1-2013

Water-Use Strategies of Japanese Knotweed (Fallopia japonica)

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Recommended Citation

Cummins, Lisa Nicole, "Water-Use Strategies of Japanese Knotweed (Fallopia japonica)" (2013). *Theses, Dissertations and Culminating Projects*. 805.
https://digitalcommons.montclair.edu/etd/805

MONTCLAIR STATE UNIVERSITY

Water-use strategies of Japanese knotweed (*Fallopia japonica*)

by

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A Master's Thesis Submitted to the Faculty of

Montclair State University

In Partial Fulfillment of the Requirements

For the Degree of

Master of Science

January 2013

College/School College of Science and Mathematics

Department Biology and Molecular Biology

[redacted]

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Abstract:

Japanese knotweed, *Fallopia japonica,* is an herbaceous perennial that is invasive on many continents, including North America. Stands of Japanese knotweed are often located in riparian regions, disturbed sites, and along roadways. Recent studies have evaluated the impact of Japanese knotweed on the hydrologic cycle. Japanese knotweed may have the ability to markedly decrease stream discharge, potentially because of its high LAI. In the summer of 2010, a two-part study was conducted to determine the impact of water availability on the physiology and morphology of Japanese knotweed. A greenhouse study of Japanese knotweed measured transpiration and other factors that may impact water-use, including photosynthesis, stomatal conductance, vapor pressure deficit, leaf water potential, leaf specific conductance, and instantaneous water use efficiency. Leaf and root biomass allocation was examined as well. Via a field study of Japanese knotweed growing under contrasting moisture regimes, designated *dry*, *intermediate*, and *wet*, LMA, node length and diameter, and stem based hydraulic conductance were compared for each moisture regime.

The greenhouse study results demonstrated that Japanese knotweed adjusted parameters to optimize use of water when available. Leaf specific hydraulic conductivity was significantly lower for drought-treated plants, at 0.20±0.01 mmol/s/m^2/MPa, compared to 0.34±0.01 mmol/s/m^2/MPa for watered plants (P=0.0001). Instantaneous water use efficiency increased significantly following drought treatment, with a mean of 24.22±2.05 µmol/mmol for drought-treated plants, and a mean of 17.92±1.4 µmol/mmol for the watered plants (P=0.0109). Such findings were supported by field study results. Hydraulic conductivity on a stem area basis increased significantly between wet site plants, at 1.16x10^6±0.126x10^6 mmol/s/MPa/m^2 , compared to 6.69x10^5±1.0x10^5 mmol/s/MPa/m^2 for the intermediate site (P=0.0047) and 4.94x10^5±0.556x10^5 mmol/s/MPa/m^2 for the dry site (P=0.0001). Significant differences in LMA and internode length were also found between sites, indicating that variations in morphology may promote successful water use and transport in varied environmental conditions. Taken together, the results of these studies show that Japanese knotweed could impact water supply in invaded areas, whether dry or wet, through alterations in physiological responses and biomass allocation that allow for optimal water use under short-term and long-term moisture conditions.

WATER-USE STRATEGIES OF JAPANESE KNOTWEED (*FALLOPIA JAPONICA)*

A THESIS

Submitted in partial fulfillment of the requirements

For the degree of Master of Science

by

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Montclair State University

Montclair, NJ

2013

Acknowledgements

This thesis would never have been complete without the support of many. I offer my sincere gratitude to the faculty and staff of the Department of Biology and Molecular Biology for their incredible support. What began as an amazing opportunity to teach as a graduate assistant led to an even greater appreciation for the scientific process, thanks to the guidance of wonderful professors. This, combined with the welcoming atmosphere of Montclair State, provided the inspiration to pursue a Masters of Science. Special thanks to Dr. Adams for opening the door to this pursuit, and for always taking the time to listen. Thank you Dr. Vanderklein, for introducing me to plant ecophysiology, and supporting this research. You have offered endless support, patience, and unyielding encouragement throughout the entire process. Thank you to Dr. Galster, for taking the time to give advice, and introduce me to the fascinating world of GIS. Thank you to Dr. Wu, for your insight and for expanding my ecological knowledge. I would also like to thank the graduate, undergraduate, and high school students who lent their assistance at various stages of this research. Finally, I would like to thank my family, for their constant support, at every step of the way.

Section *Page*

List of Figures and Tables

List of Tables

Introduction

The goal of this study was to measure water used by Japanese knotweed as well as the physiological and biophysical characteristics associated with water-use by Japanese knotweed. In order to address this goal, it was necessary to measure the plants in the lab under controlled conditions and to measure the plants in the field under ambient conditions. The greenhouse study allowed us to 1) determine the water used by Japanese knotweed from dawn until photosynthetic peak at mid-day, 2) calculate and analyze transpiration rate, leaf specific hydraulic conductance, and water-use efficiency of Japanese knotweed, 3) compare data for watered plants over the growing season to that of the same plants following a late summer drought treatment, and 4) collect biomass data. The field study samples were gathered from areas of varied water availability located within a 3.5 km radius of each other. This aspect of the study allowed us to 1) compare morphological features such as leaf mass per area (LMA) and stem structure among plants from different sites, and 2) to determine hydraulic conductance for stems from each site. Together, the greenhouse and field studies provided data regarding Japanese knotweed water-use strategies over the course of a day and in response to drought treatment, and the effect of environmental hydrologic conditions on plant morphology and water-use traits.

Japanese knotweed, *Fallopia japonica,* an herbaceous perennial native to Japan, China, and Tawain, is considered an invasive species in introduced ranges, including the mid-Atlantic region of the United States (Talmage & Kiviat, 2004). Japanese knotweed grows in dense, monospecific stands and is characterized by rapid growth and expansion (Shaw & Seiger, 2002). Common to riparian regions and disturbed sites, the presence of Japanese knotweed may result in altered biogeochemistry, decreases in biodiversity, disturbances to food webs (Aguilera et al., 2010; Gerber et al., 2008; Lecerf et al., 2007; Maerz et al., 2005), and decreased baseflow of invaded stream sites (Vanderklein et al., in review). Previous research illustrated the prodigious water-use capabilities of Japanese knotweed and its subsequent impact on stream hydrology in the Bonsal Preserve, in Montclair, NJ (Vanderklein et al., in review). In this study, stream base flow along the Third River, located in the Bonsal Preserve in Montclair, NJ, was found to be significantly higher post-harvesting of a Japanese knotweed patch along the river, both during daily highs and lows (Vanderklein et al., in review). The study by Vanderklein et al. also found the leaf area index of Japanese knotweed to be 4.96 m^2. The purpose of this research was to elucidate the relationship between the water-use and physiology of Japanese knotweed. The study was conducted from May through September of 2010, a period marked by elevated temperatures and annual peaks of photosynthetically active radiation. Two parts, a greenhouse study and a field study, were used to assess either water-use parameters over time or across sites, respectively. The results of the greenhouse study indicated that Japanese knotweed is capable of continuing photosynthesis across watered and drought treatments, via physiological adjustments. The field study results were significantly different in both morphology and hydraulic conductivity across varied moisture regimes. Taken together, the greenhouse and field studies demonstrate the ability of Japanese knotweed to extract water across a range of moisture availabilities, both in the short and long term.

Japanese Knotweed History

Japanese knotweed, alternately classified as *Polygonum cuspidatum,* and *Reynoutria japonica,* is an herbaceous perennial of the Polygonaceae family (Bailey &

Conolly, 2000). Other common names include Mexican bamboo and Donkey rhubarb (Child & Wade, 2000). It grows in silt, loam, and sandy soils with a pH ranging from 4.5 to 7.3 (Shaw & Seiger, 2002). Japanese knotweed has elongated, ovate leaves, with cuspidate tips and truncate bases, arranged alternately on hollow, woody stems (Bailey & Conolly, 2002). The plant may reach 3 meters in height (Shaw & Seiger, 2002). Greenish-white inflorescences emerge from axial tips (Child & Wade, 2000). Reproduction in the native range is by seed, its winged fruit dispersed by animals and wind (Child & Wade, 2000). Vegetative growth by long rhizomes, up to 6 meters in length, and dispersed rhizome and stem fragments, are primary means of spread in introduced ranges (Child & Wade, 2000).

The expansive range of a single male infertile specimen, which covers many areas of the United Kingdom, clearly depicts the success of this strategy (Hollingsworth & Bailey, 2000). Clones of this plant, identified by DNA analysis, are located in the United States (Gammon et al., 2010), demonstrating the extent to which this plant, without genetic variety, can still have a global impact. Though clonal growth has been documented widely, the dioecious nature of Japanese knotweed means that ability to reproduce by sexual means remains a viable option in introduced ranges (Gammon et al., 2007), a phenomenon which may provide opportunities for selection in novel habitats.

First described by Houttuyn in 1777 and classified as *Reynoutria japonica*, Japanese knotweed is native to areas of Japan, northern China and Taiwan (Bailey & Conolly, 2000). The avid plant collector and physician Phillipe von Siebold imported the specimen referred to as *Polygonum cuspidatum* from Japan through his company, Von Siebold & Co. Knotweed was initially introduced in Britain as an ornamental plant in the

1850s and sold as such by the Royal Botanical Gardens at Kew (Bailey & Conolly, 2000). The popularity of Japanese knotweed in this introduced range gave way to notoriety when it naturalized and spread, ultimately attaining invasive species status. In 1981, it became a criminal offense to knowingly introduce Japanese knotweed in the United Kingdom (Hollingsworth and Bailey, 2000). It has subsequently been reported in the United States, Britain, Germany, France, Russia, New Zealand, Canada, and the Czech Republic (Talmage & Kiviat, 2004).

A pioneer species in its native range (Adachi et al., 1996), Japanese knotweed can be found along railway tracks, bare areas, and in volcanic regions (Talmage & Kiviat, 2002). In the United States and Britain, it is frequently located along roadsides, railways, disturbed sites, and riparian areas (Shaw & Seiger, 2002). It has even recently been found in salt marshes (Richards et al., 2008). The invasive potential of Japanese knotweed enhances its potential for range expansion.

Where Japanese knotweed is found, biodiversity may be at risk. Increases in height and coverage of invasive plant species have been associated with an increased reduction in biodiversity (Hedja et al., 2009). Japanese knotweed, with its dense canopy, rapid growth rate, and potential to reach three meters in height, meets these criteria. Japanese knotweed can successfully compete with native plants by limiting access to light (Siemens & Blossey, 2007). Consequences of the introduction and spread of Japanese knotweed have historically mirrored the reductions in biodiversity associated with previous species invasion. Maerz et al., (2005), found that green frogs in knotweed patches demonstrated reduced foraging success, which could ultimately cause extinction and a reduction in amphibian diversity across invaded ranges. Japanese knotweed has also been shown to decrease arthropod (Aguilera et al. 2010; Gerber et al., 2008) and plant diversity within stands (Gerber et al., 2008). Reduced arthropod biomass has also been observed in invaded areas (Gerber et al., 2008).

Japanese knotweed alters biogeochemical cycles and soil quality. Reduced litter quality is manifested in an increased C:N ratio in knotweed stands due to resorption of foliar nitrogen to rhizomes and by increased lignin concentrations, which may slow decomposition rates and therefore nutrient cycling (, Aquilera et al., 2010; Urgenson et al., 2009). The presence of allelopathic biochemicals has also been detected in Japanese knotweed. Extracts from rhizomes contain phenolic compounds that inhibit germination capabilities of white mustard seeds upon exposure (Vrchotová & Šerá, 2008). These biogeochemical alterations are contributing factors to the invasion potential of this species and may promote changes in the community structure, which could potentially alter energy flow through trophic levels and disrupt ecosystem balance.

Species Invastion, Water Availability, & Ecohydrology

Climate change is predicted to have specific impacts on regional aquatic ecosystems, with the mid-Atlantic region poised to become warmer and drier (Meyer et al., 1999). In the Northeast region of the United States, predicted temperature increases as a result of climate change are expected to result in increased drought, and greater extremes in streamflow patterns, with flooding following ice melt and summer droughts (Frumhoff et al., 2007).

