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Propagation of the Native North American Shrub Lonicera Villosa and Trait Comparisons with Nonnative Congeneric Taxa

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**PROPAGATION OF THE NATIVE NORTH AMERICAN SHRUB *LONICERA VILLOSA*
AND TRAIT COMPARISONS WITH NONNATIVE CONGENERIC TAXA**

By

Darren Jay Hayes

B.S., University of Maine, 2013

A THESIS

Submitted in Partial Fulfillment of the

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Advisory Committee:

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An Abstract of the Thesis Presented
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The honeysuckles, or *Lonicera*, represent a circumboreally-distributed genus in the Caprifoliaceae family. A diverse assortment of vines, lianas, and shrubs comprise the genus, and honeysuckles have long been a staple of the horticultural industry, prized for their robustness as much as their sweet-scented flowers and colorful fruits. However, many cultivated honeysuckles of Eurasian origin have proven invasive outside of their native range, displacing native species and reducing overall diversity and ecosystem health. Planting of Eurasian *Lonicera* taxa is now often discouraged or banned throughout much of North America. Conversely, native North American *Lonicera* species are often sparsely distributed and of conservation concern throughout their native range. Given the historic popularity of Eurasian honeysuckles in cultivation in North America, their tendency to become invasive pests, and the sparse populations of native *Lonicera*, we identified two avenues of inquiry: 1) to identify means of efficiently propagating native *Lonicera* species, for potential conservation or industry application, and 2) to screen Eurasian honeysuckle species and cultivars for invasiveness.

First, we conducted parallel studies evaluating the feasibility of propagating the North-American native wetland shrub *Lonicera villosa*, found throughout much of Canada and sparsely in New England and the Great Lakes regions of the United States, by stem cuttings. In 2017, we collected softwood cuttings from a native population in Maine, wounded them on one side, treated them with 0, 4000, 8000, or 12000 mg·L⁻¹ of K-IBA in water, and stuck the cuttings in rooting media composed of 1:1, 1:3, or 0:1 peat:perlite by volume. In one study, cuttings were irrigated by overhead mist, while the other utilized a simple subirrigation system. Rooting percentages were high in both systems and were not found to vary significantly with treatments. Root quality significantly improved with the addition of K-IBA and with increasing proportions of perlite in the media but did not improve significantly with increasing K-IBA application rates. These findings indicate that *L. villosa* can be propagated to the high standards necessary for commercial production or conservation purposes.

Second, we conducted two comparative studies contrasting the growth of *Lonicera caerulea* cultivars, bred from Eurasian genotypes and marketed as an agricultural crop in North America, with the regionally invasive congeners *L. tatarica* and *L. xylosteum*, and the regionally native *L. villosa*. The first study evaluated the comparative growth of these honeysuckles (sans *L. xylosteum*) across five levels of applied slow-release fertilizer. *Lonicera caerulea* produced significantly more dried biomass than *L. villosa* at all but the highest rates of fertilizer application, and less dried biomass than *L. tatarica*, yet resembled *L. tatarica* more strongly in height and leaf area. In a second study, the four honeysuckle taxa were co-planted in large 20-gallon pots and subjected to either flooded, container capacity, or drought moisture treatment regimes. *Lonicera caerulea* significantly outperformed *L. villosa* and compared favorably with its invasive congeners in terms of dried biomass, height, and leaf area. Taken together, these

studies suggest that the non-native *Lonicera caerulea* cultivars are not functionally equivalent to their related native taxa and we advise caution and further screening for invasiveness prior to their widespread release.

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CHAPTER 1

LITERATURE REVIEW

1.1. A history of *Lonicera* in cultivation

The genus *Lonicera* (Caprifoliaceae) contains approximately 200 species of shrubs and woody vines distributed throughout the Northern Hemisphere (Rehder, 1903; Theis et al., 2008). The bulk of *Lonicera* species diversity is found throughout Asia, and it is likely the clade originated in Asia, with some members eventually dispersed throughout Europe and North America (Smith, 2009). At present, there is an estimated 34 species in North America, of which 18 are native and 16 are introduced (Lieurance and Cipollini, 2013).

The history of *Lonicera*, or honeysuckles, in the horticultural trade is a lengthy one. The early 20th century Standard Cyclopaedia of Horticulture by L.H. Bailey describes honeysuckles as belonging “to our most popular ornamental shrubs” and “of easy cultivation and propagation... quite hardy” with flowers that “though rather small, are profusely produced, mostly of pleasing and delicate colors varying from white or yellow to pink, purple, or scarlet, and followed by attractive red, yellow, white, blue, or black fruits” (Bailey, 1919). Bailey lists *L. tatarica*, *L. maackii*, and *L. morrowii*, all species commonly observed today, as “some of the handsomest in cultivation by the mid-1700s, when it was introduced into Europe and North America (Barnes and Cottam, 1974). *Lonicera maackii* (Rupr.) Herder, the Amur honeysuckle, is reported, anecdotally, to have been cultivated in gardens throughout its native range in China prior to its formal description by European botanists and introduction into European and North American markets in the mid to late 1800s (Luken and Thieret, 1996). The first recorded introduction of

Lonicera maackii into the United States occurred in 1898, as part of ongoing plant introduction experiments.

More recently, interest in the genus *Lonicera* within North America has shifted in part from horticultural to agricultural. *Lonicera caerulea* L., commonly known as blue honeysuckle, honeyberry, or Haskap (Bors, 2008), is a nearly circumboreal honeysuckle with subspecies found throughout Eurasia and North America. Historically, *Lonicera caerulea* may have been utilized as a food source by the indigenous Ainu of Hokkaido, Japan (Iketani, 2016). Domestication of *L. caerulea* as an agricultural crop is an area of active research, with various breeding programs producing and releasing cultivars from plant accessions and intra-specific hybrids created using material collected from subspecies found throughout much of *L. caerulea*'s native range in Eurasia (Plekhanova, 2000; Thomson and Chaovanalikit, 2003; Bors, 2009). Studies indicate that the fruits of *L. caerulea* are high in vitamins and antioxidants (Thomson and Chaovanalikit, 2003; Celli et al., 2014; Wang et al., 2016), and breeders advocate their culinary potential in the production of jams, confections, wines, and other assorted comestibles, promoting cultivation of honeyberry as an alternative to blueberries in regions not suitable for blueberry production.

1.2. A history of *Lonicera* as biological invaders

Many of the traits that contribute to the horticultural appeal and success of the many *Lonicera* species in cultivation also contributed to the emergence of the genus as a veritable font of biological invaders. Although the exact definition of an invasive species differs between individuals and disciplines, the label generally refers to a species that colonized an area outside its natural distribution due to human agency (intentional or otherwise) and persisted and spread beyond the scope of its original point of introduction (Simberloff 2013).

The role of horticulture and agriculture in the development and distribution of pestiferous invasive species has only been recently appreciated (Reichard and White, 2001), despite prior observations and anecdotes that suggested introduced plants may be capable of altering ecosystems. *Lonicera maackii*, for example, spread by sexual reproduction beyond the scope of its initial planting in the Morton Arboretum as early as the 1920s (Luken and Thieret, 1996). Observations continued of *L. maackii*'s gradual proliferation and naturalization through the 1950s, 1960s, and 1970s. This sort of time-lag between introduction and widespread invasion is a common motif in biological invasions (Crooks et al, 1999), and gradual accumulation of genetic diversity following multiple introductions, mounting propagule pressure, life history and invader time to reproductive maturity, and selection of competitive genotypes have all been implicated as contributing factors to this time-lag (Simberloff 2013).

The tendency for non-native honeysuckles to proliferate freely was viewed as a boon by plant breeders in the industry, academia, and the government. For example, breeders at the USDA continued hybridizing and releasing cultivars for widespread planting as part of the USDA Soil Conservation Service until the 1980s (Luken and Thieret, 1996). Now, many introduced bush and vining honeysuckles are widely considered invasive pests (Woods, 1993; Hartman & McCarthy, 2008). Even with the mountains of evidence against them, the historically popular bush honeysuckles are still widely planted, and states have only recently begun taking legislative action to curb the spread of invasive *Lonicera*. For example, in the Northeastern U.S., these plants have been banned or prohibited for sale in Connecticut, Massachusetts, New Hampshire, Vermont, and most recently, Maine (USDA, 2018).

While not widely considered invasive, *Lonicera caerulea* cultivars have not been exempt from similar observations and it may be naive to view the species as entirely benign. A

naturalized population of *L. caerulea* near Duluth, Minnesota, was reported by Schimpf et al. (2011). In a subsequent visit to that same site by Peterson et al. (2016), the naturalized population of *L. caerulea* was reported to exhibit both natural layering and seedling recruitment as mechanisms for population growth. In addition, Peterson et al. (2018) identified individual plants distributed well outside the initial area reported by Schimpf et al. (2011). *Lonicera caerulea* also features prominently on the Norwegian Biodiversity Information Centre's Black List, ranking it among the worst invaders of Norway in an entire category of severity above known noxious invaders such as *L. tatarica*, *L. morrowii*, and *L. maackii* (Gederaas et al., 2012). This difference in severity may result from the cold tolerance of *L. caerulea*, owing to a more northern native distribution. The reputation of *L. caerulea* as an invader of northern forests (Gederaas et al., 2012; Tyler et al., 2015) suggest continued introduction into North America is not without risk, a conclusion supported by Peterson et al.'s (2016) application of checklist-based screening tools for potential invasive species, which found significant risk of invasion.

Lonicera caerulea cultivars on the market are developed from germplasm over a wide geographic distribution and represent admixtures of genotypes from many different populations (Bors, 2009), a process that is also believed to contribute to the genesis of invasive genotypes of plants that are historically more benign (Schierenbeck and Ellstrand, 2009). The case of *Lonicera caerulea* is complicated further by uncertainty, even controversy, surrounding its taxonomic relationship to North American species. *Lonicera caerulea* has been considered a single polymorphic, circumboreal species on and off throughout the 19th and 20th centuries, with many varieties described to account for the high degree of polymorphism observed among populations (Rehder 1903). However, *L. caerulea* has at times also been subdivided into a number of different species due to this significant level of polymorphism, with North American

representatives divided into two species, *Lonicera villosa* (mountain fly honeysuckle) with a northeastern distribution and *Lonicera cauriana* (blue fly honeysuckle) in the west (Fernald 1925). These two species have, at times, been further divided into subspecies and varieties.

Some proponents for the widespread planting of honeyberry cultivars view the potential classification of mountain fly honeysuckle as a North American native subspecies or variety of *Lonicera caerulea* as evidence supporting the safety of their introduction (Bors 2009), although these same proponents also underscore the differences between the genotypes, especially the greater size and productivity of honeyberry over native North American genotypes. While the matter is not settled concerning *Lonicera caerulea* taxonomy (see Naugžemys et al. 2011, Holubec et al. 2015), the degree of relatedness and capacity for hybridization between Eurasian and North American taxa may be cause for greater concern, rather than evidence supporting the safety of introducing these cultivars. Concerns include the potential for replacement of native genotypes by cryptic invasion (*sensu* Saltonstall 2002), reduction of native population fitness and the potential for a subsequent population crash due to outbreeding depression (*sensu* Crispo et al. 2011), or the creation of invasive genotypes by reduced genetic load, heterosis, or evolutionary novelty of hybrid lineages (*sensu* Ellstrand and Shierenbeck 2000).