The field of ecohydrology provides a framework with which to study the interactions of ecosystem components, particularly as they pertain to water cycling and usage. The benefits of evaluating both the ecology and hydrology of an area are that a consideration of ecological processes pertaining to the water cycle may yield more sustainable solutions and a decrease in extreme hydrological events associated with disruption of biological processes (Zalewski, 2002). Specifically, this approach may help determine alterations in water supply and demand in the presence of invasive species. Studies on the feedback effects of water supply on ecosystem productivity and nutrient cycling and the effects that biotic processes have on hydrologic processes may yield valuable insights (D'Odorico et al., 2010).

Vegetation serves to regulate evapotranspiration and precipitation, and can affect runoff and soil moisture (D'Odorico et al., 2010). Interception of precipitation by plants, combined with the ability of plants to extend roots below the typical evaporative region of soil and maintain transpiration rates, can affect the water budget of an area (Loik et al., 2004). Woody plants have the potential to alter stream flow and evapotranspiration rates in some regions (Huxman et al., 2005). The degree and direction of alteration is dependent on a variety of factors such as landscape features, climate, runoff, and subsurface water supply (Huxman et al., 2005). Conversely, river flow can impact species composition, since different plants are adapted to specific hydrologic conditions (D'Odorico et al., 2010). Given the close relationships of vegetation and hydrology, and water flow and quality, a method of evaluation that integrates these factors would prove useful in determining the effect of invasive species on hydrologic processes. In order to determine these effects, however, it is first necessary to determine water use of the invasive species in question, under a variety of water supply regimes.

Invasive Plants and Water-Use

An invasive species is an organism that has been introduced to an area, naturalized, and expanded its range (Mack et al., 2000). The ability of invasive species to use more water as compared to native species (Calder & Dye, 2001) is a detrimental effect that may result in ecosystem alteration. The field of ecohydrology may be used to study the interactions between the environmental factors of water supply and climate, and regional vegetative composition (D'Odorico et al., 2010). Riparian areas are especially vulnerable to invasion, which can impact the hydrology of these areas (Tickner et al., 2001). To compound the issue, water can promote the spread of invasive species (Tickner et al., 2001). Climate change models predict the spread of invasive species, which could further alter ecosystem functions such as nutrient cycling and productivity in aquatic regions (Meyer et al., 1999). Given the necessity of sustaining water supply in the face of climate change and increased demand, the potential depletion by invasive species is a viable threat.

Invasive species can negatively impact the water cycle via increased evapotranspiration resulting in decreased water supply for other organisms. This has been especially apparent in Africa, where use of water by invasive plants has decreased water supply dramatically in areas that are already under stress due to drought (Gorgens & van Wilgen, 2004). In a biome scale assessment, invasive species were found to cause a 7% reduction in runoff, resulting in reduced groundwater recharge and livestock production (van Wilgen et al., 2008).

Water-use by invasive plants may differ from that of native species for a variety of reasons (Calder & Dye, 2001). For plant species, ability to propagate vegetatively, increased means of seed dispersal, rapid growth, tall stature, and high specific leaf area are traits that have been associated with increased invasive potential (Lake & Leishman, 2004; Pysek et al., 2009) that may either directly or indirectly result in increased water demand and use. Invasive species may also possess traits that promote faster growth, including increased foliar nitrogen and phosphorus levels, leaf area ratio (LAR), and assimilation rate when compared to natives (Leishman et al, 2007). Again, water must supply these plants as they grow and photosynthesize. On a leaf area scale, invasive plants may have increased stomatal conductance, and increased sapflow per unit ground area (Cavaleri & Sack, 2010). Invasive exotics are associated with altered water-use and, consequently, hydrologic alterations to water sources of invaded ecosystems.

Salt cedar or tamarisk (*Tamarix ramossima*) is a prominent invader in the southwestern United States, predominantly in riparian areas (Sala et al., 1996). Increased water-use by *Tamarix* relative to that of native plants has been the primary concern in this arid region. This high water-use has been attributed to high leaf area index (LAI) and stand density (Sala et. al., 1996) and increases linearly with leaf area. This pattern persists even under water-limited conditions (Nippert et al., 2010, Sala et al., 1996) possibly due to a shift in water source to deeper soil levels (Nippert et al., 2010). Additionally, a comparative study of *Tamarix* water-use to that of native species suggested that use of groundwater during periods of water stress allowed the invasive to maintain transpiration levels while the native species could not (Busch et al., 1992).

In contrast, evidence of equal water-use (compared to native vegetation) but increased salt tolerance by *Tamarix* also has been put forth as an explanation for its persistence in arid regions (Glenn et al., 1998). *Tamarix*'s salt tolerance was cited as an advantage when compared to native species such as *Populus fremontii*, which exhibits reduced sapflow under saline conditions (Pataki et al., 2005). A comparative study of hydraulic conductance between native and invasive species under water stress by Pratt and Black (2006) showed that values for this were not consistently higher in invasive species. In fact, native *Salix amygdaloides* actually possessed greater resistance to cavitation than *Tamarix* (Pratt & Black, 2006), which implies that it should be able to conduct water under greater water stress conditions. Overall, however, the potential of *Tamarix* to exacerbate problems caused by limited water resources has provided impetus to quantify its water-use.

Increased water-use and alternate water-use strategies by invasive plants is not restricted to the case of *Tamarix*. *Shinus terebinthifolius,* an invasive species found in Florida, exhibits increased tolerance to flooding during wet seasons compared to native species, as demonstrated by steady pre-dawn water potentials (Ewe & Sternberg, 2002). *Phragmites australis* grows well in flooded areas, but is able to tolerate a broad range of water conditions via adaptations such as reduced leaf area during drought periods (Pagter et al., 2005). In the state of Washington, the exotic *Centurea diffusa,* can utilize water from different soil layers at different times of the season compared to native species. Specifically, *Centurea diffusa* accesses water in shallow soil layers early in the season and extracts water with deep taproots later in the season, depleting resources prior to germination for native plants such as *Pseudoroegneria spicata* (Kulmatiski et al., 2006).

The exotic vine, *Celastrus orbiculatus,* establishes specific conductivity later in the growing season than native species, and maintains green leaves longer (Tibbets and Ewers, 2000). The Hawaiian grasses, invasive *Pennisetum setaceum* and native *Heteropogon contortus,* both exhibit a decrease in net photosynthesis with decreasing leaf water potential, and an increased allocation to root biomass under drought conditions (Williams & Black, 1994). Invasive species may be able to tolerate a broad range of water conditions due to physiological and temporal adaptations or altered water-use strategies, which may promote invasion and continued water-use under conditions unfavorable to natives, or at least a competitive presence.

Based on its preference for riparian regions and ability to transpire large quantities of water, Japanese knotweed has the potential to deliver major hydrological impacts. The extent to which the invader may impact this aspect of the Mid-Atlantic region, the highly populated North Jersey metropolitan and surrounding areas in particular, remains unknown. Also unknown are the mechanisms behind this impact.

Ecophysiology & Water-use Parameters

Efficient use of water and maintenance of hydraulics may determine a plant's ability to thrive in an environment. Seasonal and site variations in water availability may necessitate altered water-use strategies to facilitate successful establishment of flora. The survival and spread of exotics across ranges requires that they successfully extract and use water in the introduced ranges.

Many factors interact to determine the water-use of a plant. Given the wide range of hydrological conditions that support knotweed growth, it is likely that this invader has maximized water-use properties by implementing a variety of strategies across sites. Plant water-use may be determined by properties such as hydraulic conductance and differences in water potential, regulated by stomatal conductance and leaf area (Hubbard et al., 2001; Sperry et al., 2002). One potential limitation to plant water-use occurs at the root/soil interface, where hydraulic conductivity decreases as water potential decreases (Sperry et al., 1998). Drought tolerant species may exhibit lower hydraulic conductivity, and decreased stomatal sensitivity (Sperry et al., 1998). Water may not move quickly, but the leaves are supplied with water with reduced risk of cavitation, and photosynthesis continues even under high vapor pressure deficits.

In species with lower drought tolerance, an increase in stomatal sensitivity may act to protect plants from hydraulic failure (Sperry et. al., 1998; Zimmermann, 1983). Comparative studies have demonstrated that varied moisture conditions may result in varied water-use strategies, even within species. In populations of *Acer grandidentum* Nutt. growing in adjacent slope and riparian sites, the slope site maintained lower stomatal conductance and turgor loss points (Alder et al., 1996). In the slope population, stem xylem showed no significant difference in vulnerability to cavitation, while root xylem possessed increased vulnerability to cavitation (Alder et al., 1996).

Differences in environmental factors may result in altered leaf morphologies and water-use habits. In a study by Kogami et al. (2001), leaf structure and CO_2 transfer conductance of low and high altitude leaves were compared, and high altitude leaves were found to possess a greater leaf mass per area (g/m^2). Under contrasting water environments, *Cakile edentula* fitness levels vary according to leaf size and water-use efficiency, with large leaf size and intermediate water-use efficiency providing an advantage in a wet environment, and small leaf size and high water-use efficiency favored under dry conditions (Dudley, 1996).

Plant form and function may be impacted by rainfall and water availability. In some cases, adjustments by the plant are a seasonal response to altered water availability, at which the plant initiates transient water-use strategies (Ackerly, 2004; Stratton et al., 2000; Zeppel et al., 2006). In Australia, invasive *Eucaplyptus creba* used a constant fraction of water relative to rainfall, assessed by comparing evapotranspiration and LAI values relative to rainfall, giving it an apparent advantage over native *Callitris glaucophylla* (Zeppel et al., 2006). For charparral shrubs, hydraulic conductivity and stem hydraulics were related to minimum daily leaf water potential in the rainy season (Ackerly, 2004). Morphological traits and function may differ as well. Hydraulic conductivity per stem cross-sectional area at different internodes along the shoots of grapevine plants decreased from the base to the apex (Lovisolo & Schubert, 1998). The difference was greater in irrigated plants than in plants subjected to drought treatment (Lovisolo & Schubert, 1998).

Physiological responses to water availability and traits related to hydraulic efficiency interact to determine a plant's overall water-use habits. For example, in a comparative study of Hawaiian species, *S. terebinthifolius* possessed high leaf specific conductivity and hydraulic efficiency, and maintained a relatively high leaf water potential during the wet season despite maintaining a high rate of stomatal conductance (Stratton et al., 2000). In the dry season, this conductance decreased, indicating a physiological shift that allowed for maintenance of leaf water potential under contrasting moisture conditions (Stratton et al., 2000). Seasonal and diurnal variations in leaf water potential were related to maximum photosynthetic rates, hydraulic efficiency, and leaf specific conductivity (Stratton et al., 2000). Water-use habits and plant water status can impact physiological processes such as photosynthesis, a key function that must be maintained under a range of water conditions.

Ecohydrology and Ecophysiology of Japanese Knotweed

Despite its prominence along waterways, few studies exist that document water-use by Japanese knotweed in these areas. Rhizomatous spread via waterways, from as little as 0.7 grams of rhizome (Seiger & Merchant, 1997), renders these habitats both prone and conducive to invasion. In some instances, invasion by Japanese knotweed has been associated with decreased streamflow and increased flooding (Snyder & Kaufman, 2004). With a high leaf area, dense stand formation, extensive root system, and rapid growth rate, it has the potential to utilize great quantities of water (Lake and Leishman, 2004; Talmage & Kiviat, 2004). Additionally, given its tolerance for a broad range of water regimes, from dry to riparian regions, the effect of this invasive may vary depending on location, season, and water availability. Evidence of salt tolerance, as found in *Tamarix,* may allow the introduction of Japanese knotweed in areas that may already be water-stressed (Richards, 2008). An understanding of the quantity of water used by Japanese knotweed and the strategies employed to obtain this resource may aide in determining potential impacts on the hydrology of a region as well as the means by which such changes are wrought.

Japanese knotweed is known to have a high LAI and the ability to transpire large amounts of water. (Vanderklein et al., in review). Thus, Japanese knotweed has the potential to deliver major hydrological impacts in water limited environments and riparian sites. The extent to which the invader may impact riparian ecosystems of the Mid-Atlantic region, the highly populated North Jersey metropolitan and surrounding areas in particular, remains unknown. Also unknown are the sources that allow for the mechanism (transpiration) behind this impact.