1.3. Impacts of invasive *Lonicera*

Biological invasions are now generally understood to have myriad negative consequences for native ecosystems, even if certain species interactions lead to positive facilitation effects for some native species (Simberloff 2013). Invasions by nonnative *Lonicera*, particularly by *Lonicera mackii* and *Lonicera x bella*, a putative hybrid between *L. tatarica* and *L. morrowii*, have been well documented and have many reported consequences for native communities. *Lonicera mackii* is, in some ways, an ecosystem engineer that facilitates increased transpiration

and water loss from plant communities compared with native shrubs. In a study site in Kentucky, USA, the contribution of *L. mackii* to overall transpiration amounted to roughly 10% of the water throughput of the stream draining the study site (Boyce et al. 2011). Boyce et al. (2011) concluded that this increased transpirational water loss was likely to shorten the duration of ephemeral spring water features necessary for many organisms, especially amphibians, to complete their life cycles, noting the existence of many sites with much higher basal areas and capacities for transpiration than those in the study. Invasion by *Lonicera mackii* may also have harmful effects on native amphibian populations due to the leeching of harmful water-soluble phytochemicals, which may interfere with amphibian respiratory physiology (Watling et al. 2011a). Invasion by nonnative honeysuckles has also been shown to alter microclimates in ways that reduced amphibian species richness (Watling et al. 2011b), outcompete native plants and reduce plant growth and species diversity under its canopy through extended leaf retention and freeze resistance and the release of allelopathic compounds (McEwan et al., 2009; Dorning and Cipollini, 2005), and even pose a health risk by providing a resource for white-tailed deer (*Odocoileus virginianus*) and by extension aggregating ticks and increasing incidence of tickborne diseases (Allan et al. 2010).

The negative effects of invasive honeysuckles on overall plant richness can be dramatic, with a 53% reduction in richness and 63% reduction in overall plant cover, increasing in severity with longer residence time by invasive honeysuckles, reported by Collier et al. (2001). The dense understory formed by invading *Lonicera* species has been shown to alter densities of understory birds (McCusker et al. 2009), and honeysuckles have at times been advertised as benefitting native bird communities. However, they are now more widely considered an ecological trap, providing low-quality nesting sites (Schmidt and Whelan 1999), and have been demonstrated to

reduce the number of fledged young in some species (Schmidt and Whelan 1999; Rodewald et al. 2010).

1.4. Traits, drivers, and risk factors of invasive species

While the negative consequences of invasion by introduced species are fairly well documented, the mechanisms by which certain species are able to invade are less so, confounding the effective screening for, and exclusion of, invasive species. Mechanisms ranging from greater phenotypic plasticity (Pyšek & Richardson 2008), preadaptation (Skálová et al. 2012), and rapid evolution of increased fitness (Blossey and Notzold 1995), to simply greater values of competitive and performance-related traits in invasive vs. non-invasive taxa (van Kleunen et al. 2010, Matzek 2012) have been proposed.

The role of phenotypic plasticity, or the ability of an organism to change phenotypic expression in response to a variety of environmental conditions, has long been thought to confer an adaptive potential that could allow introduced species to invade a wide range of habitats due to their “general-purpose genotypes” (Baker, 1965). This concept was refined by Richards et al. (2006) into a set of specific strategies by which phenotypic plasticity could contribute to the competitiveness of invasive species. These strategies include the “jack-of-all-trades” strategy, in which plasticity allows species to tolerate unfavorable conditions with a minimized loss of fitness; the “master-of-some” strategy, in which plastic responses enable species to take greater advantage of favorable conditions; and the “jack-and-master” strategy, in which both previous strategies hold true to some degree.

Despite the prevalence of the concept that phenotypic plasticity contributes to invasiveness in plant species, meta-analyses of invasiveness studies comparing plastic responses

in plant traits conclude that the evidence supporting plasticity as an extensible predictor of invasiveness is inconsistent. A 2011 meta-analysis of 35 studies comprising 93 comparisons of phenotypic plasticity by Palacio-López and Gianoli concluded that invasive and non-invasive species displayed similar functional responses to environmental conditions. They concluded that differences in phenotypic plasticity may not play a role in plant invasions, or that plasticity may only play a role in early invasions by allowing plants to establish in novel environments, after which plasticity is reduced by the selection of more adaptive genotypes.

In contrast, Davidson et al. (2011) conducted a different meta-analysis comparing 75 invasive/non-invasive species pairs and concluded that invasive plants displayed greater phenotypic plasticity than non-invasive plants at high levels of resource availability (i.e., they exhibited the “master-of-some” strategy), but that the plastic traits only sometimes correlated with increased fitness. They also concluded that non-invasive plants actually displayed equal or greater plasticity and possessed greater fitness in resource-limited environments.

While these meta-analyses underscore the difficulty in making kingdom-level generalizations for predicting invasiveness, identifying traits that are predictors of invasiveness (including differences in plasticity) has been more informative at a lower taxonomic level, with comparisons between native, introduced invasive, and introduced non-invasive congeneric species allowing for relative assessments of invasiveness risk (Pyšek & Richardson 2008; Skálová et al. 2012).

A 2010 meta-analysis of 117 studies comparing 125 invasive and 196 non-invasive plant species, conducted by van Kleunen et al., tested the association of invasiveness with various trait groups, as well as the impact of study-type, biogeographical region, and biological factors on these associations. Van Kleunen et al. (2010) concluded that invasive species scored significantly

higher in the six trait categories tested, which included physiology, growth rate, plant size, fitness, leaf-area, and shoot allocation, and that this difference held true regardless of continent of origin and test environment. They also concluded that there were no significant differences between invasive species and native species that were invasive elsewhere, indicating that species were preadapted for invasion and that their invasiveness was not an emergent behavior following introduction. They did, however, detect an effect of study type on trait differences, with congeneric and confamilial studies detecting differences that higher levels of taxonomic comparisons did not (van Kleunen et al., 2010).

Overall, the meta-analysis of van Kleunen et al. (2010) indicates that trait values for performance-related functional traits are useful in predicting invasive potential in plants, even if comparisons of phenotypic plasticity are less consistent. This conclusion was shared by Matzek (2012), who compared 10 closely related *Pinus* species of known invasive status. Known invasive *Pinus* species had higher values than non-invaders for 13 of the 17 compared functional traits, while no significant difference in plasticity was observed between invasive and non-invasive species for any trait.

The contribution of multiple introductions and hybridizations to population-level increases in genetic diversity has also been implicated as an important factor in the development of invasive potential in some taxa (Schierenbeck and Ellstrand, 2009). An example of this phenomenon can be found in common reed (*Phragmites australis*), which has a long history in North America and paleoecological records supporting its presence in North America for thousands to tens-of-thousands of years (Orson 1999). Historical herbarium records described *Phragmites australis* as rare in North America, a status that changed rapidly between the early 1900s and the present. *Phragmites australis* is now considered a noxious invader of disturbed

wetlands in North America (Orson 1999), with invasive populations characterized by a modern, widespread haplotype of apparently recent Eurasian origin. Invasions like these underscore the widespread population and ecosystem consequences of human mediated dispersal of an exotic genotype of an otherwise native species, including reduced plant diversity (Stalter and Baden, 1994), suppression of native competitors through allelopathic exudates (Uddin et al., 2014), changes to soil organic matter and microbial activity (Song et al., 2015), alterations to microbial communities (Yarwood et al. 2016), and changes in avian abundance and diversity (White et al., 2015).

In a comprehensive review, Sakai et al. (2001) implicated several population-genetic processes as contributors to biological invasions. Among these is the accumulation of genetic diversity, which may be necessary to produce robust and adaptable invasive populations over the course of multiple introductions. The role of genetic diversity seems to be exemplified by the invasive histories of North America's most successful invasive birds, the house sparrow (*Passer domesticus*) and the European starling (*Sturnus vulgaris*), which each required many introductions before they became successful invaders (Sakai et al., 2001).

Rapid evolution following hybridization may be another potential mechanism for the development of invasiveness in plants (Ellstrand and Schierenbeck 2000) and animals. In the Rhine, invasive lineages of sculpins originated from hybridization between co-occurring species of *Cottus* that were formerly reproductively isolated (Nolte et al. 2005), with heterosis of hybrids generating traits outside the normal range for either parent species (Cheng et al. 2015). Similarly, hybridization has been implicated in the invasive success of reed canary grass, (*Phalaris arundinacea*) and California wild radish (*Raphanus sativus*). Reed canary grass seems to have acquired its invasive potential through accumulated genetic diversity from multiple introductions

for a variety of different purposes, resulting in intraspecific hybrids with traits and tolerances from many different lineages (Lavergne and Molofsky 2004), while the invasive California wild radish is a hybrid between two non-native, naturalized radish species that are not, themselves, noxious invaders (Ridley and Ellstrand 2009).

As briefly explored in the invasive history of honeysuckles, *Lonicera* are no exception to these processes. A history of multiple introductions for a variety of different horticultural and environmental applications is likely to have played a key role in the development of robust populations of *Lonicera morrowii* with the traits necessary to escape cultivation and invade native ecosystems on a widespread and damaging scale. Additionally, morphological evidence indicates that hybridization between *L. morrowii* and *L. tatarica* has given rise to invasive hybrid swarms of intermediate forms under the nomen *Lonicera x bella*, a conclusion that has yet to be confirmed or rejected by genetic analysis (Barnes and Cottam, 1974; Green 1966; Schierenbeck and Ellstrand, 2009). This putative hybrid has been described in at least 30 U.S. states (BONAP) and several Canadian provinces, with populations concentrated in the Great Lakes region and the Northeast. Against a backdrop of unanswered questions about the invasion biology of *Lonicera*, the increasing popularity of *L. caerulea* as a crop for North America raises additional questions and concerns.

1.5. Native plant markets and a future for *Lonicera* in horticulture

With the mounting scientific evidence and growing public awareness surrounding invasive plant species and their potentially deleterious effects, the market for native alternatives to popular-but-noxious horticultural staples is growing, and surveys suggest a willingness among consumers to pay a premium for native species and genotypes (Yue et al. 2011).

North America is home to 18 native species of *Lonicera* (Lieurance and Cipollini, 2013). Unlike the Eurasian honeysuckles that have become widespread and pestiferous in North America, native honeysuckles are observed to be locally rare (Lieurance and Cipollini 2013, USDA NRCS 2018). This reputation for sporadic occurrence may be partly responsible for a lack of efforts to assess the suitability of native species and genotypes for the horticultural trade. Given the historical and contemporary interest in nonnative *Lonicera*, a closer inspection of North American representatives seems prudent. The sparseness of native *Lonicera* species in natural ecosystems should not be a deterrent to investigating their suitability, as many range-limited species have proven to be more tolerant of anthropogenic conditions than expected. For instance, the native North American River Birch (*Betula nigra* L.) is restricted to riverbanks and moist soils and is classified as threatened in the northern extremes of its range (USDA NRCS), but is known to be hardy and drought tolerant in horticultural landscapes (Gu et al. 2007) and is resistant to pests that plague other *Betula* species in cultivation (Nielsen et al. 2011). Many taxa restricted largely to wetlands have proven to be more adaptable than native habitats or contemporary ranges might suggest. For example, Lubell (2013) investigated the performance of several native shrubs in the landscape and found that the wetland plants *Myrica gale* L. and *Cephalanthus occidentalis* L. performed especially well in a typical urban setting.

Among the first steps toward the assessment of native North American *Lonicera* for cultivation are the development of protocols for efficient propagation and the evaluation of potential field performance of native genotypes. Asexual propagation by stem cuttings is a common method for producing plants both for sale in the horticultural industry (Hartmann et al. 2011) and for use in ecosystem remediation and restoration projects (Everett et al. 1978). Many factors influence the efficiency with which plants can be propagated in this fashion, and

individualized protocols for suitable cutting phenology, method of irrigation, medium composition, and treatment with plant growth regulators may be required to optimize production on a taxon-specific basis (Dirr and Heuser 2009, Hartmann et al. 2011).

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CHAPTER 2

VEGETATIVE PROPAGATION OF A NORTH AMERICAN NATIVE BLUE HONEYSUCKLE, *LONICERA VILLOSA*, BY OVERHEAD MIST AND SUBIRRIGATION

2.1. Abstract

With growing consumer awareness of the ecosystem costs of invasive plants and interest in native plants, it is important for the horticultural industry and the researchers that support it to identify, screen, and develop native plants of interest for market. Given the long history of demand for Eurasian honeysuckles (*Lonicera* spp.), many of which have proven to be invasive, the development of native *Lonicera* species as alternatives seems prudent. We assessed adventitious root formation on stem cuttings of mountain fly honeysuckle (*Lonicera villosa* (Michx.) Schult.) treated with different concentrations of K-IBA (indole-3-butyric acid) and stuck in media with different proportions of perlite and milled peat moss. In two independent experiments using overhead mist or subirrigation, we assessed cuttings for propagation success (a combination of rooting success and survival), root dry weight, total root volume, and total number of root tips. Percentage rooting was high and not significantly affected by treatments. Root quality, as measured by root dry weight, root volume, and number of root tips, increased with K-IBA application and proportion of perlite in the substrate. K-IBA application rates from 8000 to 12000 mg·L⁻¹ and a porous mineral substrate produced well-rooted plants with the high success rate necessary for commercial propagation, regardless of propagation system.

2.2. Introduction

Horticulture has long been a pathway for the introduction of invasive plant species across the globe (Reichard and White, 2001), due in part to industry pressures to provide selections of

robust and adaptable plants that can be grown by consumers with little management (Anderson et al. 2006). Eurasian honeysuckle species, such as *Lonicera maackii* (Rupr.) Herder and *Lonicera tatarica* L., are textbook examples of this trend, with a long history as valued and widely-planted horticultural crops and components of the urban landscape. Both have been prized for their flowers, sweet scent, persistent colorful fruits, and wide tolerance of climactic conditions, since the introduction of robust species from Asia to Western Hemisphere in the late 1800s to early 1900s (Bailey, 1919; Luken and Thieret, 1996). The tendency for Eurasian honeysuckles to escape cultivation and cause ecological harm in North America was first noticed in the mid-1900s (Luken and Thieret, 1996), but only recently has public perception of these species and cultivars shifted to the point that they are being removed from nursery inventories and even banned in some parts of the U.S. (USDA NRCS, 2018). Invasion by non-native honeysuckles and other pestiferous species is associated with a wide range of environmental and ecological impacts, including reductions in plant, animal, and microbe diversity (Stalter and Baden, 1994; Yarwood et al., 2016; Whyte et al., 2015), loss or alteration of ecosystem functions and services (Weidenhamer and Callaway, 2010), and facilitation of further biological invasion (Flory and Bauer, 2014).

As the scientific and public understanding of the negative impacts of invasive species grows, so too does interest in native alternatives. Though customers are willing to pay a premium for plants labeled as native (Yue et al. 2011), options for native landscape plants remain relatively limited. However, this is itself an opportunity to identify and develop native plants that may have horticultural potential and provide more environmentally and ecologically responsible options for the horticultural industry. Given the historical popularity of *Lonicera* and contemporary interest in edible blue honeysuckles (*Lonicera caerulea*) from Eurasian stock

(Gerbrandt et al. 2017), the assessment of native North American relatives seems of particular interest.

In contrast with their Eurasian congeners, even the most widespread *Lonicera* native to North America generally form sparse populations, are frequently species of conservation concern, or are extirpated in parts of their native range (Lieurance and Cipollini 2013, USDA NRCS 2018). Some, such as the mountain fly honeysuckle, can be quite charming in character and yet remain absent from commerce. Mountain fly honeysuckle is endemic to much of Canada, with a range that extends into the Northeastern and Great Lakes regions of the United States, though it is presumed extirpated in Ohio and is endangered in Pennsylvania (USDA NRCS 2018). It is most often found in bogs, fens, and mesic forests. It is a small compact shrub ranging from 1 to 4 feet in height, with rugged dark-green leaves with short stiff hairs and a pale underside, and reddish-brown to coppery stems and bark that exfoliates into persistent strips as the stems age. Plants produce small paired yellow flowers in early spring, and edible-but-tart oblong blue fruits that ripen in early summer. Fruits are also attractive to birds but are usually produced in low abundance. The restriction of mountain fly honeysuckle primarily to bogs and fens might account for its obscurity in horticulture, as it persists in environments in which it and its competitors are stunted, spindly, and resource-starved. Does it grow worth a darn in horticultural landscapes?

Propagation of native plants of interest via asexual or sexual means is a necessary first step toward developing native plants for horticultural or conservation purposes. Given the sparse distribution and low density of wild populations of mountain fly honeysuckle, the small stature of plants, and low abundance of fruits, an efficient means of asexual propagation will be necessary to produce plants in useful quantities. Stem cuttings often are rooted to produce plants

both for sale in the horticulture industry (Hartmann et al. 2011) and for restoration of natural ecosystems (Everett et al. 1978). Cutting phenology, mode of irrigation, media composition, and plant growth regulator treatments all influence rooting success and often need to be optimized for species of interest (Dirr and Heuser 2009, Hartmann et al. 2011). Because the factors that influence adventitious rooting within a cutting are numerous, the responses of cuttings to auxin is often taxon-specific. Excessive auxin application can have an inhibitory effect on adventitious root formation and root growth (Leakey et al. 1982).

Here, we assessed the efficacy of propagating *mountain fly honeysuckle* from stem cuttings under two modes of irrigation, varying levels of exposure to auxin in the form of the potassium salt of indole-3-butyric acid (K-IBA), and in media that varied in their proportions of coarse perlite and milled peat moss.

2.3. Materials and Methods

On 28 June 2017, we collected 384 softwood terminal stem cuttings from seventeen robust plants of mountain fly honeysuckle indigenous to a roadside population near Lubec, ME, USA (GPS Coordinates: N 44°48'03.4" W 67°07'35.4"). Cuttings averaged 6.3 cm and contained 2-3 nodes. Leaves were removed from the basal node of each cutting, and stems were wounded lightly by scraping the basal one to two cm of the stem on one side with a razor blade, a procedure observed to increase rooting quality in a preliminary study. Cuttings were treated with one of four rooting hormone treatments by dipping them for five seconds in solutions of 0, 4000, 8000, or 12,000 mg·L⁻¹ K-IBA dissolved in water. Cuttings were subsequently stuck in 50-cell propagation sheets (Dillen-ITML, Middlefield, Ohio) filled with media containing 50%, 75%, or 100% perlite by volume, and milled peat moss comprising the remaining volume. This resulted

in a 4x3 full factorial design with 12 treatment combinations. Cuttings were watered in, and then placed in one of two propagation systems, overhead mist irrigation or subirrigation.

Space limitations precluded replication on the level of the mist irrigation system, so separate experiments were conducted in parallel using each irrigation system. Cuttings in the experiment irrigated via overhead mist were arranged in their propagation cells in a completely randomized design, with 20 replications per factorial treatment combination (N=240). The 50-cell propagation sheets, which were inserted into netted flats, were placed flush to form a functionally continuous area. Cuttings were irrigated with eight seconds of mist at ten-minute intervals for the duration of the experiment.

In the experiment irrigated via subirrigation, 50-cell propagation flats were cut to create 12-cell units (three cells by four cells). Each unit was placed in its own subirrigation unit consisting of an 8" x 8" aluminum tray lined with clear plastic wrap. Hormone and substrate treatment combinations were randomly assigned to each cell, with one replicate of each combination per subirrigation tray. The experiment was a RCBD with 12 replicate trays serving as blocks with one replicate per factorial combination (n=12; N=144). Trays remained unirrigated for 12 hours to reduce the potential for leaching of applied rooting hormones, after which they were filled with tap water to a depth of 3 cm and refilled to the same depth daily. Although the potential existed for biologically significant hormone interactions between cells to confound the effects of prescribed treatments, the influence of auxin concentration was not ambiguous.

The two experiments were conducted on a single bench under 25% mylar shade cloth in the glass-glazed Roger Clapp Greenhouses at the University of Maine, Orono, with natural photoperiods. Temperature on the bench was logged using a Watchdog 1450 micro station with

radiation shield (Spectrum Technologies, Aurora, IL) located under the shade cloth, near the height of the cuttings in the subirrigation experiment. The temperature averaged 25.4 °C for the experimental period with a maximum instantaneous temperature of 38.8 °C. Photosynthetically active radiation (*PAR*) under the shade cloth was measured once every ten minutes using a quantum light sensor attached to the same datalogger, and daily light integral (DLI) was calculated from these data. The average DLI was 7.36 mol m⁻² day with a maximum instantaneous *PAR* reading of 667 μmol m⁻² s⁻¹. Cuttings from the overhead mist irrigation experiment were harvested the week of 7 August, while cuttings from the subirrigation experiment were harvested the week of 14 August.

In each experiment, propagation success and root-system quality were assessed via the same protocol. First, cuttings were uprooted and rinsed gently to remove substrate. Each cutting was rated on success of propagation in a binary fashion, with a score of 0 assigned to cuttings that died or failed to root, and a score of 1 assigned to cuttings that both survived and formed at least one adventitious root exceeding 1 cm in length. Roots were trimmed from each cutting using a scalpel and arranged on an Epson Expression 1680 flatbed scanner with transparency unit (Epson, Suwa, Nagano Prefecture, Japan). Roots were arranged to minimize overlap and crossing. Roots were scanned and analyzed using WinRHIZO software version 2003b, which mathematically calculated root system volume and total number of root tips per cutting, and has been demonstrated to provide accurate measurements of these parameters (Bouma et al. 2000). Roots were then dried to constant weight in open paper bags in a hot drying room maintained at ~68 °C and weighed to determine root dry weights.

Data analysis was conducted using the statistical software R version 3.3.2 (R Core Team 2016). Propagation success was analyzed via logistic regression, with overall effects of

treatments on propagation success analyzed using the Wald test conducted using the *aod* version 1.1-32 (Lesnoff and Lancelot 2012) package for R. Least square difference (LSD) tests were conducted using the *agricolae* version 1.2-4 (de Mendiburu 2016) package for R, following detection of significant treatment effects by analysis of variance at an α of 0.05. For cuttings rooted in overhead mist, square root transformations were performed on root volume, root dry weight, and root tip counts to improve normality. For cuttings rooted by subirrigation, a cube root transformation was performed on the root dry weights, and a square root transformation was conducted on the root tip counts. All treatment means were back-transformed for standardized reporting of LSD results.

2.4. Results

Treatments did not have a significant effect on the probability of propagation success in either experimental system (Table 2.1). Rooting of cuttings that received overhead mist was between 95 and 100 percent, regardless of treatment combination. Although the rooting success of cuttings that received subirrigation ranged from 58 to 100%, it did not vary significantly with treatments (Table 2.1).

Table 2.1. Propagation success of mountain fly honeysuckle stem cuttings treated with K-IBA and rooted in overhead mist and subirrigation systems. Propagation success did not differ significantly among K-IBA treatments within each system.

K-IBA (mg·L ⁻¹)	Overhead Mist			Subirrigation		
	50 % Perlite	75% Perlite	100% Perlite	50 % Perlite	75% Perlite	100% Perlite
0	95%	100%	100%	67%	100%	100%
4000	100%	100%	95%	67%	100%	100%
8000	95%	100%	100%	58%	83%	100%
12000	95%	95%	100%	75%	100%	67%

Among cuttings rooted in the overhead mist system, all K-IBA treated cuttings exhibited significantly greater root volume, root dry weight, and number of root tips than the untreated controls (Table 2.2). However, mean root volume, root dry weight, and number of root tips did not differ among cuttings receiving K-IBA in concentrations of 4000, 8000, and 12000 mg·L⁻¹. Collectively, these three treatments outperformed cuttings that received 0 mg·L⁻¹ K-IBA by approximately a factor of two in all parameters. Choice of substrate likewise affected rooting, with cuttings in media consisting of 100% perlite forming root volumes and root dry weights of 1.5 to 2 times those in media with less perlite (Table 2.2). Number of root tips did not differ significantly with the percentage of perlite in the rooting media.