The study reported here-in is a multi-pronged approach to characterizing the water-use strategies of Japanese knotweed. One method employed was a greenhouse study of plants selected from the Bonsal Preserve in Montclair, NJ. Water-use and hydrologic impact of Japanese knotweed at this site has been previously studied (Vanderklein et al., in review). By growing Japanese knotweed in the greenhouse, water-use by the plant could be measured independently of confounding factors found in the field, such as other vegetation. Physiological measurements of photosynthesis, water potential, stomatal conductance, transpiration rate, and water-use were measured. From these, traits such as leaf specific hydraulic conductivity and water use efficiency could be assessed. Leaf area and leaf and root biomass were also determined to provide insight regarding the role of resource allocation and its possible relation to water-use over the course of the study period.

The second part of the study examined the hydraulic conductivity of Japanese knotweed under a range of naturally occurring water supply regimes. Hydraulic conductivity plays a critical role in the ability of plants to maintain photosynthesis, and largely determines plant water status. Therefore, an analysis of this trait may provide insight into the success of Japanese knotweed in hydrologically diverse sites. Stem morphology and leaf biomass data were also compared among sites.

Between the two studies, questions are addressed, such as: How much water does Japanese knotweed use under varied moisture conditions? Why is Japanese knotweed a strong competitor under varied water regimes? How does the plant react to water stress? In turn, this information may be used to target regions that are at risk for invasion, estimate hydraulic costs in terms of water use, predict future impact from both a financial and ecological standpoint, and weigh the cost benefit ratio of control and eradication of established stands of Japanese knotweed.

Materials and Methods

1. Greenhouse Study:

Plant Material

In late May, 2010, Japanese knotweed specimens were removed from the Third River Basin of the Bonsal Preserve, located in Montclair, NJ, 40.850 ° N, 74.187 °W, elevation 64 masl (Figure 1). Plastic containers (39.7 x 33.3 x 33.7 cm; 44.6 liters in volume) were filled to a height of 6 cm with ½ inch pea gravel, to act as a reservoir for water (Figure 2). Approximately 12 cm of soil from the site, roughly assessed to be a sandy loam with a sizeable organic component based on visual appraisal, was added to the containers. Root clumps of twenty emerging plants standing about one half meter in height were removed from roughly the center of a stand measuring about 100 m^2 and planted in the containers on site.

The twenty Japanese knotweed root clumps were grown in the Science Hall greenhouse on the Montclair State University Campus. Upon arrival, plants were well-watered and kept in a low light corridor outside of the greenhouse to prevent excess desiccation and heat shock. For the first week, plants were moved to the greenhouse for several hours in the morning, then removed from full-light around midday. Once the plants had established themselves in the containers, they were moved to the greenhouse for the duration, with the exception of several excessively hot days. Plants were watered at least every two days, the soil kept moist and the gravel reservoir wet, based on visual assessment. In August, the plants were subjected to a drought treatment, during which they received water only once in course of the week, to prevent the soil from drying completely.

Methods

Day-long measurements of photosynthesis, stomatal conductance, transpiration, and leaf water potential were conducted in 2010 on 6/23, 7/16, 7/27 and 9/4 for ten randomly selected plants out of nineteen established plants. The 9/4 measurements were taken on plants following drought-treatment. For all other dates, the plants were watered. The night before each measurement, the plants were watered, soil was covered with plastic, and plants were covered in black plastic bags for the purpose of maintaining dark conditions for each plant until initial readings were taken beginning at sunrise the following day.

Physiological Measurements

Gas exchange measurements included photosynthesis, stomatal conductance, and vapor pressure deficit (VPD). Gas exchange measurements were taken using a LiCor 6400 (LiCor, Lincoln, NE) portable infrared gas analyzer (IRGA), ($[CO_2]_{ref}$=400ppm), at roughly one-hour intervals from sunrise to sunset. Leaves in ambient full light were used for the readings. Water potential was measured using a Scholander-type pressure chamber (PMS Instrument Co., Albany, OR) at predawn and midday. Leaves toward the upper end of the stem (non-terminal leaves located mid-canopy) were cut using a razor, and re-cut immediately prior to placement of the leaf within the chamber. Pre-dawn water potential was assumed to equal soil water potential. At midday, the area and mass of the removed leaves were also measured so as to ensure accuracy of total leaf area and water use data.

Transpiration rate and leaf specific hydraulic conductivity were calculated using data collected from the measurement period. Transpiration rate (mmol/m^2/s) was determined for each plant on three dates. Amount of water used, time, and total leaf area were used to calculate transpiration rate on a leaf area basis for the plants. On 7/16, 7/27, and 9/4, water use was determined by weighing containers containing the plants at sunrise and at midday. The soil was covered with plastic so as to eliminate evaporation from the soil. Therefore, the difference between the two measurements equaled the weight of water lost through transpiration. Leaf specific hydraulic conductivity, K_L (mmol H_2O/m^2/s/MPa) was calculated by dividing transpiration rate on a leaf area basis by leaf water potential difference between the pre-dawn and mid-day measurements and the time period between the morning and afternoon water potential readings.

Biomass Analysis

Leaf area was measured using a CI-202 Leaf Area Scanner (CID, Inc. Vancouver, WA.). Within seven days of each day course, the areas of all un-furled leaves were measured. At the end of the experimental period, all plants were harvested. Of the original 20 plants, 18 were used for the biomass analysis. Leaves were removed, dried in a forced-air oven for a minimum of one week, at 52 degrees C, and weighed. Roots were dried as described for leaves and weighed both as a total clump and as coarse and fine roots separately. Fine roots were considered anything under roughly 0.2 mm.

2. Field Collection of Japanese Knotweed

Plant Material

Plants from sites of varying moisture conditions were collected (Figure 3). These were labeled as dry, intermediate, and wet. Characterization of sites was based upon apparent distance from the water table, visible water source, and prevailing light conditions. The wet site was located at a midstream delta, roughly equal to the water table, the same site from which the greenhouse plants were obtained. The intermediate site was located at the shaded end of a street known to be slightly above the water table on average, on a dry day, based on personal observation an a history of flooding. The dry site was located on the top of a hill in a sunny clearing.

Measurements

Stem Hydraulic Conductivity

Intact stems of approximately 50 cm long were cut from all three field sites and immediately put in water (n=18 for each site). Once in the lab, stems from the main shoot were re-cut under water to reestablish hydraulic connection, and to contain at least 3 nodes. Japanese knotweed possesses a hollow stem structure, divided into nodes and separated by what is assumed to be an impermeable septum at each node. For added precaution, the thickest, most basal end was plugged to prevent water transport through the hollow stem segment instead of the xylem. Physical examination of bisected stems revealed that the node segments were transected with a solid tissue, indicating that perhaps plugging might be bypassed in future studies. This basal end was then fitted to a length of tubing. A balance was located at the distal end. A solution of degassed water and 0.1 molar KCl flowed through the tube at a pressure of approximately 0.5 MPa (Sperry et al., 1988). For each sample, hydraulic conductance was measured by using gravity to push the 10% solution of KCl through a segment of stem containing three nodes, and measuring the rate of flow. The rate of flow was determined by collecting water from the distal end of the stem and weighing it simultaneously while keeping track of the time elapsed between starting and ending the weighing. Length of the stem, diameter at mid-node, and thickness of the stem were measured. Cross-sectional area of the stem was calculated using these figures. The stem was then trimmed, and the procedure was repeated for two nodes and then one node. Cuts were always made mid-sheath between nodes.

Biomass Analysis

Leaf and stem morphology were studied to compare differences between sites. Different leaf and stem structures may directly impact water use. Between 20-30 leaves were collected from each site, and scanned for leaf area. Dry mass was measured following drying in a forced air oven at 52 degrees C for at least 48 hours. Ten stems each were collected from the dry, intermediate and wet sites. Total stem segment length, number of nodes, distance between internodes, and mid-internode diameter were measured for each stem.

3. Statistical Analyses

Statistical analyses were performed using JMP 9.0 software (2010, SAS Institute, Inc.) For comparison of single parameters across treatments, one-way ANOVA's were performed. Multivariate correlations were modeled using a scatterplot matrix. Means, standard error, P-values, and R^2 were also calculated using JMP 9.0.

Results

The data obtained from the greenhouse and field studies indicated significant differences between plant physiology and structure under varying moisture conditions. Key traits and water-use strategies were revealed through an examination of the greenhouse data for watered and drought-treated dates. IRGA measurements and plant water use data for watered and drought-treated plants, when combined with measurements taken for varying moisture sites, pointed towards significant differences in water-use strategy across environmental conditions pertaining to water availability.

1. ***Greenhouse Study***

Gas Exchange Measurements, Water-Use Results, and Biomass Analyses

Gas exchange measurements revealed that while average stomatal conductance for drought-treated plants was significantly lower than watered plants ($P=0.056$), average photosynthesis for both treatments was not significantly different (Figure 4). Average stomatal conductance for the drought-treated plants was $9.1\text{x}10^{-2}\pm0.9\text{x}10^{-2}$mmol/m^2/s and $0.111\pm5.0\text{x } 10^{-3}$ mmol/m^2/s for the watered treatment. Average photosynthesis was 2.92 ± 0.18 µmol/m^2/s for the water treatment and 3.04 ± 0.32 µmol/m^2/s for the drought treatment. Average vapor pressure deficit, VPD, varied significantly between the drought and watered treatments at 2.15 ± 0.07 kPa and 1.81 ± 0.04 kPa, respectively ($P=0.0001$) (Table 1). The fact that photosynthesis was maintained during drought treatment indicates a potential compensatory mechanism.

The daily course of photosynthesis and stomatal conductance for July 27th are plotted in Figure 5. The other dates follow a similar curve, with a peak reached around mid-day followed by a slow decline. On the July 27th date, a mid-day depression was recorded, with a steep drop mid-day for both photosynthesis and stomatal conductance, followed by a slight elevation in both towards late afternoon. This decoupling occurred on a day with elevated temperatures and full sun.

Transpiration rate exhibited a significant (P=0.0001) decline when the plants were subjected to drought treatment. Transpiration means by treatment were 0.13±0.005 mmol/m^2/s for the drought treatment and 0.19±0.004 mmol/m^2/s for the water treated plants (Figure 6). Average transpiration for July 27th (0.20 ±0.004 mmol/m^2/s)nand September 4th (0.13±.005 mmol/m^2/s) were significantly different (P=0.0001). Conditions on July 27th, led to adjustments in stomatal conductance and photosynthesis throughout the day, did not lead to a decline in transpiration rate, indicating that water availability may have limited transpiration during the September 4th drought treatment.

Though pre-dawn and mid-day leaf water potentials were significantly lower for the drought-treated plants, compared to the average for all watered plants (P=0.0001), change in water potential was not significantly different, and was in fact very close to identical. Average pre-dawn leaf water potential for watered plants was -0.02±0.04 MPa. The value for drought-treated plants was $-0.74\pm1.7\times10^{-2}$ MPa. Mid-day value for watered plants had was -0.68±0.01 MPa, while drought-treated plants had a value of -1.39±0.02 MPa. Change in water potential for watered plants was 0.659±0.01 MPa, and for drought-treated plants was 0.655±0.02 MPa.

Leaf specific conductivity was lower following drought treatment (Figure 7) indicating a reduced ability of the plants to supply water to the leaves on September 4th. For the drought treatment, mean K_L was 0.20±0.01 mmol/s/m^2/MPa. The drought treatment was significantly different from the pooled water treated dates (P=0.0001), for which the average K_L was 0.34±0.01 mmol/s/m^2/MPa (Figure 7). The K_L for drought-treated plants was also significantly lower (P=0.0001) than that of the last watered date, for which average K_L was 0.39±0.01 mmol/s/m^2/MPa.

Instantaneous water use efficiency (photosynthesis divided by transpiration) varied significantly (P=0.0308), between treatments, with a value of 17.92±1.41 μmol/mmol for water treated plants, compared to the drought treated value of 24.22±2.05 μmol/mmol (Figure 8).

Following the study, the harvest biomass comparison showed a close correlation between leaf mass and root mass, and also leaf mass and fine root mass (Figure 9). Leaf mass correlated positively with both total root mass (R^2=0.62, P=0.0002) and fine root mass (R^2=0.61, P=0.0002).