Among cuttings rooted in subirrigation trays, root volume and number of root tips differed significantly with K-IBA application (Table 2.2). The highest K-IBA application rate yielded cuttings with the greatest root volume and number of root tips, about a 50% increase over controls that did not receive K-IBA. Root volume, root dry weight, and number of root tips also varied significantly with the proportion of perlite in the rooting media. Values for all three

parameters were greatest for the cuttings in 100% perlite, which produced values about twice those of cuttings in 75% perlite and thrice those of cuttings in 50% perlite (Table 2.2).

Table 2.2. Influence of K-IBA application (top) or perlite content of the rooting medium (bottom) on root volume, root dry weight, and number of root tips on stem cuttings of successfully rooted mountain fly honeysuckle. Cuttings were rooted in overhead mist and subirrigation systems.

K-IBA (mg·L ⁻¹)	Overhead Mist			Subirrigation			
	Root Volume (cm ³) *z	Root Dry Weight (g) *z	Number of Root Tips *z	Root Volume (cm ³) *	Root Dry Weight (g) ^y	Number of Root Tips *z	
	0	0.086 b	0.028 b	219.781 b	0.249 b	0.054	465.999 b
4000	0.181 a	0.054 a	413.960 a	0.284 ab	0.067	561.548 ab	
8000	0.194 a	0.058 a	468.160 a	0.335 a	0.085	634.586 a	
12000	0.194 a	0.055 a	491.465 a	0.355 a	0.078	689.063 a	
Percentage Perlite	Root Volume (cm ³) *z	Root Dry Weight (g) *z	Number of Root Tips ^z	Root Volume (cm ³) *	Root Dry Weight (g) * ^y	Number of Root Tips *z	
	50	0.129 b	0.040 b	380.874	0.166 c	0.033 c	340.218 c
	75	0.128 b	0.039 b	377.952	0.258 b	0.055 b	515.108 b
100	0.229 a	0.065 a	407.192	0.460 a	0.137 a	900.180 a	

*Significant treatment effect at $p \leq 0.05$

^zData square-root transformed for statistical analysis. Treatment means back-transformed for reporting.

^yData cube-root transformed for statistical analysis. Treatment means back-transformed for reporting.

^xMeans within each column and factor followed by the same letter are not significantly different at $\alpha = 0.05$

2.5. Discussion

Rooting success was high in both experiments, indicating that stem cuttings of mountain fly honeysuckle are suitable for propagation of clones for research, industry, or restoration purposes. Rooting percentages were between 95 and 100 percent for the overhead mist experiment, but more variable in the subirrigation experiment. Despite variable propagation success ranging from 58 to 100 percent for subirrigation, neither substrate composition nor K-IBA application significantly influenced propagation success. It is worth noting that no cuttings that produced roots in the subirrigation experiment subsequently died; mortality always occurred before the formation of adventitious roots. Survival and rooting success could potentially be increased by simple methods to reduce transpirational loss of water by the cuttings, such as the use of humidity domes or tents, as management of cutting water status is often key to cutting survival and rooting success (Hartman et al. 2011). In our experiment with subirrigation, trays and cutting were exposed to the ambient temperature and humidity of the greenhouse, with mylar shade cloth to reduce solar radiation by 25% representing the only means to slow transpiration. Although individual clones within species may differ in their tolerance to subirrigation during propagation (Svenson, 2018), this approach can produce results for some taxa that are similar to, or superior to, overhead mist (Peterson et al., 2018; Zhang and Graves, 1995). Subirrigation has added benefits of reduced water usage (Peterson et al., 2018), improved phytosanitary conditions (Preece 2003), and the flexibility offered when a mist system is not available.

Auxin application significantly increased root volume, root dry weight, and number of root tips on cuttings in overhead mist, and root volume and number of root tips on cuttings in subirrigation (Table 2.2). The effect of auxin on these parameters was generally binary, with a significant increase in these measures between cuttings that received no auxin and the cuttings

that received 4000 to 12000 mg·L⁻¹ K-IBA. Although there were few commercially significant differences in adventitious root formation among the cuttings that received K-IBA, those treated with the greatest auxin concentration also showed no adverse effects to high auxin exposure (Table 2.2). Therefore, we could not rule out the possibility that greater auxin concentrations, beyond the 12000 mg·L⁻¹ K-IBA we tested, may yield more robustly rooted plants than those that receive lower application rates. Regardless, the lower application rates from 4000 to 8000 mg·L⁻¹ K-IBA produced well-rooted plants.

Although the experimental design precludes direct statistical comparison between the two experimental systems, it is worth noting that cuttings in the subirrigation system performed better than cuttings in the overhead mist system for the metrics examined in this study. While rooting percentages for some treatment combinations in the subirrigation experiment were low, overall rooting for the system averaged across all treatments was an appreciable 85 percent, a rate that could be potentially increased with management of transpirational water loss. As such, subirrigation combined with pure perlite media and auxin application rates greater than or equal to 8000 mg·L⁻¹ would allow for the low-tech, accessible production of well-rooted cuttings of mountain fly honeysuckle for research or industry. Though there was a week difference in collection dates between the two systems, the roots of the cuttings in the subirrigation system were observed to have already substantially outgrown their pots and branched throughout the system during the overhead mist system's earlier collection dates, which was not observed for any cutting rooted in the overhead mist system. Cuttings rooted in the subirrigation system produced longer, thicker, more highly branched roots than those irrigated by overhead mist.

2.6. Conclusions

Efficient clonal propagation of the mountain fly honeysuckle, a small native shrub honeysuckle of potential horticultural and conservation interest, can be achieved using stem cuttings rooted in an overhead mist propagation system, or by using a simple and accessible subirrigation approach without mist. In this study, rooting success rates were high for cuttings irrigated both by overhead mist and in subirrigation trays and was not significantly impacted by the percentage of perlite in the rooting media or the concentration of the rooting hormone auxin applied in the ranges covered in this study. However, both treatment factors significantly improved measures of root system vigor, as cuttings treated with greater auxin concentrations of 8000 to 12000 mg·L⁻¹ K-IBA and stuck in media consisting of 100 percent perlite produced robust root systems with the greatest dry weight, total root volume, and number of root tips. Further studies and system-level replications are needed for direct comparisons between irrigation methods and to determine the post-transplant health and vigor of plants produced under different treatment combinations, but rooted cuttings with greater measures of root dry weight, root volume, and number of root tips are expected to better acclimatize and establish once transplanted into field or landscape conditions. In our experience, rooted cuttings of mountain fly honeysuckle adapt readily to both container culture and mineral soils in the landscape, despite its restriction primarily to bogs and fens in the wild.

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CHAPTER 3

THE EFFECTS OF SUBSTRATE FERTILITY AND MOISTURE ON THE GROWTH OF A NON-NATIVE HONEYSUCKLE, *LONICERA CAERULEA* L., COMPARED WITH NATIVE AND INVASIVE CONGENERS

3.1. Abstract

Eurasian honeysuckles have a long history of introduction into North America and have been popular shrubs in the horticultural industry for centuries. However, honeysuckles of Eurasian origin have proven to be noxious invasive pests time and time again, with deleterious effects on native ecosystems. While most honeysuckles of Eurasian origin are appearing on increasingly more ban lists in North America and other parts of the world, cultivars of the edible-berried blue honeysuckle (*Lonicera caerulea* L.), marketed as honeyberry, Haskap, or sweetberry honeysuckle, continue to be developed for agricultural use in North America with surprisingly little scrutiny considering the invasive history of Eurasian honeysuckles in general and of *L. caerulea* in forests in Norway. We assessed the growth of *Lonicera caerulea* grown alongside the related North American blue-berried honeysuckle *Lonicera villosa* and the known invasive Eurasian honeysuckles *L. tatarica* and *L. xylosteum* as a first step in assessing the performance of *Lonicera caerulea* relative to these congeners. In Experiment 1, *L. villosa*, *L. caerulea*, and *L. tatarica* plants were grown under applied fertilizer treatments of Osmocote Pro 17-5-11 4-month controlled release granular fertilizer at rates of 5, 10, 15, 20, and 25 grams of fertilizer per gallon (equivalent to 0.85, 1.70, 2.55, 3.40, and 4.25 g N). *Lonicera caerulea* significantly outperformed *Lonicera villosa* by a factor of 2 for root and shoot dry weights across all fertilizer treatments, though did not display the degree of growth or responsiveness to increased substrate fertility demonstrated by *L. tatarica*. However, *L. caerulea* resembled *L.*

tatarica more strongly in form, producing leaves of a much greater individual size and producing significantly taller primary stems than *L. villosa*, both of which are evidence of a more competitive growth prioritization. In Experiment 2, plants of the four representative taxa were grown together in communal #20 trade-gallon pots under drought, container capacity, and flooded moisture regimes. Measures of growth differed substantially among taxa, but significant quantitative within-taxon variation across moisture treatments was not detected. As in Experiment 1, plants of *L. caerulea* in Experiment 2 produced greater dry biomass than plants of *L. villosa* and resembled the invasive Eurasian honeysuckles more strongly in size and form. We recommend further comparative studies between *L. caerulea* and its native and known invasive congeners in North America, to better understand the potential risks of introducing additional members of a taxon with a history of invasiveness.

3.2. Introduction

Honeysuckles (*Lonicera* spp.) introduced from Eurasia have a long history of popularity in the horticultural trade in North America. Tatarian honeysuckle (*Lonicera tatarica* L.) from Asia was in widespread horticultural cultivation in Europe and North America by the mid-1700s (Barnes and Cottam 1974), while another popular honeysuckle, *Lonicera maackii* (Rupr.) Herder, was introduced into the United States from China by 1898. *Lonicera maackii* was introduced in the context of plant introduction experiments, and its widespread breeding and development as a horticulture crop was driven in part by efforts by the USDA's Soil Conservation Service to develop the species for widespread use as a control for erosion (Luken and Thieret 1996). The Standard Cyclopaedia of Horticulture by L.H. Bailey, which enjoyed many reprintings in the early 20th century, describes honeysuckles as plants "of easy cultivation and propagation... quite hardy", and amongst "our most popular ornamental shrubs", and as

having flowers that “though rather small, are profusely produced, mostly of pleasing and delicate colors varying from white or yellow to pink, purple, or scarlet, and followed by attractive red, yellow, white, blue, or black fruits” (Bailey 1919). Bailey went on to list *L. tatarica*, *L. maackii*, and *L. morrowii*, all species commonly observed today in yards, landscapes, unintentional elements of natural ecosystems, and as products of the horticultural industry, as “some of the handsomest in bloom” and notes their persistent decorative fruits. The popularity of introduced ornamental bush honeysuckles continued into the 21st century, despite evidence as early as the 1920s suggesting that they tended to expand beyond the extent of their intentional cultivation (Luken and Thieret 1996). Now, many introduced bush and vining honeysuckles of Eurasian origin are widely considered invasive pests (Woods 1993, Hartman and McCarthy 2008), and recently have become the targets of state-level bans in parts of the US (USDA 2018).