2. Field Study

Hydraulic conductivity was assessed on a stem area and stem length basis, by site type, and by number of nodes (Figures 10, 11, 12). Stem based hydraulic conductivity decreased exponentially as number of nodes increased from one to three for three sites (Figure 10). Discrepancies for the initial wet site resulted in removal of these data from the final analysis. On a stem area basis, the dry site possessed a significantly lower hydraulic conductivity (Figure 11). Stem area based hydraulic conductivity was only significant between the wet and the other two sites. However, there was a trend of increasing stem area-based conductivity with increasing moisture. The average for the dry site was $4.94\times10^5 \pm 0.556\times10^5$ mmol/s/MPa/m^2 the intermediate site value was

$6.69\text{x}10^5 \pm 1.0\text{x}10^5$ mmol/s/MPa/m^2 and the wet site value was $1.16\text{x}10^6 \pm 0.126\text{x}10^6$ mmol/s/MPa/m^2. The average values for stem area based hydraulic conductivity between the intermediate and wet sites were significantly different (P=0.0047). Average stem area based hydraulic conductivity was also significantly different between the wet and dry sites (P=0.0001). Length based hydraulic conductivity was not significantly different between any of the sites. Values were 79.6±17.4 mmol/s/MPa/m for the dry site, 58.9±13.9 mmol/s/MPa/m for the intermediate site, and 88.7±19.3 mmol/s/MPa/m for the wet site.

Internode length comparisons between the dry, intermediate and wet sites revealed that the internode length for the dry sites was significantly less than those of the intermediate and wet sites (Figure 12). The dry site had an average internode length of $6.3\text{x}10^{-2} \pm 0.002$ m, compared to $9.2\text{x}10^{-2} \pm 0.3\text{x}10^{-2}$ m and $0.101 \pm 3.0\text{x}10^{-3}$ m for the intermediate and wet sites, respectively. The ratio of diameter at mid-node to length of the corresponding node was also significantly higher for the dry site, with a value of $6.8\text{x}10^{-2} \pm 0.1\text{x}10^{-2}$ (Figure 13) compared to $5.2\text{x}10^{-2} \pm 0.1\text{x}10^{-2}$ and $5.1\text{x}10^{-2} \pm 0.1\text{x}10^{-2}$ for the intermediate and wet sites, respectively. This difference was apparent based on visual appraisal as well (Figure 14).

A trend of increased leaf area with increasing site moisture was present (Table 2). The wet site possessed larger leaves $6.9\text{x}10^{-3} \pm 0.3\text{x}10^{-3}$ m^2, compared to dry site values of $3.3\text{x}10^{-3} \pm 0.3\text{x}10^{-3}$ m^2 and intermediate site values of $5.2\text{x}10^{-3} \pm 0.4\text{x}10^{-3}$ m^2. The only significant difference was between values for the dry site and wet site (P=0.0001). Leaf mass per area increased with moisture. Only the dry site differed significantly from the other three sites (P=0.0001). Leaf mass per area ratios for the dry, intermediate, and wet sites were 86.5±3.5, 43.2±6.7, and 39.3±1.0, respectively (Table 2).

Table 1. Average photosynthesis, stomatal conductance, and VPD by date for the greenhouse study.

Date	Photosynthesis	Stomatal Conductance	VPD
	μmol/m²/s	mmol/m²/s	kPa
23-Jun	2.26±0.28	0.14±0.01	1.58±0.06
16-Jul	3.81±0.35	0.13±0.01	1.57±0.08
27-Jul	3.01±0.29	0.07±0.01	2.25±0.06
4-Sep	3.04±0.32	0.09±0.01	2.15±0.07

Table 2. Leaf area and LMA for field sites and greenhouse harvest.

	Leaf Area (m^2)	LMA (kg/m^2)
Dry Site	$3.3x10^{-3}$±$1.4x10^{-3}$	86.5 ± 3.5
Intermediate Site	$5.2x10^{-3}$±$1.9x10^{-3}$	43.2± 6.7
Wet Site	$6.9x10^{-3}$±$2.1x10^{-3}$	33.2 ± 0.9
Greenhouse	$3.4x10^{-3}$±$2.2x10^{-3}$*	n.a.

* Greenhouse data was for leaf area of plants from the 9/04 readings and leaves harvested from these plants only.

Figure 1. Site of collection for greenhouse study samples. In May of 2010, samples were obtained from the patch indicated by the black rectangle.

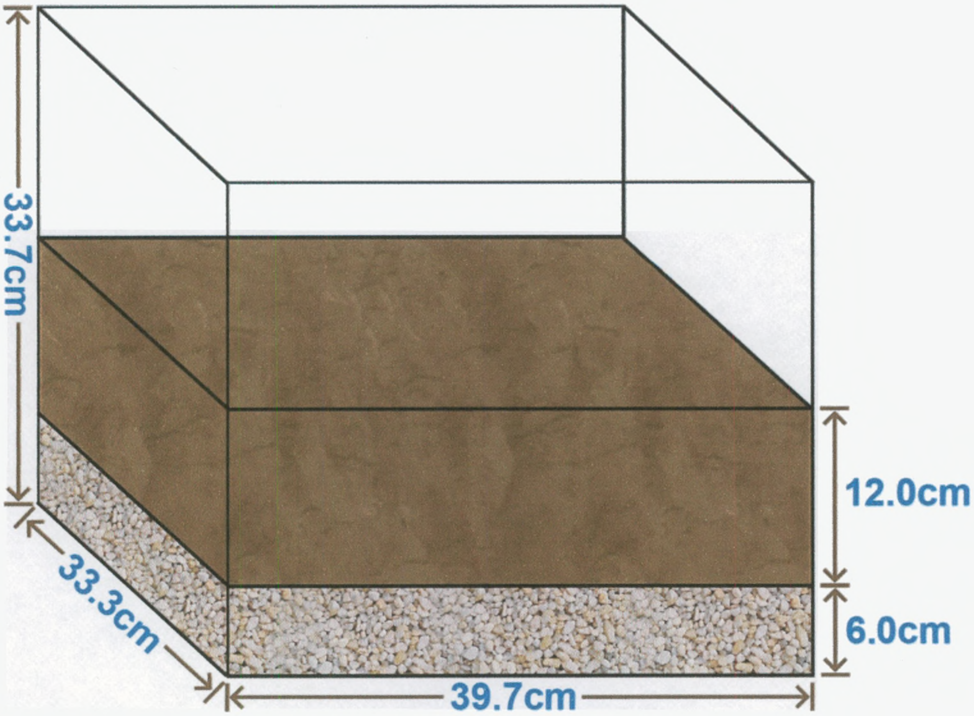


Figure 2. Diagram of container contents used in the greenhouse study. Bottom was filled with 6.0 cm of gravel to act as a reservoir. Roughly 12 cm of soil from the Bonsal Preserve site was added above the gravel.

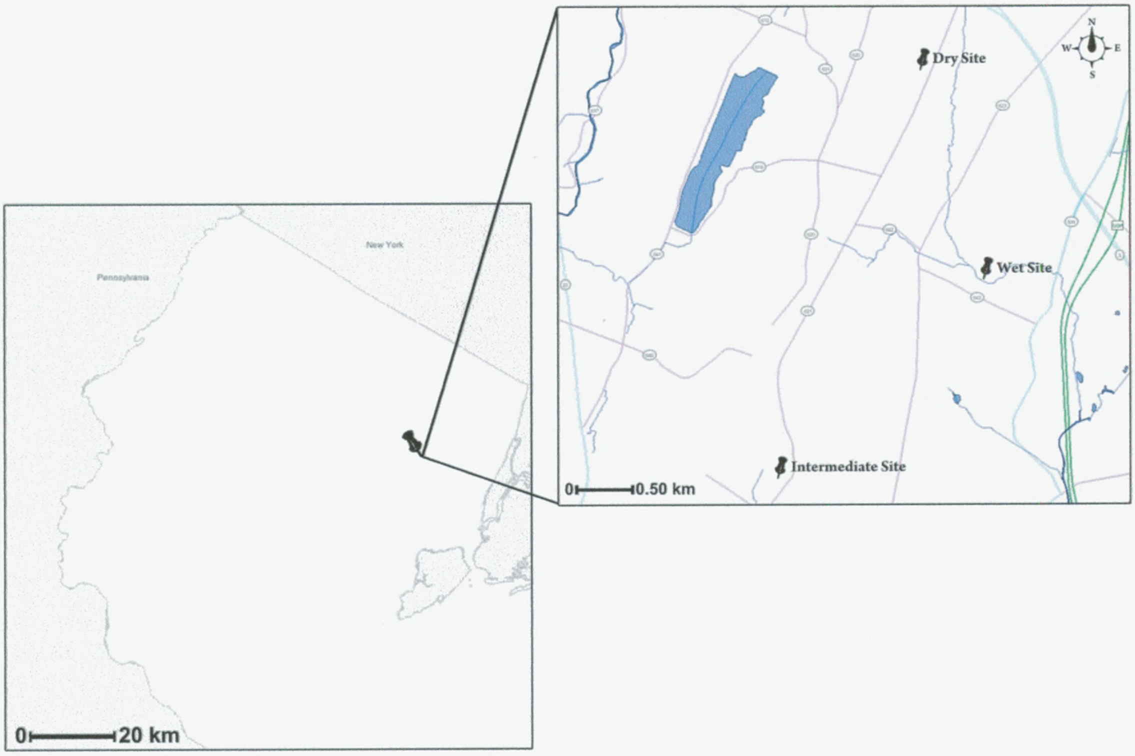
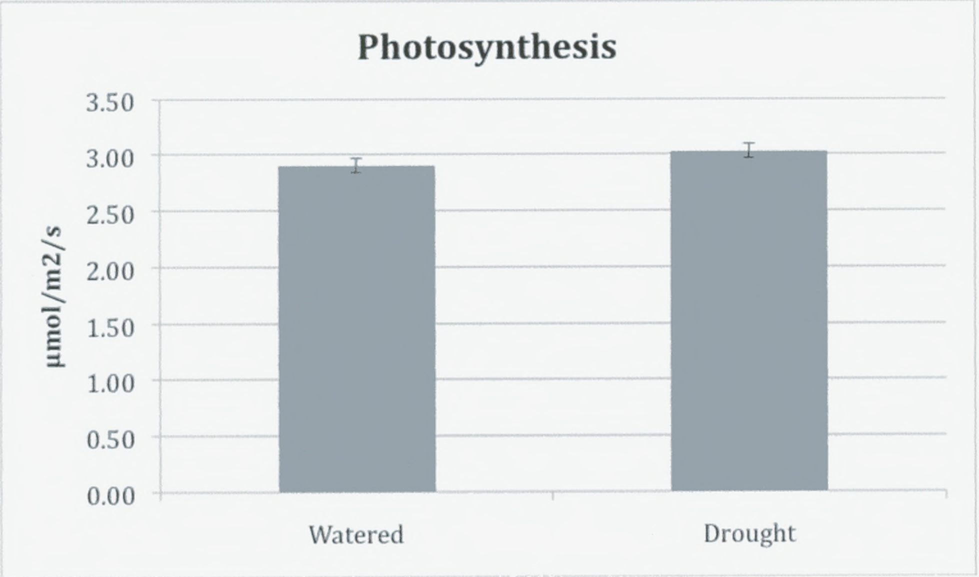


Figure 3. Locations of varied moisture sites for field study. Samples were harvested in August of 2010. Measurements of stem based hydraulic conductivity were taken on the date of harvest.



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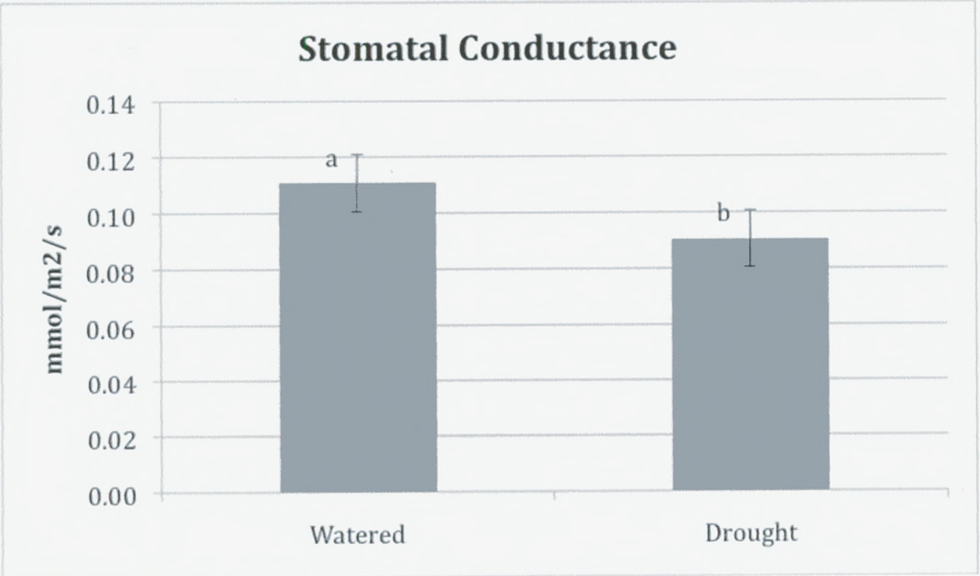

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Figure 4a and b. Greenhouse Study: Photosynthesis and stomatal conductance by treatment. Bars are the mean ±1 SE. **4a.** Change in photosynthesis between the watered and drought-treated plants. For photosynthesis, there was not a significant statistical difference between the two treatments. **4b**. Change in stomatal conductance between the watered and drought-treated plants. For stomatal conductance, a significant statistical difference existed between treatments (P=0.0001). Note that though there was a decrease in stomatal conductance following drought treatment, the rate of photosynthesis was not significantly different between treatments.

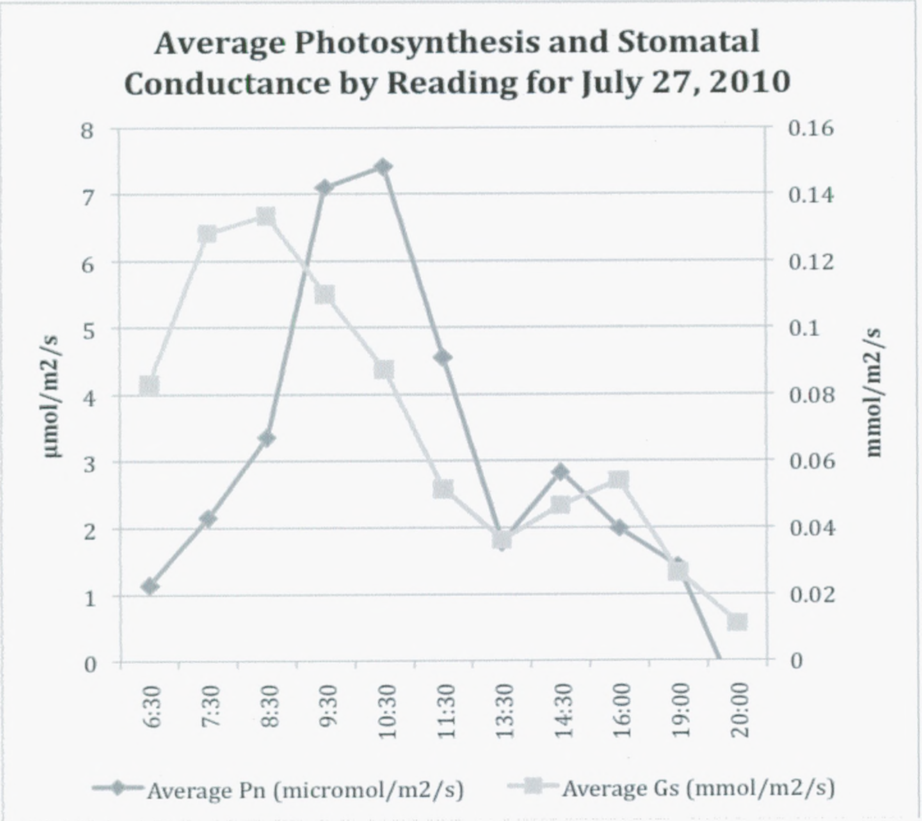


Figure 5. Greenhouse Study: Average photosynthesis and stomatal conductance for each reading on July 27th 2010. There was a mid-day depression and mid-afternoon peak on July 27th.

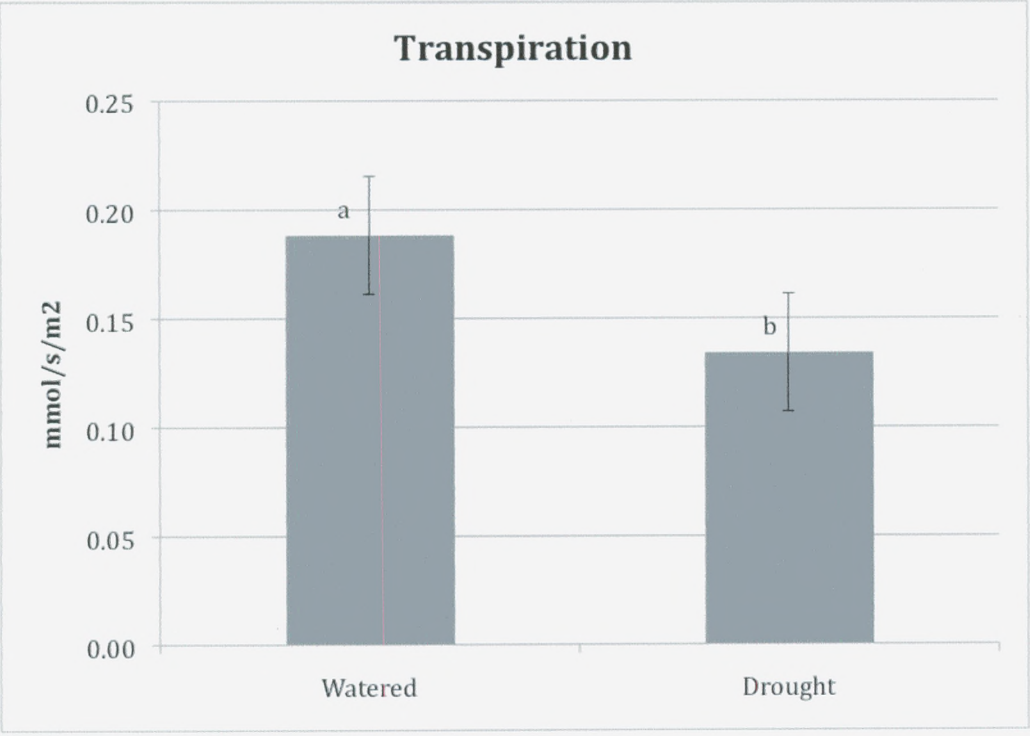


Figure 6. Greenhouse Study: Transpiration rate on a leaf area basis by treatment. Bars are the mean ±1 SE. Values were significantly different between treatments (P=0.0001). A decrease in transpiration followed drought treatment.

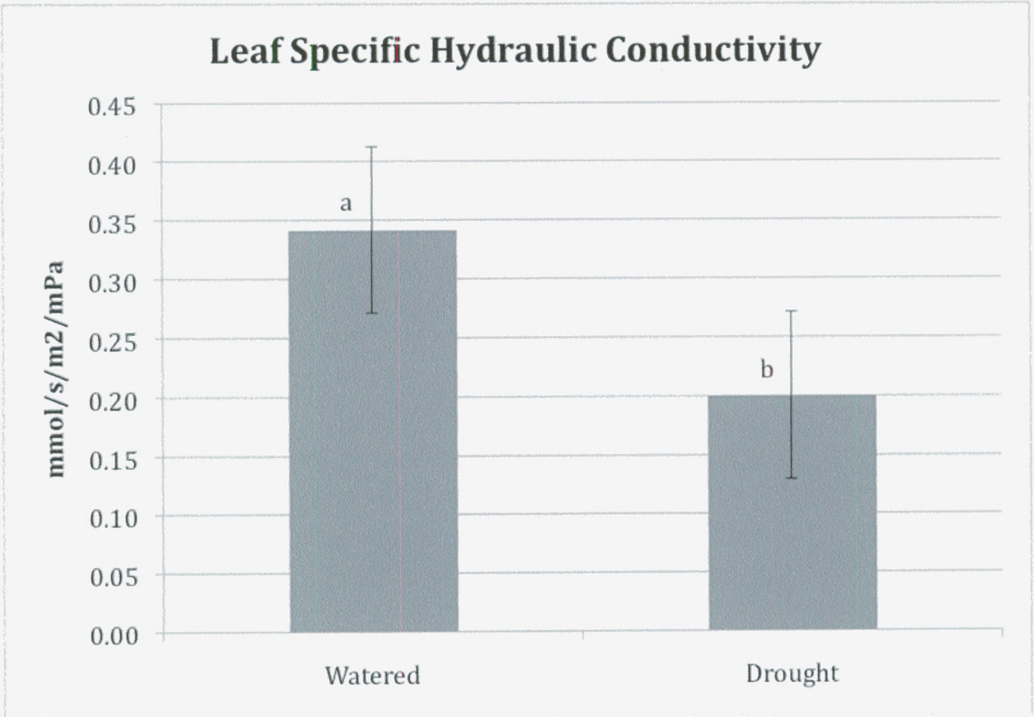


Figure 7. Greenhouse Study: Leaf specific hydraulic conductivity by treatment. Bars are the mean ±1 SE. The mean K_L for the September 4th drought treatment was significantly different from the pooled water treated dates ($P=0.0001$). A decrease in leaf specific hydraulic conductivity followed drought treatment.

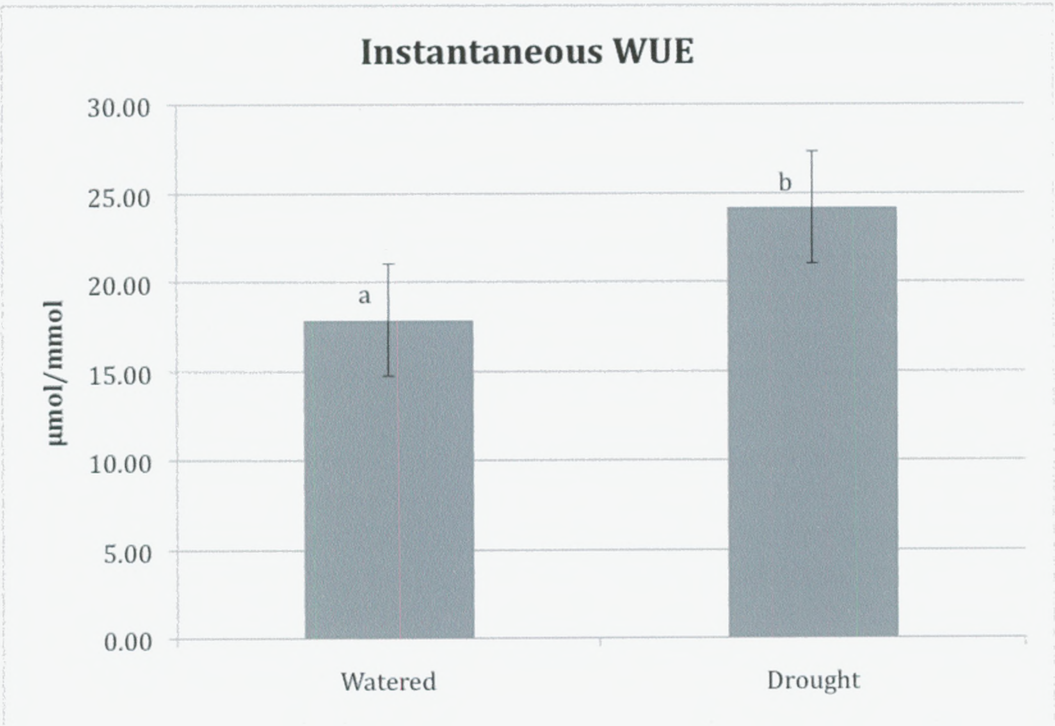
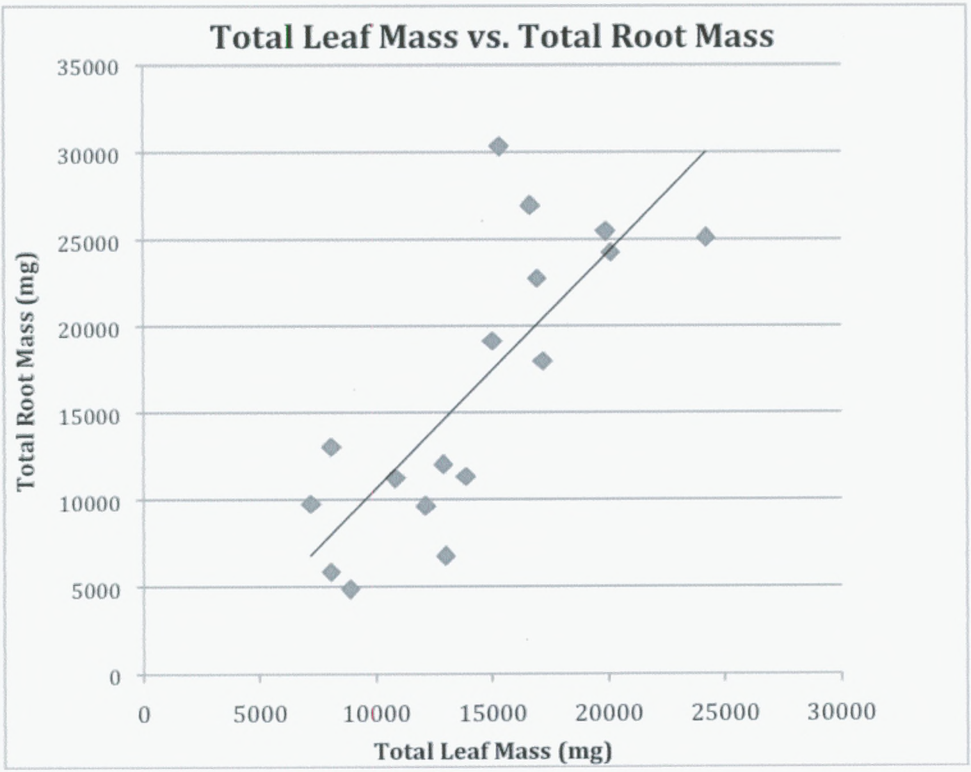