Many of the same traits that made Eurasian *Lonicera* attractive as ornamentals, enhanced further by breeding efforts, enabled them to become serious invasive pests in their introduced range in North America. This motif is not unique to *Lonicera*, as horticulture and agriculture are famous sources of nonnative, invasive plants (Reichard and White 2001). Recently, plant scientists have developed models to guide selection of candidate taxa in an effort to reduce the proportion of introduced plants that become invasive (Anderson et al., 2006; Conser et al., 2015; Koop et al., 2011). Despite the broad concerns about invasive species introductions in general, and the invasive history of Eurasian *Lonicera* in particular, cultivars of honeysuckle developed from Eurasian stock, including *Lonicera tatarica*, *Lonicera xylosteum*, *Lonicera nitida*, *Lonicera japonica*, and others, continue to be sold in North America. Recently, interest has grown in the development of vigorous and productive cultivars of the edible blue honeysuckle, *Lonicera caerulea* L., using germplasm collected from a wide range in mainland Asia and Japan

(Gerbrandt et al. 2017). These cultivars are marketed under the names honeyberry, Haskap, or sweetberry honeysuckle, and as an agricultural berry crop for cold climates, with berries finding use in value-added products such as wines, jams, and confections (Celli et al. 2014). These cultivars are sometimes advertised as alternative crops to blueberries (Bors 2009b), and studies indicate that the fruits of *L. caerulea* are high in vitamins and antioxidants (Wang et al. 2016). However, *L. caerulea* also features prominently on the Norwegian Biodiversity Information Centre's Black List, where it ranks among Norway's invasive plants with highest impact, in a category of severity above known noxious, invasives like *L. tatarica*, *L. morrowii*, and *L. maackii* (Gederaas et al. 2012). Schimpf et al. (2011) reported a naturalized population of honeyberry near Duluth, Minnesota, and a subsequent visit to the site by Peterson et al. (2018) reported evidence of spread by both natural layering and seedling recruitment. Applications of checklist-based invasive plant screening tools by Peterson et al. (2016) indicated that blue honeysuckle cultivars from Eurasian stock pose a high risk of becoming invasive in North America, even with conservative ratings based on the limited data available on the growth, habit, and reproduction of *Blue honeysuckle*.

The exact taxonomy of the honeysuckles is still the subject of debate (see Naugžemys et al. 2011, Holubec et al. 2015), and some consider the mountain fly honeysuckle *L. villosa* (Michx.) Schult to be a variety or subspecies of *L. caerulea* (Fernald 1925, Schimpf et al. 2011). North American honeysuckles, including *Lonicera villosa*, generally form sparse populations and are often species of conservation concern in their native range (Lieurance and Cipollini 2013, USDA NRCS 2018). To some, this relationship is evidence that introduced genotypes of *L. caerulea* are unlikely to become invasive in North America (Bors 2009a), despite long-standing documentation of the morphological differences between Eurasian and North American

blue honeysuckles that to others justifies classification of North American taxa as separate species (Fernald 1925). In fact, the degree of relatedness and known capacity for hybridization between Eurasian *L. caerulea* and *L. villosa* (Bors 2009a) may be cause for greater concern, rather than evidence supporting the safe introduction of Eurasian blue honeysuckle, and here we will refer to Mountain Fly Honeysuckle as *L. villosa* for the sake of clarity. For example, potential population genetic consequences of introducing nonnative blue honeysuckle genotypes near native populations of mountain fly honeysuckle might include cryptic invasion (*sensu* Saltonstall 2002), reduction of population fitness by outbreeding depression (*sensu* Crispo et al. 2011), or the creation of invasive genotypes by reduced genetic load, heterosis, or evolutionary novelty of hybrids (*sensu* Ellstrand and Shierenbeck, 2000).

Here we address, in part, the need for further study and vetting *L. caerulea* cultivars by assessing traits such as root and shoot biomass, root-shoot ratio, average leaf size, specific leaf area, and plant height of *L. caerulea* in comparison to the known invader *L. tatarica*, and the native edible-berried blue honeysuckle *L. villosa*, as well as potential responses of these traits to changes in substrate fertility. In a second study we assessed these traits in response to different substrate moisture treatments in *L. caerulea*, *L. tatarica*, *L. villosa*, and *L. xylosteum* L., a more range-restricted invasive considered a noxious weed in the Northeastern US (USDA NRCS 2018).

3.3. Materials and Method

3.3.1. Experiment 1

Twenty-five cuttings each of the taxa *Lonicera tatarica*, *L. caerulea*, and *L. villosa* were propagated from semi-hardwood cuttings collected from containerized stock plants maintained at the University of Maine in Orono. Cuttings were collected in July 2016, treated with 4000 mg·L⁻¹

¹ of the potassium salt of indole-3-butyric acid (KIBA) and rooted in a 50:50 peat-perlite mix under intermittent mist. *Lonicera tatarica* stock plants represented locally invasive genotypes collected from the Fay Hyland Botanical Garden (GPS Coordinates: N 44°53'45.0" W 68°40'27.8"), while stock plants of *L. villosa* were propagated from material collected near Lubec, ME (GPS Coordinate: N 44°48'03.4" W 67°07'35.4"). *Lonicera caerulea* stock plants were grown from rooted cuttings purchased from a wholesale nursery in Manitoba, Canada. Cuttings were overwintered in cold storage from November 2016 until March 2017, then repotted into #1 trade-gallon plastic pots filled with 2:1:1 (by vol.) milled peat:vermiculite:coarse perlite, amended with 15 g of finely ground dolomitic limestone per pot.

Plants were grown in a glass-glazed greenhouse until they had put on an initial flush of new growth, after which plants were observed to enter ecodormancy as substrate fertility was exhausted (*sensu* Lang et al. 1987). Fertilizer treatments were initiated on April 27 2017. Fertility treatments were applied as top-dressed Osmocote Pro 17-5-11 4-month controlled release granular fertilizer (Scotts Miracle-Gro Company, Marysville Ohio, US) at rates of 5, 10, 15, 20, and 25 grams of fertilizer per pot (equivalent to 0.85, 1.70, 2.55, 3.40, and 4.25 g N), for a total of 5 replications per fertilizer treatment per taxon. Temperature on the bench was logged using a Watchdog 1450 micro station with radiation shield (Spectrum Technologies, Aurora, IL) at about the average leaf height of the honeysuckles. The temperature averaged 25 °C for the study period and reached a maximum of 47.2 °C. Photosynthetically active radiation (*PAR*) was measured once every ten minutes using a quantum light sensor attached to the same datalogger, and daily light integral (DLI) was calculated from these data. The average DLI was 19.6 mol m⁻² day with a maximum instantaneous *PAR* reading of 2324 μmol m⁻² s⁻¹. Plant placement was randomized at the start of the experiment and re-randomized weekly for the first five weeks of

the experiment, until the large size of some of the plants made re-randomizing too cumbersome. Plants were initially spaced on a one-foot center, but spacing was increased to a two-foot center on the final randomization to accommodate further growth. Western flower thrips [*Frankliniella occidentalis* (Pergande)] were observed during routine scouting in June, and plants were treated with Marathon II 1% granular pesticide on 16 June and on three-week intervals for the duration of the experiment.

To monitor fertilizer release and substrate fertility, electrical conductivity (EC, $\text{mS}\cdot\text{cm}^{-1}$) of the substrate was measured using the PourThru extraction method (*sensu* Cavins et al. 2000) and an HI991300 portable pH/EC/TDS meter (Hanna Instruments, Woonsocket, Rhode Island) on 18 June, 18 July, and 25 August. Plants were harvested the week of 28 August. We measured the length of the longest primary stem of each plant (*Lonicera* often form multi-stemmed shrubs), as well as the average size of twenty-five fully developed leaves randomly selected from each plant, by digitally photographing them and measuring stem length and the size of each leaf (cm^2) using ImageJ version 1.51 (Schneider et al., 2012). Roots were washed to remove substrate, and roots, stems, and leaves were dried to constant weight in a room maintained at ≈ 68 °C for three days prior to weighing. Stem and leaf weights were added to calculate total shoot dry weights, and specific leaf area ($\text{cm}^2 \text{g}^{-1}$) was calculated on an area per dry weight basis.

Statistical calculations were conducted using R version 3.3.2 (R Core Team 2016). Analysis of Variance (ANOVA) F-values were calculated at an alpha of 0.05 from linear models using the *car* package (Fox and Weisberg 2011) to test for the effects of taxon, fertilizer rate, and taxon by fertilizer interactions on the response variables. ANOVA assumptions were assessed visually using residual histograms, Q-Q normal plots, and residual versus fitted values plots. Shoot dry weights and root dry weights were square-root transformed to improve normality and

homoscedasticity, while primary stem length, root-to-shoot ratio, and EC measurements were \log_{10} transformed. Post-hoc least-square means with 95% confidence intervals were calculated for each response model using the package *lsmeans* (Lenth 2016), omitting terms for which ANOVA F-tests failed to reject the null hypothesis. All LS Means and confidence intervals were back-transformed and reported in their original units.

3.3.2. Experiment 2

Fifteen cuttings each of *L. tatarica*, *L. caerulea*, *L. villosa*, and *L. xylosteum* were propagated from semi-hardwood cuttings. Cuttings of *Lonicera tatarica* were from a locally invasive genotype growing in the Fay Hyland Botanical Garden (GPS Coordinates: N 44°53'45.0" W 68°40'27.8"), and cuttings of *L. xylosteum* were from plants cultivated in the Lyle E. Littlefield Ornamentals Trial Garden, both located at the University of Maine, Orono, ME. Cuttings of *L. villosa* were collected from stock plants originating from an indigenous population near Lubec, ME (GPS Coordinates: N 44°48'03.4" W 67°07'35.4"), and cuttings of *L. caerulea* were collected from stock plants of *L. caerulea* 'Svetlana' purchased from a wholesale nursery in Manitoba, Canada. Cuttings were collected in July 2015, treated with 4000 mg·L⁻¹ KIBA and rooted in a 50:50 (by vol.) peat:perlite mix under intermittent mist. Cuttings were overwintered in cold storage from November 2015 to April 2016. Rooted cuttings were transplanted into 4-inch pots filled with 1:1 peat:coarse perlite and grown through 2016. Plants were overwintered again in cold storage from November 2016 until April 2017, and transplanted into #1 trade-gallon plastic pots (Manufacturer) filled with 2:1:1 (by vol.) peat:vermiculite:coarse perlite, amended with 15 g of finely ground dolomitic limestone and top-dressed with 10 grams of Osmocote Pro 17-5-11 4-month controlled release granular fertilizer (Scotts Miracle-Gro Company, Marysville Ohio, US) per pot. On 13 June, the honeysuckles were transplanted into

#20 trade-gallon plastic pots (Manufacturer) with one plant of each taxon per pot, for a total of four plants per pot, pruned to a uniform height of 10 cm, and grown in a polyfilm-glazed hoop-house under 25% shade cloth. Planting order was randomized for each pot, and *Lonicera* were spaced evenly within the pots, resulting in a randomized split-plot design. Plants were fertigated twice weekly with Peters Professional 20-10-20 General Purpose fertilizer at a rate of .075 g N L⁻¹ throughout June and July. Western flower thrips [*Frankliniella occidentalis* (Pergande)] were observed during routine scouting in June, and plants were treated with Marathon II 1% granular pesticide on 16 June and on three-week intervals for the duration of the experiment. Plants were also treated with Hot Pepper Wax Insect Repellent (Hot Pepper Wax Inc., Greenville PA, US) in August and September to control for two-spotted spider mites [*Tetranychus urticae* (Koch)].

Moisture treatments were initiated on 1 August 2017. Pots were randomly assigned to one of three treatments: drought, container capacity, and flooded. Pots in the drought treatment were not watered after 1 August 2017, while pots in the container treatment continued to be watered to container capacity twice a week. Pots in the flooded treatment were set inside 20-gallon plastic pails and the water level was brought to the surface of the medium and maintained there for the duration of the study.

Plants were harvested the week of 10 October 2017. We measured plant height (cm), leaf size, and total leaf area (cm²) by digitally photographing them and processing the images using ImageJ version 1.51 (Schneider et al., 2012). Roots were washed to remove substrate, and roots, stems, and leaves were dried to constant weight in a room maintained at ≈68 °C for a week prior to weighing. Stem and leaf weights were added to calculate total shoot dry weights, and specific leaf area (cm²·g⁻¹) was calculated on an area per dry weight basis. *Lonicera villosa* was excluded from leaf measurements due to high rates of leaf senescence in the final weeks of the experiment.

Two replicates of *L. tatarica* were discarded from the container capacity treatment due to persistently poor performance following transplant to #20 plastic pots, prior to the initiation of moisture treatments.

Statistical calculations were conducted using R version 3.3.2 (R Core Team 2016). Analysis of Variance (ANOVA) F-values were calculated at an alpha of 0.05 from mixed effect models using the *lme4* package (Bates et al. 2015) to test for the effects of taxon, moisture treatment, and taxon by moisture interactions on the response variables. ANOVA assumptions were assessed visually using residuals histograms, Q-Q normal plots, and residual vs fitted values plots. Root dry weights, leaf dry weights, shoot dry weights, root system lengths, and plant heights were \log_{10} transformed and stem dry weights were square-root transformed to improve normality and homoscedasticity to meet ANOVA assumptions. Post-hoc least-square means with 95% confidence intervals were calculated for each response model using the package *lsmeans* (Lenth 2016) using Satterthwaite-adjusted degrees of freedom. Terms for which ANOVA F-tests failed to reject the null hypothesis were omitted from marginal mean difference calculations. All marginal means and confidence intervals were back-transformed and reported in their original units.

3.4. Results

3.4.1. Experiment 1

Based on ANOVA F-statistics (Table 3.1), we rejected the null hypotheses for the effect of taxon on each plant trait and conclude that the responses differ across the taxa in the study. Similarly, we rejected the null hypotheses for the effect of fertilizer application on root dry weight, shoot dry weight, and root-to-shoot ratio and conclude that responses differ across levels of applied fertilizer. We also rejected the null hypothesis for taxon by fertilizer-rate interactions

with respect to shoot dry weight and concluded that the three taxa responded differently to the applied fertilizer. Significant fertilizer and taxon effects were also detected for substrate EC on the first (F-values 96.09 and 5.55 respectively, sig. at $p \leq 0.001$ and $p \leq 0.01$) and second (F-values 26.33 and 17.04 respectively, sig. at $p \leq 0.001$) collection dates, as well as fertilizer effects and fertilizer by taxon interactions for the third collection date (38.96 and 4.99 respectively, sig. at $\alpha = 0.001$).

Table 3.1: ANOVA F-statistics for the Effects of Taxon and Fertilizer Application Rate on Growth of Three Honeysuckles.

Source	Root Dry		Root:Shoot	Leaf Size (cm ²)	Specific	Primary
	Weight (g)	Shoot Dry Weight (g)			Leaf Area (cm ² /g)	Stem Length (cm)
Taxon	207.943	514.166	5.780	106.894	6.015	70.231
	***	***	**	***	**	***
Fertilizer	2.892	7.645	5.152	0.950	0.346	1.081
Rate	*	***	**			
Taxon x	1.366	5.937	0.585	0.597	0.924	0.760
Fertilizer		***				
Rate						

*Significant treatment effect at $p \leq 0.05$

**Significant treatment effect at $p \leq 0.01$

***Significant treatment effect at $p \leq 0.001$

Lonicera tatarica produced the greatest dried biomass, with nearly five times the shoot dry weight and root dry weight of *L. caerulea*, which in turn produced about twice the dried shoot biomass of *L. villosa* across all but the highest fertilizer application levels (Fig. 3.1 A). *Lonicera tatarica* exhibited a strong response to increased soil fertility in terms of shoot dry weight, producing ≈ 80 grams of combined stems and leaves at a fertilizer application rate of 20 g CRF per #1 container, over a two-fold increase in shoot dry weight over the lowest fertilizer

application rate of 5 g. The maximum rate of fertilizer application appeared to have a deleterious effect on the dry shoot biomass produced by Tatarian honeysuckle.

Neither *L. villosa* nor *L. caerulea* displayed a significant response to increased fertilizer application rate with respect to shoot dry weight. Similarly, the three taxa differed significantly in mean root dry weight across the fertilizer treatments (Fig. 3.1 B). *Lonicera caerulea* produced 2-3 times the dry root mass of *L. villosa* at 5 to 10 grams of applied fertilizer (0.85 to 1.7 g N) but only one fourth the dry root mass of *L. tatarica*. Plants produced the greatest average root dry mass at 10 grams of applied fertilizer (equivalent to 1.7 g N), above which increased fertilizer applications appeared to have a slight inhibitory effect on root production. *Lonicera caerulea* and *L. tatarica* produced the greatest ratio of root dry weight to shoot dry weight (Fig. 3.1 C), and the root to shoot ratio of the two taxa were not statistically different. The root-shoot ratio of *Lonicera villosa* was significantly lower than that of the others, indicating the production of less root dry mass per unit of shoot dry mass, and the root-shoot ratio of each taxon decreased with increasing fertilizer application rate.

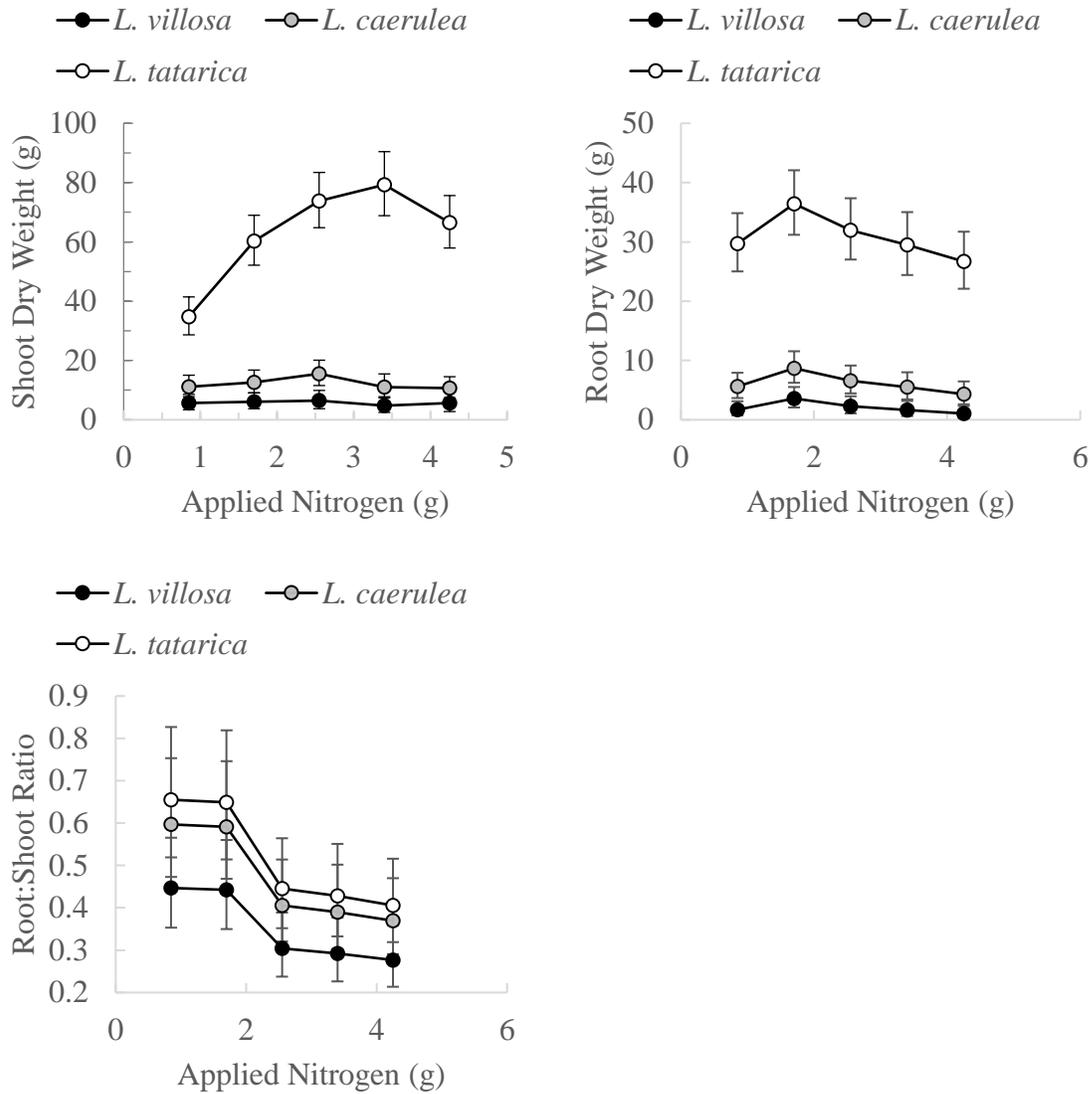


Figure 3.1: Least-square means of shoot dry weight (A), root dry weight (B), and root:shoot (C) $\pm 95\%$ CI of *Lonicera villosa*, *L. caerulea*, and *L. tatarica* across five fertilizer application rates. *Lonicera tatarica* differed significantly from the other two taxa in terms of mean root and shoot dry weights for all fertilizer application rates. *Lonicera caerulea* differed significantly from *Lonicera villosa* for all but the highest application rate. *Lonicera tatarica* and *L. caerulea* did not differ significantly from each other in terms of root:shoot, and both differed significantly from *L. villosa*.

Average leaf size, specific leaf area, and primary stem length varied significantly by taxon (Table 3.1), but not by fertilizer application rate, and there was no interaction. *Lonicera tatarica* produced leaves of the greatest average size (20.9 cm²), followed by *Lonicera caerulea* (16.7 cm²), with those of *L. villosa* at 6.9 cm² (Fig. 3.2 A). *Lonicera villosa* produced leaves with the greatest specific leaf area (SLA; 121.1 cm²/g), while *Lonicera tatarica* produced leaves with the lowest SLA (109.1 cm²/g; Fig. 3.2 B). The SLA of *Lonicera caerulea* was not significantly different from the SLA of *L. villosa* or *L. tatarica*. Primary stem length did not differ significantly between *L. caerulea* and the invasive *L. tatarica*, both of which produced primary stems of a length more than double those of *L. villosa* (Fig. 3.2 C; 68.9 cm, 71.1 cm, and 31.4 cm respectively).

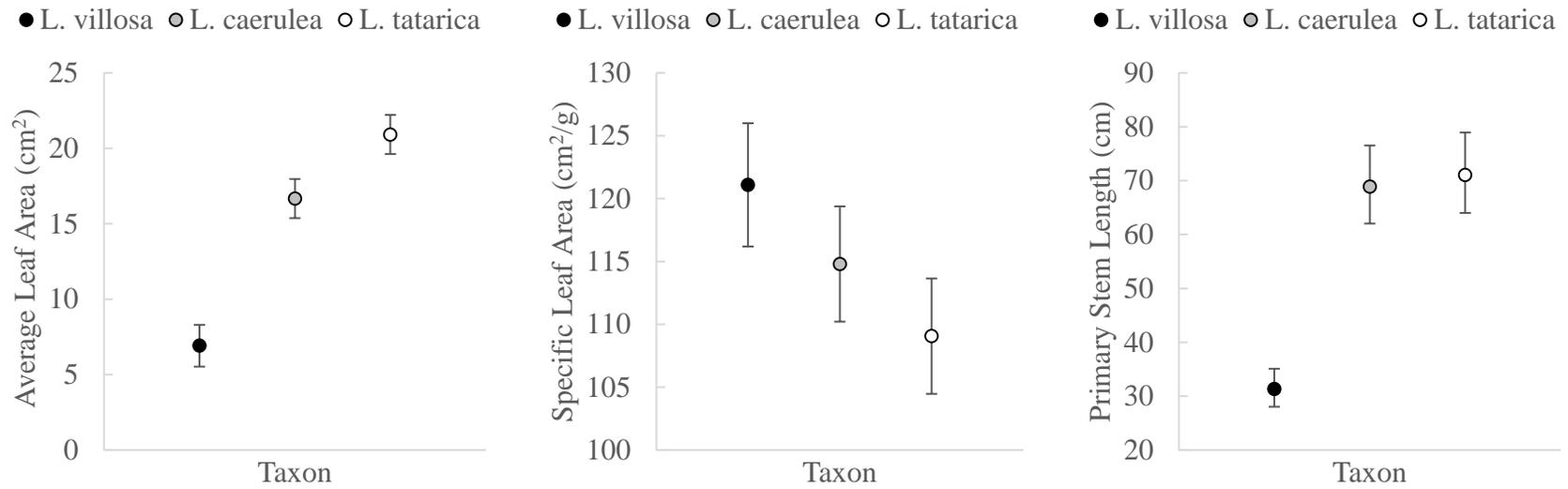


Figure 3.2: Least-square means average leaf area (A), specific leaf area (B), and primary stem length (C) \pm 95% CI of *Lonicera villosa*, *L. caerulea*, and *L. tatarica* averaged over levels of fertilizer application.