Figure 8. Greenhouse Study: Instantaneous water use efficiency by treatment. Bars are the mean ±1 SE. Mean instantaneous WUE was significantly different between treatments (P=0.0109). There was an increase in instantaneous WUE following drought treatment.



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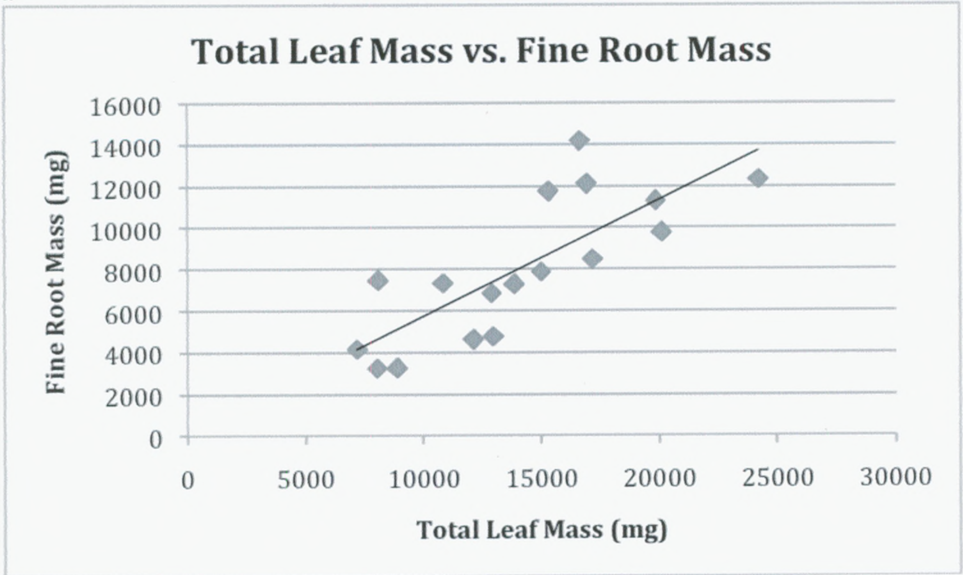

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Figure 9a and b. Greenhouse Study: Comparison of total root and fine root between leaf biomass allocation. 9a. Leaf mass correlated positively with both total root mass, ($y=1.362x - 2942$, $R^2=0.62$, $P=0.0002$). **9b.** Leaf mass also correlated positively with fine root mass ($y=0.562x + 100.8$, $R^2=0.614$, $P=0.0002$).

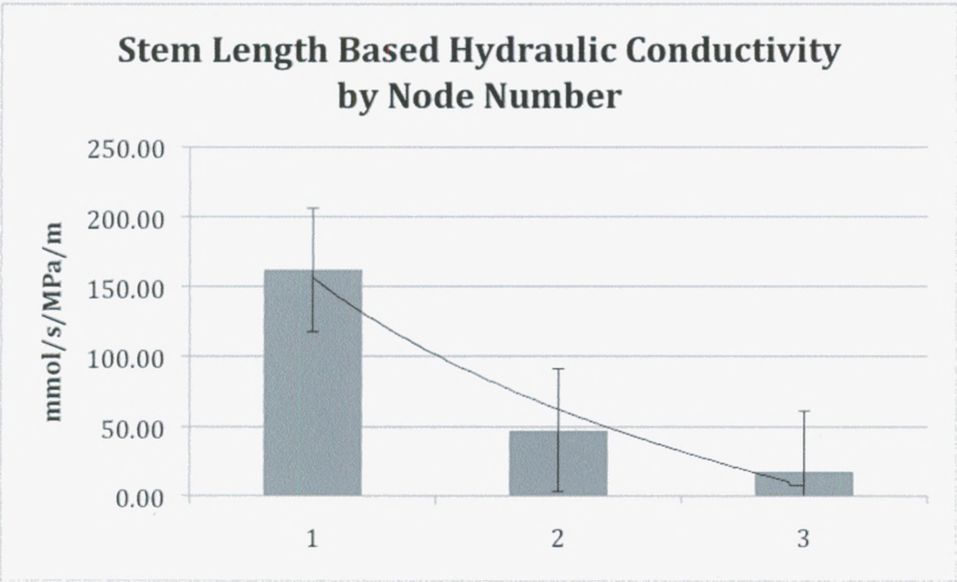


Figure 10. Field Study: Hydraulic conductivity on a length basis by number of nodes. Values decreased exponentially as the number of nodes increased ($y = -135 \ln(x) + 156.6$, $R^2=0.969$).

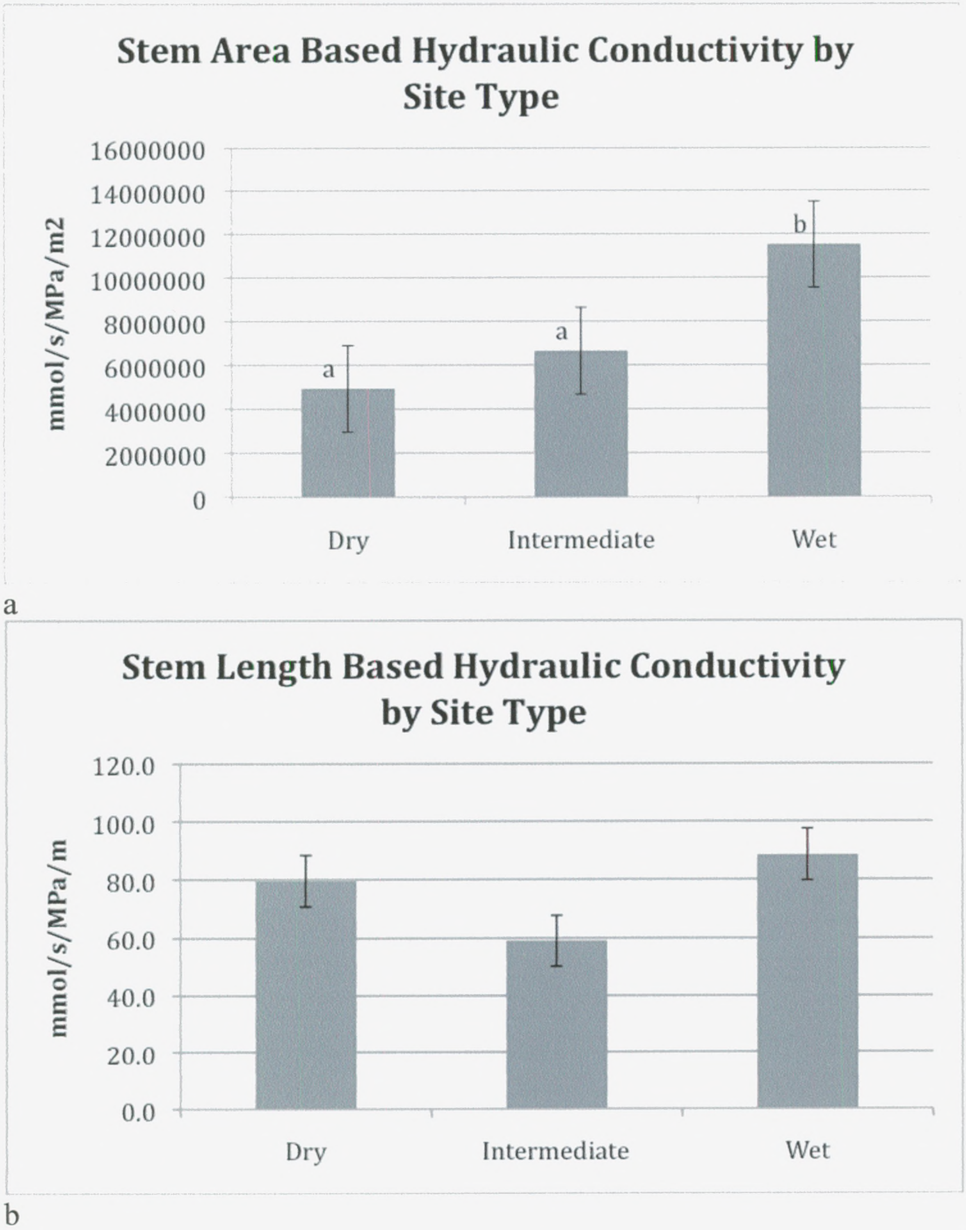
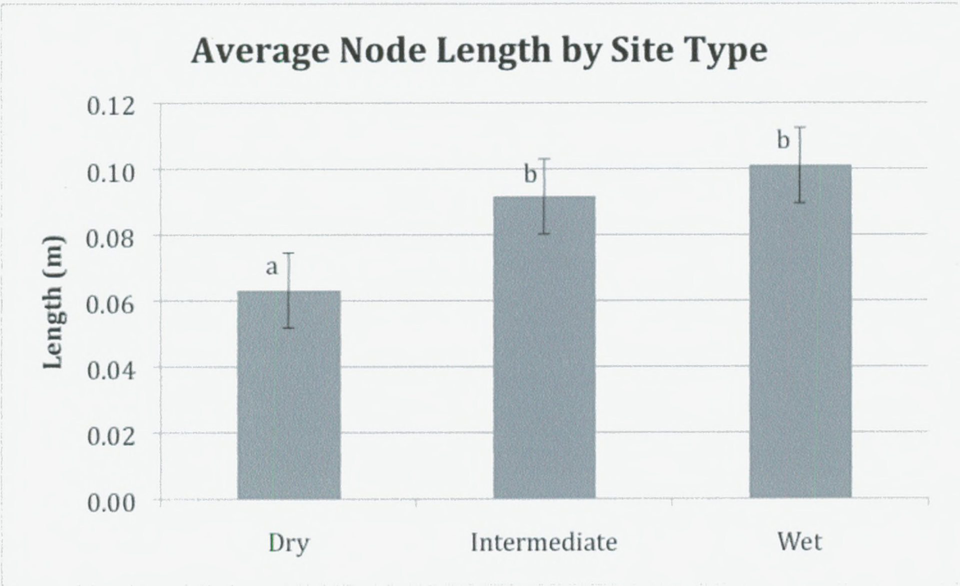


Figure 11a and b. Field Study: Stem hydraulic conductivity for varied moisture sites. Bars are the mean ±1 SE. **11a: A significant statistical difference in** stem area based hydraulic conductivity existed only between the wet site and the dry and intermediate site (P = 0.0356). **11b:** Length based hydraulic conductivity did not differ significantly between sites. On a stem area basis, hydraulic conductivity increased significantly for the wet site as compared to the dry and intermediate sites.