Substrate EC measured on 18 June, 2017 followed the expected increasing linear trend with respect to CRF rate (Fig. 3.3 A). The substrate EC of pots planted with *Lonicera tatarica* was greater than that of pots planted with *L. villosa* or *L. caerulea* at all fertilizer application rates, indicating that Tatarian honeysuckle influenced either the breakdown of the CRF or fertilizer persistence in the substrate. Substrate EC declined between 18 June and 18 July but remained greatest in pots planted with *Lonicera tatarica*. By the end of the experiment on 25 August, substrate EC had declined further, with substrate EC of pots planted with *L. tatarica* reading lower than those planted with *L. caerulea* or *L. villosa*, a reversal of earlier trends (Fig 3.3 C). Given the significantly greater biomass of *L. tatarica* by the end of the experiment, it is likely that *L. tatarica* had exhausted the available fertilizer, though the increased demand for irrigation to replace water lost to transpiration by the comparatively large invasive honeysuckles also could have resulted in increased leaching of substrate nutrients.

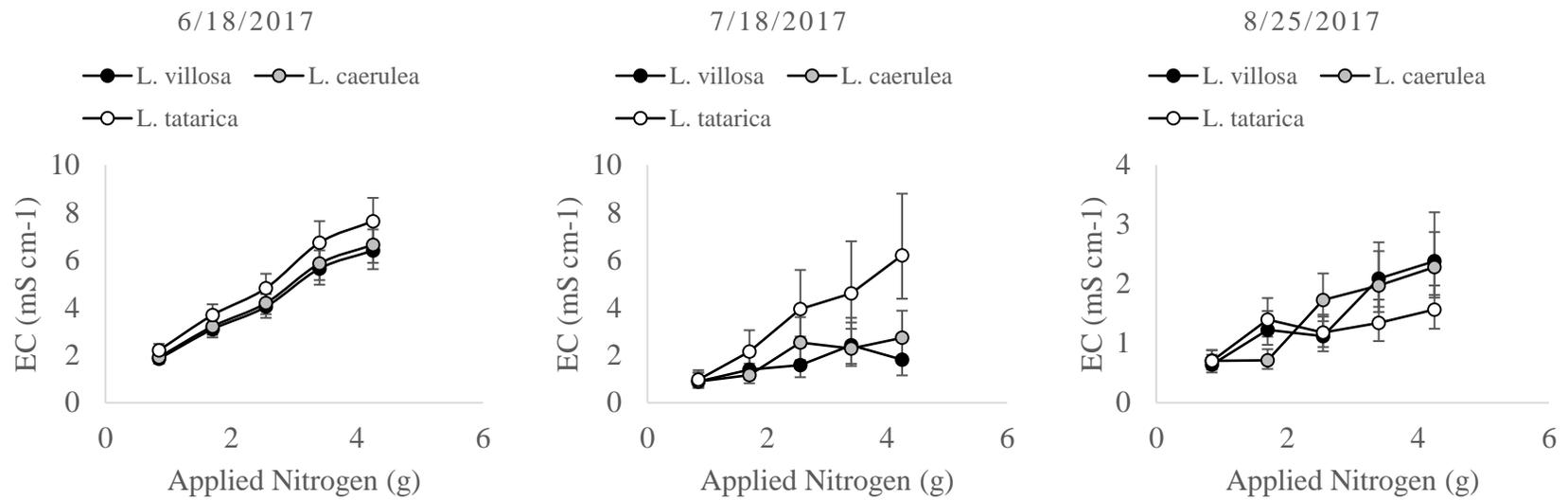


Figure 3.3: Least Square Means of substrate electrical conductivity (mS cm⁻¹) ± 95% CI of substrates supporting the growth of three honeysuckles (*Lonicera villosa*, *L. caerulea*, and *L. tatarica*) on three measurement dates.

3.4.2. Experiment 2

Significant differences were not detected among moisture treatments for any of the plant traits examined at an α of 0.05 (Table 3.2.), though nearly significant differences were detected on root system length ($F(2,12) = 3.293$, p-value 0.0725). However, we detected significant differences across the honeysuckle taxa with respect to all response variables, as well as significant moisture treatment by taxa interactions for root dry weight, stem dry weight, root system length, and a nearly significant interaction term for specific leaf area. These significant interaction terms indicate that while moisture treatments did not have a significant quantitative effect on the response variables within each taxon, there were significant qualitative differences in the relationship among the honeysuckle taxa over the moisture treatments, indicating changes in the relationship between the different taxa across the moisture treatments.

Of the four taxa examined, the native *Lonicera villosa* produced the least dry biomass, equivalent only to the less widespread invader *Lonicera xylosteum* under flooded conditions (Fig. 3.4 A, B: 2.33 g and 3.31 g respectively for root dry weight, 3.39 g and 5.02 g for stem dry weight) and to *Lonicera caerulea* in terms of stem dry weight under drought conditions (2.81 and 5.82, respectively). *Lonicera caerulea* produced dry root biomass equivalent to that of the widespread invader, *L. tatarica*, under all moisture treatments, and produced dry stem biomass equivalent to the invasive *L. xylosteum* under drought and container capacity conditions and to *L. tatarica* under flooded conditions (Fig. 3.4 A, B). *Lonicera caerulea* also produced leaf biomass equivalent to *L. tatarica* (2.87 g and 4.67 g, respectively), while both taxa produced greater leaf biomass than *L. xylosteum* (1.04 g). However, *Lonicera caerulea* produced less above-ground biomass per unit of belowground biomass than the two invasive taxa (Fig 3.4 D).

Table 3.2: ANOVA F-statistics and Degrees of Freedom (df) for the Effects of Taxon and Moisture Treatment on Growth of Four Honeysuckles.

Source	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Root:Shoot	Root system length (cm)	Plant Height (cm)	Leaf Size (cm ²)	Specific Leaf Area (cm ² /g)
Moisture level F-value	0.3012	0.1956	0.55929	2.6642	3.293	0.275	1.9426	0.7095
Moisture level df	2	2	2	2	2	2	2	2
Error A df	12	12	12	12	12	11	11	11
Taxon F-value	47.9486 ***	31.1817 ***	14.77809 ***	6.9619 **	46.545 ***	90.764 ***	46.2399 ***	4.2333 *
Taxon df	3	3	2	2	3	3	2	2
Moisture level x Taxon F-value	2.9294 *	2.7171 *	1.88413	1.5375	2.950 *	1.422	2.0506	2.4798
Interaction df	6	6	4	4	6	6	4	4
Error B df	34	34	22	22	34	31	20	19

*Significant treatment effect at $p \leq 0.05$

**Significant treatment effect at $p \leq 0.01$

***Significant treatment effect at $p \leq 0.001$

Lonicera caerulea also performed similarly to *L. xylosteum* for rough and container capacity treatments and *L. tatarica* (for Flooded treatments) in terms of root system length, producing root systems that were over twice the length of those of *L. villosa* (Fig. 3.5 A).

Lonicera tatarica produced plants with the longest root systems under drought and container capacity moisture conditions, over twice the length of the other Eurasian honeysuckles and four

times the length of *L. villosa*. *Lonicera caerulea* plants also rivalled *L. tatarica* in height, reaching 70.22 cm and 76.23 cm respectively (Fig. 3.5 B), approximately four times the height achieved by the North American native *L. villosa* (17.33 cm). The leaves of *Lonicera caerulea* were intermediate in size compared with the other Eurasian honeysuckles, with an area of 13.0 cm² vs. 7.6 cm² for *L. xylosteum* and 17.7 cm² for *L. tatarica* (Fig. 3.5 C). The leaves of *Lonicera caerulea* did not differ significantly from the other non-native honeysuckles in terms of specific leaf area, while *L. xylosteum* produced leaves of the greatest area per gram of leaf dry weight and *L. tatarica* produced leaves of the least area per gram of dry weight (Fig. 3.5 D).

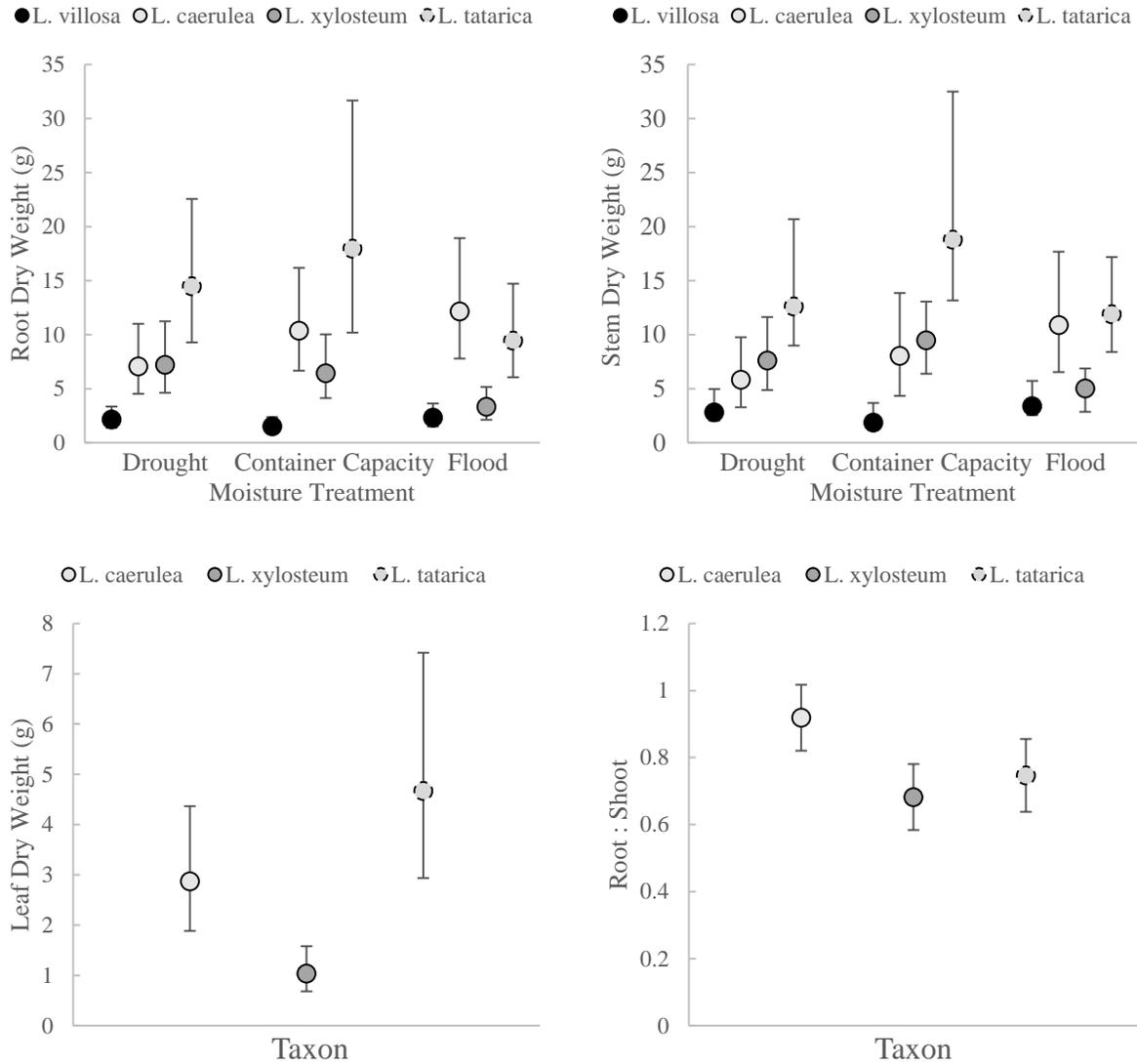


Figure 3.4: Least-square means of root dry weight (A), shoot dry weight (B), leaf dry weight (C), and root:shoot (D) \pm 95% CI of four *Lonicera* species across three moisture treatments. *Lonicera villosa* was excluded from leaf measurements due to early leaf senescence. *Lonicera villosa* produced the least root and stem dry biomass and was only statistically equal to *L. xylosteum* in the flooded treatments and *L. caerulea* in the drought treatments in respect to stem dry weight. *L. caerulea* produced root and shoot dry biomass on par with *L. xylosteum* and *L. tatarica* drought and container capacity treatments, and *L. tatarica* on flooded treatments. *Lonicera caerulea* produced greater dry leaf biomass than *L. xylosteum* and equivalent to *L. tatarica* but produced greater dry root mass in proportion to dry shoot mass than the invasive honeysuckles.

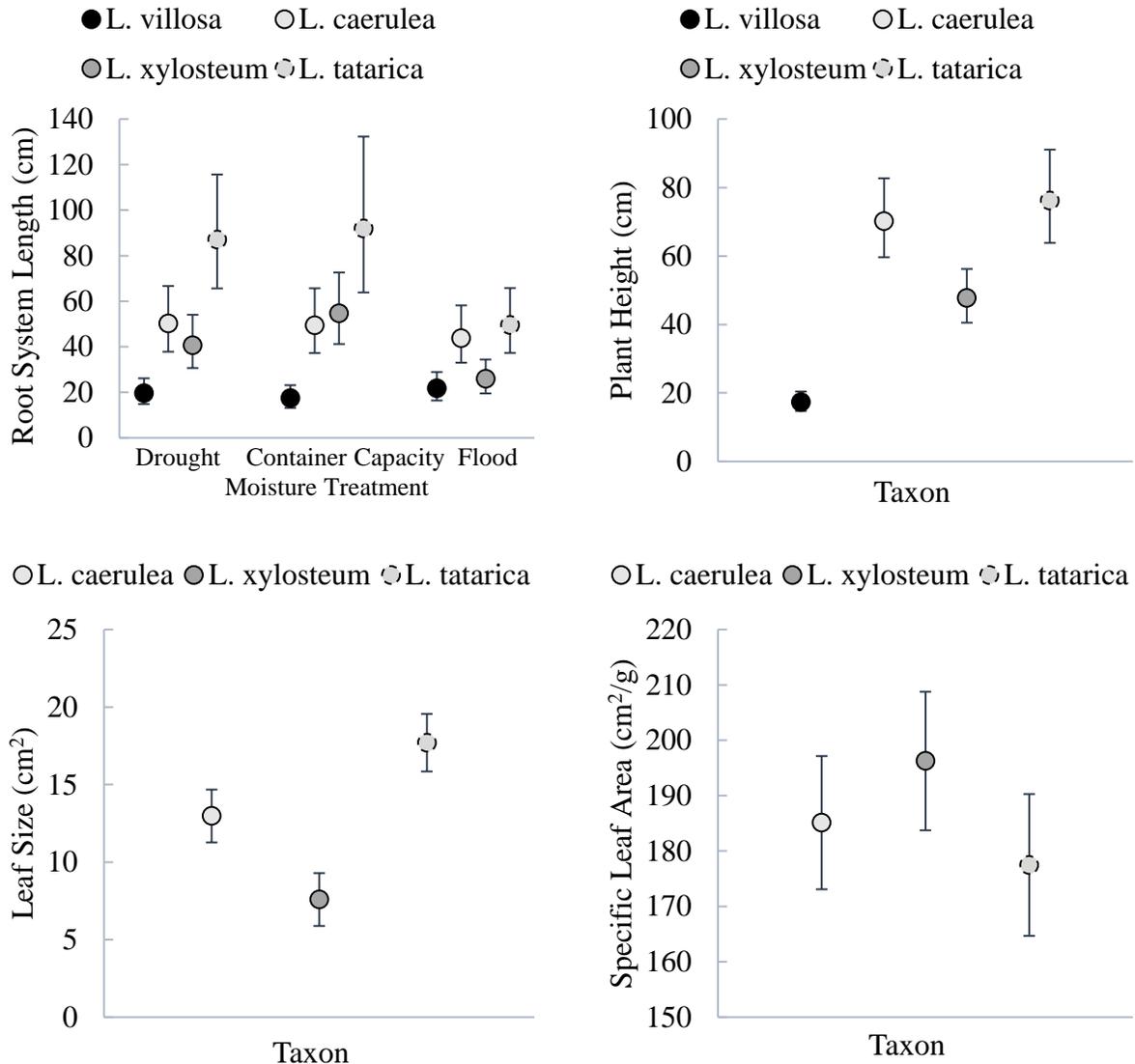


Figure 3.5: Least-square means of root system length(A), plant height (B), leaf size (C), and specific leaf area (D) \pm 95% CI of four *Lonicera* species across three moisture treatments. *Lonicera villosa* was excluded from leaf measurements due to early leaf senescence. *Lonicera villosa* produced root systems with the shortest length, matched only by *L. xylosteum* under flooded conditions, and produced plants of the shortest stature. *Lonicera caerulea* matched *L. xylosteum* for root system length for drought and container capacity treatments, and *L. tatarica* for flooded treatments and for plant stature. *Lonicera caerulea* produced leaves that were intermediate in size between the two invasive honeysuckles, and with an SLA that was statistically equivalent to that of both invaders. *Lonicera tatarica* produced leaves with a significantly lower SLA than *L. xylosteum*.

3.5. Discussion

Though measures of root and shoot dry weights between introduced the cultivar of *Lonicera caerulea* and native accession of wild *L. villosa* were unresponsive to fertilizer application rates in the first experiment and were closer in magnitude than to the known invasive *L. tatarica*, the two blue honeysuckles differed significantly over many of the fertility treatments in the study, especially over the low to medium scale of fertilizer treatments (5 to 15 grams 17% N fertilizer). Over this range *L. caerulea* produced twice the dry biomass of *L. villosa* in a single four-month growing season. In the second experiment these differences between the introduced *L. caerulea* cultivars and native *L. villosa* were more pronounced, and *L. caerulea* was observed to be more like the two invasive Eurasian taxa than the native. Though quantitative differences in moisture treatment response were not detected within the taxa over the duration of Experiment 2, the significant interaction terms and qualitative differences between taxa in response to moisture treatment suggest that such differences would be detected in an experiment with less variation, a greater duration, or designed for increased sensitivity to these effects.

The blue honeysuckles also differed significantly in form and resource allocation: the agricultural cultivar of *L. caerulea* rivalled the primary stem length of *L. tatarica*, achieving the same height despite only producing 20 to 25 percent of the total shoot dry weight in Experiment 1 and 50 percent of the total shoot dry weight in Experiment 2. This may indicate a prioritization for vertical growth as a competitive strategy, a common trait in competitive forest trees and shrubs (Gaudet and Keddy, 1988). A prioritization for vertical growth to shade out competitors and monopolize light resources is also a common competitive strategy in invasive plants (Pyšek and Richardson 2007) that may in part explain the success of *L. caerulea* as an invader of established forests in Norway. The production of larger leaves seen in *L. caerulea*, closer in

magnitude to the surface area of *L. tatarica* than its fellow blue honeysuckle, could further support this strategy by shading out competitors once it has gained a height advantage. The low specific area of *L. tatarica* indicates a greater investment of resources in leaf construction, which is often associated with increased leaf lifespan (Reich et al. 1991). Species that maintain their leaves later in the year may capitalize on a longer growing season to access light and resources during a period of reduced competition (Fridley 2012). This competitive strategy is observed in the similarly invasive honeysuckle *L. maackii* (Trisel 1998) and is thought to be a contributing factor in many forest species invasions (Fridley 2012). Leaves with low SLA also tend to be more resistant to herbivory (Grime et al. 1996), a trait that is thought to contribute to the invasion success of invasive Eurasian honeysuckles (Lieurance and Cipollini 2013). The specific leaf area of *L. caerulea* was intermediate between *L. tatarica* and *L. villosa* in Experiment 1 and *L. tatarica* and *L. xylosteum* in Experiment 2 but was not statistically different from either taxon at an alpha of 0.05 and the degree of variation seen in these studies. The SLA of *L. villosa* could not be calculated in Experiment 2 due to near-complete leaf senescence of these plants before any leaf senescence was observed in the Eurasian taxa, providing evidence that leaf retention and functional growing season may differ between the native and introduced taxa.

The root to shoot ratio of *L. caerulea* also compared more favorably to *L. tatarica*. High root-shoot ratios are also correlated with increased resistance to drought, as well as greater ability to access soil resources, traits one would expect in a cultivar selected for agricultural conditions. The low root-shoot ratio of *L. villosa* is consistent with its life history as a plant of bogs, fens, and wet-mesic forests.

3.6. Conclusions

While *L. caerulea* did not exhibit growth or response to fertility to the extent of the confirmed high-impact invader *L. tatarica* in the context of Experiment 1, the agricultural cultivar performed better than the native *L. villosa* in terms of dry biomass produced over the course of both experiments and was more similar in growth form, size, and resource allocation to *L. tatarica* and *L. xylosteum*. While it is difficult to predict invasiveness based on trait studies, in our opinion the agricultural blue honeysuckle crops developed from Eurasian taxa should not be considered equivalent to the native North American blue honeysuckle due to observed differences in morphology and physiology, and that it would be erroneous to infer the potential distribution and behavior of *Lonicera caerulea* cultivars in North America based on the distribution and abundance of *Lonicera villosa*. When considered alongside the invasive status of *Lonicera caerulea* in Norway, the long invasive history of Eurasian *Lonicera* in North America, the high risk assessment using screening tools, and the potential population genetic consequences for the North American native *Lonicera villosa*, we believe this study illustrates the need for further trait studies to be conducted before the widespread planting of *Lonicera caerulea* cultivars in North America.

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BIOGRAPHY OF THE AUTHOR

Darren J. Hayes was born in Millinocket, Maine on March 19, 1986. His love for the biological sciences was instilled in him in large part by his grandfathers, one an avid gardener and devourer of National Geographic television programming, the other an outdoorsman. Darren took a circuitous route to the formal study of the Horticultural sciences, first pursuing interests in other disciplines and earning a B.S. in Biology with a concentration in Neuroscience in 2013. All the while hobbyist horticultural pursuits provided an outlet for independent study and self-expression, culminating in the decision to return to academia and refocus his efforts.

Darren was afforded the opportunity to combine his horticultural interests and appreciation for the wilderness of Maine as an undergraduate research assistant for Dr. Bryan Peterson and transitioned in this capacity into the Horticulture M.S. program, where he was awarded numerous awards and scholarships over the course of his graduate career. He hopes to continue to conduct plant-science related research in Maine, and to continue to expand his diverse interests and extend them into possible business ventures. Darren is a candidate for the Master of Science degree in Horticulture from the University of Maine in August 2018.