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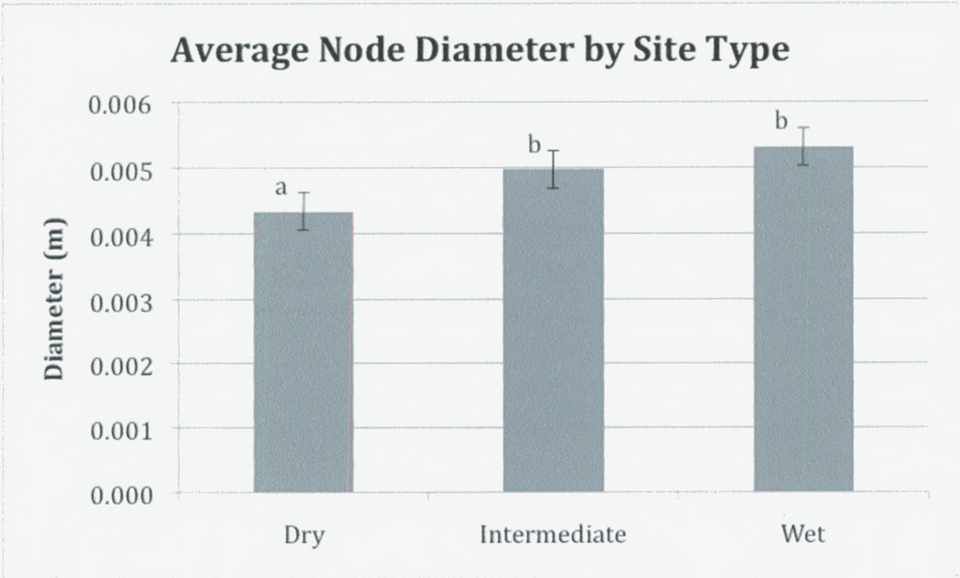

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Figure 12a and b. Field Study: Stem morphology at varied moisture sites, node length and node diameter. Bars are the mean ±1 SE. **12a:** A significant statistical difference existed between the dry site and pooled intermediate and wet sites (P=0.0001). A significant statistical difference was also present between the intermediate and wet sites (P=0.025). **12b:** A significant statistical difference in stem diameter was present between the dry site and pooled intermediate and wet sites (P=0.0097), but not between the intermediate and wet sites. Note that node length and diameter were significantly lower for the dry site.

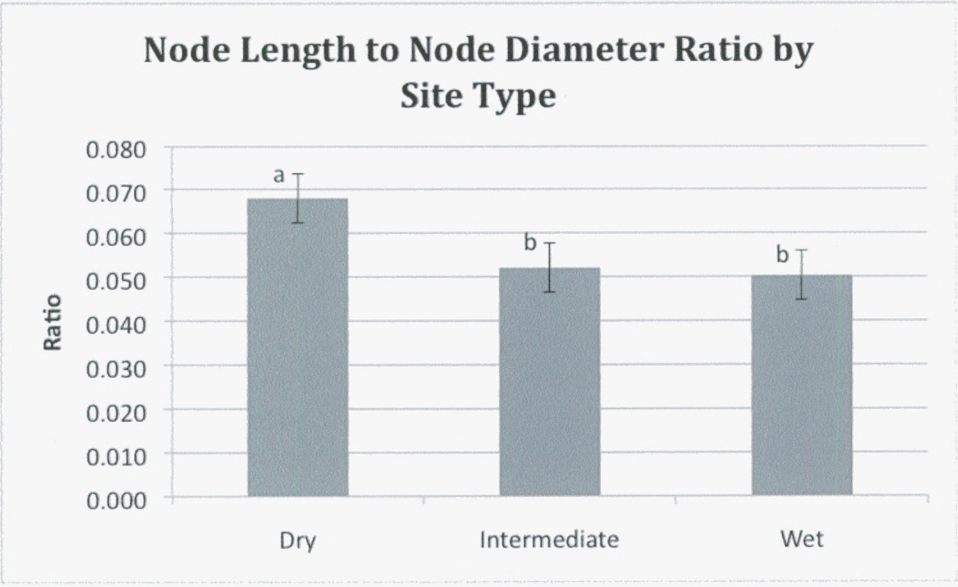

Figure 13. Field Study: Relationship of stem morphology characteristics at varied moisture sites. Bars are the mean ±1 SE. **The** diameter/length ratio was statistically significant for the dry site values as compared to the intermediate and wet site plants (P=0.0001). The increased ratio of node length to node diameter for dry site plants indicated a truncated yet wider stem structure.

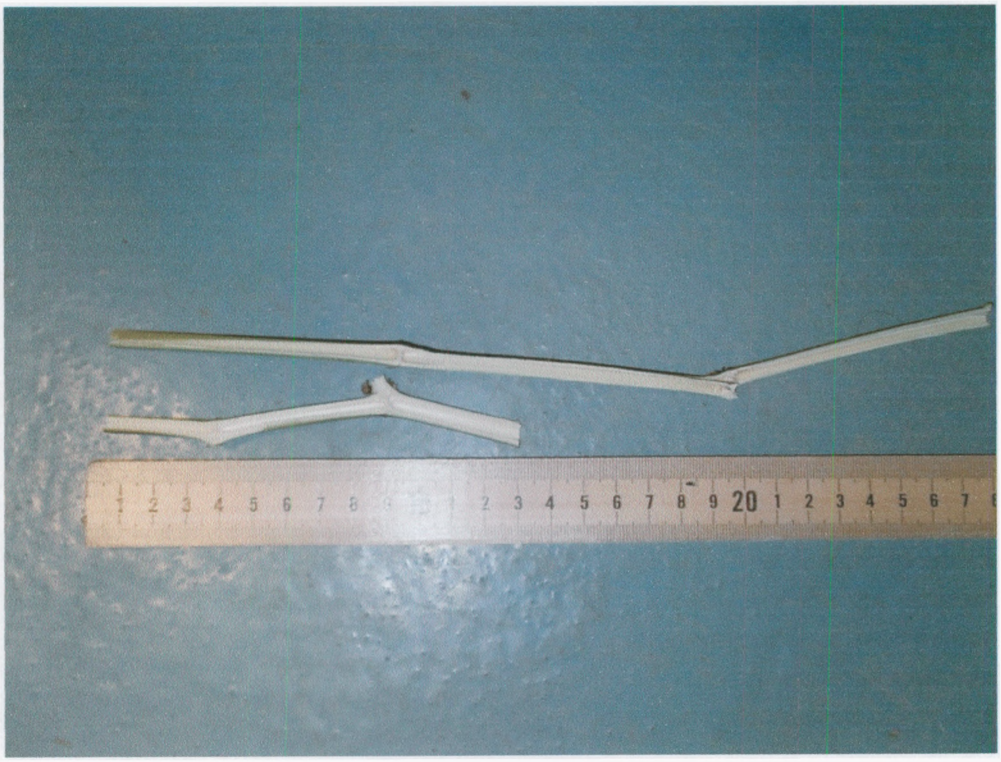

Figure 14. Field Study: Moisture varied site stem sections, top: intermediate; bottom: dry. Note the increased node length for the intermediate site.

Discussion

The success of Japanese knotweed as an invasive species may be attributed to several characteristic traits. The results of this study suggest that shifts in physiological functions under variable environmental conditions and phenotypic plasticity may, in part, contribute to the prolific range expansion exhibited by Japanese knotweed. The presence of Japanese knotweed in disturbed sites and along waterways is consistent with colonization patterns associated with other invasive plants. That Japanese knotweed may, in fact, be drought tolerant, would set it apart from some species of opportunistic exotics. One of the few widely studied invasive plants to owe some degree of success to drought tolerance is *Tamarix*. Should the ubiquitous invader Japanese knotweed fall into this category as well, the risk of water depletion under conditions of water stress might very well become an issue for the Mid-Atlantic region, particularly in a time of population growth and climate change.

Gas Exchange

The comparison of watered and drought-treated plant physiological measurements in the greenhouse revealed that Japanese knotweed is able to regulate its physiological functions in ways that allow it to persist under a range of moisture conditions. Such adjustments included decreases in stomatal conductance, transpiration rate, and leaf specific hydraulic conductivity under the drought-treatment (Figures 3, 6, and 7). An increase in instantaneous water use efficiency was seen as well (Figure 8). While the drought-treated plants in our study displayed a decreased stomatal conductance relative to watered plants, the plants exhibited no significant difference in photosynthetic rate

(Figure 4). In all, over the course of each day, photosynthesis, stomatal conductance, and water-use parameters followed characteristic patterns that typically maximize carbon gain, whether through a single or bimodal peak (Figure 5). The ability of a plant to supply water to its tissues is a limiting factor for maximum photosynthetic rates (Brodribb & Field, 2000; Bacelar et al., 2007). This may be attributed to decreases in stomatal conductance, followed by a decrease in photosynthetic rates, as exhibited by some water stressed plants. (Bacelar et al., 2007). However, increases in WUE may allow some species to adjust to low water conditions and increase their success under such circumstances (Bacelar et al., 2007).

In our study, average stomatal conductance was lower for the drought-treated plants (Figure 4). This may have been a protective mechanism. One possible explanation for decreased stomatal conductance lies in the higher mean VPD for this treatment. Average stomatal conductance was also lower on July 27th, when average VPD was higher than that of the September 4th drought-treated plants (Table 1). Other studies have shown that stomatal conductance exponentially decreases with increasing VPD, which is thought to be regulated primarily by transpiration and leaf water potential (Monteith, 1995; Oren et al., 1999). This is consistent with Alder et al. (1996), who found that plants of the same species growing on a slope (dry) site maintain lower stomatal conductance relative to those on an adjacent riparian site. An increased rate of transpiration facilitated by a high VPD would result in a lower leaf water potential, possibly causing signals to be released that trigger stomatal closure. Our results indicate a correlation between stomatal conductance and VPD. Reductions in stomatal conductance under conditions of water stress would limit transpiration and conserve water.

One other parameter that can be used to examine drought tolerance is stomatal sensitivity. Species with high stomatal sensitivity will exhibit a steeper decline in stomatal conductance with increasing VPD (Sperry et al., 1998). In species with lower drought tolerance, an increase in stomatal sensitivity may act to protect plants from hydraulic failure (Sperry et al., 1998). Data obtained for the day courses and between treatments indicate that knotweed exhibits a degree of sensitivity. A mid-day depression and mid-afternoon second peak in photosynthesis occurred on July 27th (Figure 5). Such strategies allow plants to shut down during bright, hot parts of the day, then resume function when damage to photosynthetic apparatus is less likely, thus maximizing carbon gain (Hodges, 1966). The mid-day depression under hot, sunny conditions, and reduced stomatal conductance under drought-treatment, indicate that Japanese knotweed is not impervious to water stress.

The maintenance of the photosynthetic rate across treatments (Figure 4) indicated that Japanese knotweed was able to adjust not only to the drought conditions but to actively reduce stomatal conductance as well. Japanese knotweed was able to adjust to lower water levels and continue photosynthesis at a decreased, though not ceased, rate of stomatal conductance, indicating a degree of drought tolerance. Also of note, though photosynthesis was maintained at a lower stomatal conductance, there remained a positive correlation between the two, as can be seen in the closely matched peaks (Figure 5).

Water Use

Physiology impacts the ability of a plant to transport water, and this was evident in the Japanese knotweed in our study. Water-use strategies specific to water availability were evident in both the greenhouse and field studies. In the greenhouse study, such strategies were manifested in a reduced transpiration rate and leaf specific hydraulic conductivity, and an increased instantaneous water use efficiency following drought treatment. An increased stem hydraulic conductivity on a stem area basis for wet sites and maintenance of stem hydraulic conductivity on a length basis across sites in the field study further demonstrated that Japanese knotweed exhibits varied water transport ability according to water availability (Figure 11). A corresponding increase in LMA (Table 2) and decrease in internode length (Figure 12) with decreasing water availability was also evident.

In the greenhouse, drought-treated plants transpired at a significantly lower rate on a leaf area basis than watered plants, but did not completely shut down (Figure 6). As a result, leaf specific hydraulic conductivity was also lower for drought-treated plants (Figure 7). Instantaneous water use efficiency was higher for drought-treated plants, allowing knotweed to assimilate more carbon per unit water loss than observed under well-watered conditions (Figure 8). Higher water use efficiency tends to be favored in dry environments, while intermediate water use efficiency is favored in moderately wet environments where higher transpiration rates allow for higher assimilation rates (Dudley, 1996; Donovan et al., 2007). Our findings of an increased instantaneous water use efficiency following drought treatment agree with this research.

Japanese knotweed continued to transpire and carry out photosynthesis under reduced leaf water potentials in the drought treatment (Figure 4). The lower pre-dawn water potential in drought-treated plants did not prevent further transpiration. Change in water potential between pre-dawn and midday readings was the same for both treatments. This indicates that Japanese knotweed will function at lower leaf water potential values. However, the amount of water lost is decreased under drought stress conditions. These findings are consistent with previous reporting of plants exhibiting reductions in water potential following drought stress (Wilson et al., 1980), and a subsequent decrease in photosynthetic rate, and stomatal conductance (Bacelar et al., 2007).

Water transport ability varied across sites in the field study component. Stem hydraulic conductance on a stem area basis was significantly higher for the wet site, and was lower for all others (Figure 11). On the other hand, stem hydraulic conductivity on a length basis was maintained across sites (Figure 11). Leaf area decreased as water availability decreased (Table 2). A reduction in leaf area should result in a higher leaf specific conductivity, which would reduce the driving force necessary to supply leaves with water, even under drought stress. In contrast, the drought-treated plants in the field study exhibited decreased leaf specific hydraulic conductivity. Another possible explanation, which was not measured in the current study, is that there may have been a reduction in vessel diameter, which would decrease conductivity while protecting plants from embolism (Lovisolo & Shubert, 1998).

Hydraulic conductivity varied among nodes of stems from different sites. There was an exponential increase in hydraulic conductivity with one node as opposed to three (Figure 10). This agrees with the idea that conductance may be positively related to diameter and inversely related to height (Mencuccini & Grace, 1996). In trees, resistance has been shown to increase near branch ends (Mencuccini & Grace, 1996). The single node was closer to the base of the shaft, and possessed greater area. The third node would have been nearer the plant tip, an area of greater stress and therefore subject to greater resistance. This also suggests that the nodes increase resistance. Recent work by Petit et al. (2007) shows that in trees the xylem tapers from the base to the top of the tree. This would be similar to what we are seeing here in the knotweed. The idea is that as you get closer to the tip, the hydraulic stresses increase. If the xylem diameter decreases as well, then the water column has less chance of cavitating. Given that these plants have high conductivities, this might be a mechanism to prevent cavitation under high water demand.

Stomatal conductance and photosynthesis are linked to hydraulic conductance, and hydraulic conductivity on a leaf area basis has been linked to photosynthetic rate (Brodribb & Feild, 2000). Decreases in hydraulic conductance can result in decreased stomatal conductance and subsequently a decreased photosynthesis rate (Hubbard et al., 2001). In contrasting mesic and xeric sites, higher leaf specific conductivity may result in higher primary productivity values (Van der Willigen & Pammenter, 1998). Higher leaf specific conductivity allows for better supply of water to the leaves, possibly permitting increased stomatal conductance and therefore greater growth efficiency (Pammenter & Van der Willigen, 1998). This relationship partially held for the Japanese knotweed in our study. Photosynthetic rates were not significantly different between treatments while stomatal conductance and leaf specific hydraulic conductance were significantly lower for drought treated plants. Whether this ability to maintain photosynthetic rates despite reductions in stomatal conductance would result in increased primary productivity in the long term is uncertain.

Biomass and Morphology Analyses

Leaf and stem morphology in the field varied across sites of contrasting water, and in some cases, light, availability. Leaf area, LMA, internode length, and stem diameter measured at our sites indicated characteristic morphology under specific environmental conditions. Our data agreed with functional traits found in previous research, and may explain the measurements that were obtained for hydraulic conductivity. In the greenhouse, leaf and root mass analyses indicated that knotweed effectively allocated biomass, with greater root mass corresponding to greater leaf mass (Figure 9). Thus, the water uptake tissue (the roots) was proportional to the tissue through which carbon was gained and water was lost (the leaves). Adjustments to biomass allocation and morphology are possible ways in which Japanese knotweed persists across introduced ranges.

The Japanese knotweed in our study displayed adjustments in leaf structure and physiology, indicating that this trait may determine the success of Japanese knotweed in introduced ranges. Leaf structure is a key characteristic in determining plant response to environmental conditions such as seasonal water deficit and light levels (Ackerly et al., 2002; Mitchell et al., 2008; Pierce et. al., 1994), and corresponds with photosynthetic capacity of plants (Reich et. al., 1999). Leaf structure and function can also affect the environmental impact of a plant species. Leaf area may determine the amount of water lost due to evapotranspiration, a potential environmental issue should a plant with high leaf area continue to transpire under drought conditions (Sala et al., 1996). Research by Vanderklein et al. (in review) indicates that not only does Japanese knotweed have a low LMA but that this plant can alter stream base-flow in invaded areas.

Leaf area decreased with decreasing water availability (Table 2). This may serve to minimize water loss through transpiration (Bacelar et al., 2006). Greater water supply may allow for greater transpiration rates, which would support larger leaves. Conversely, smaller leaf area may correspond with higher levels of insolation (Ackery et al., 2002), and low water supply, also supported by our data. Larger leaves are functionally ideal for shade plants in that they increase light capture. This is supported by the fact that leaf area values were lowest in our dry site, which was also the most exposed. The variable light and moisture conditions experienced by the field sites may also explain differences in leaf structure.

LMA varied across sites. LMA was greatest for the dry site leaves (Table 2). This may benefit dry site plants in several ways. Thicker leaves concentrate the photosynthetic tissue, and result in greater light capture per unit leaf area, ideal under high light, such as that found in our dry site. A higher LMA has been shown to correspond with higher levels of insolation (Ackerly et al., 2002). The higher LMA may also increase water use efficiency in dry environments (Pierce et. al., 1994). In addition, the inverse of LMA, SLA, positively correlates with photosynthetic maximum and stomatal conductance (Reich et. al., 1999).

Greater LMA for Japanese knotweed has been recorded for plants growing at higher altitudes due to greater leaf thickness, thicker mesophyll cell walls and higher mesophyll cell density (Kogami et al, 2001). As noted above, our greenhouse plants continued to transpire under low leaf water potentials following drought treatment. Modifications to LMA could result in a lower internal CO_2 transfer conductance without a change in stomatal conductance (Kogami et al., 2001). While the difference in altitude for our plants was on a much smaller scale, it is possible that similar strategies may have been invoked under water stressed conditions. Leaf structural differences may have allowed the plants to make physiological adjustments that permitted altered water potential and transpiration profiles.

The leaf area of the greenhouse plants was only slightly greater than that of the dry site plants in the field study (Table 2). The LMA value obtained fell between those of the dry and intermediate sites (Table 2). The water transport capacity and physiology of our plants, which were removed from the same patch as those used in the wet site analysis, adjusted to the environment of the greenhouse, which could be characterized by high light intensity, heat, and moderate wind speeds. Greenhouse plants exhibited smaller stature and reduced leaf area relative to field site plants from the same cohort throughout the summer (Table 2). One reason for such differences may have been because the roots of our plants were cut from parts of a more extensive underground system. Therefore, they did not have the same water extracting capacity as field grown plants. Under different conditions, transpiration rate may have been higher, since a higher LMA tends to correspond to lower stomatal conductance and higher water-use efficiency (Pierce et. al., 1994). This may also explain the fact that our greenhouse plants faired well under drought conditions.

In the greenhouse, leaf mass correlated positively with both fine and total root mass. The role of the roots in determining water supply, which can drive photosynthesis, indicates that such a complimentary relationship could be adaptive in nature. Differential allocation to biomass under drought conditions has been previously witnessed (Bacelar et al., 2006). The prolific root system and aboveground expansion of Japanese knotweed stands may be similarly correlated. The wet site plants possessed visibly larger leaves than dry site plants, and attained higher stature. The implications of this in terms of resource allocation and water-use are that Japanese knotweed could be a water hog and waster, growing as tall as hydraulic limitations will allow, while expanding outward belowground, allowing for greater water extraction. For future studies, a comparison between plants grown under drought conditions and watered conditions would provide greater insight into the biomass allocation of Japanese knotweed under different water supply regimes.

Stem morphology varied across sites as well. The most significant difference was in the reduced node length of the dry site plants (Figure 12, Figure 14). Drought treated plants have been shown to exhibit shorter internode length (Perry and Larson, 1974). This may provide a functional advantage. Xylem tapering near the tops of plants has been shown by Petit et al., (2007). While this tapering increases hydraulic resistance, it also decreases the risk of cavitation at areas of the plant that are subject to the greatest tension (Petit et al., 2007). A similar situation may be seen within shoots in our Japanese knotweed. Shorter internode length and a less steep decline in hydraulic conductance with additional nodes may serve to preserve water transport. Shorter internodes may be less prone to cavitation. If this increase in nodes does not result in a corresponding increase in resistance along the water pathway, the water-use may be facilitated, maximizing photosynthetic ability and ultimately enhancing growth and reproduction. However, our data seem to indicate that hydraulic conductance exhibits a marked decrease (Figure 10). The decrease does not appear to be more extreme for dry plants with shorter internodes than for wet site plants. This is in contrast to previous research (Lovisolo & Schubert, 1998). However, structurally, the average length of nodes for the wet site plants was greater than the average of the dry site plants.

Knotweed structure may be tied closely to function and hold key implications for the impact of knotweed on water depletion. Shorter vessel elements near the top of plants may serve as a protective mechanism against cavitation, since these areas are subject to greater tension. Longer water pathways lead to increased stress (Van der Willigen & Pammenter, 1998), which may account for shorter internodes at the dry (xeric) site. Together, the exponential decrease in hydraulic conductivity and decreased internode length in dry sites may relate to the hydraulic limitation hypothesis, as set forth by Ryan and Yoder (1997). In our study, the longer vessel length in the wet site did not result in increased stem length based hydraulic conductivity, as the shorter nodes in the drier sites may have provided an adaptive advantage. Environmental conditions determined the hydraulic architecture and therefore conductance. Adjustments in vessel length and diameter, combined with alterations in stem hydraulic conductivity, could permit Japanese knotweed to extract water efficiently across a range of water regimes. Under arid conditions, Japanese knotweed could exacerbate already drought strained resource depletion.

Biomass allocation can directly impact water use and physiology. Plant water use may be determined by properties such as hydraulic conductance and differences in water potential, both of which may be regulated by stomatal conductance and leaf area (Sperry et al., 2002). Another potential limitation to plant water use occurs at the root/soil interface, where hydraulic conductivity decreases as water potential decreases (Sperry et al., 1998). Drought tolerant species may exhibit a greater ability to extract water under water-limited environments via adaptive physiological and morphological strategies. The correlations observed in our study indicate that Japanese knotweed may adjust root biomass, stem structure and functional traits, and leaf area and structure accordingly.

The findings of this study may have significant implications in terms of water resource management. Increases in evapotranspiration in areas invaded by Japanese knotweed may result in water depletion. The presence of Japanese knotweed along riparian corridors and along roadways where it can intercept runoff allows the plants to utilize water that might otherwise supply other organisms or replenish water resources. Such depletion may prove critical in future droughts in the mid-Atlantic region.

In order to manage water resources, it is crucial to identify losses. The impacts of invasive species are varied and far-reaching, as it modifies riparian habitats and utilizes water that might have been used elsewhere. The true extent of water-use by Japanese knotweed requires further evaluation, as do strategies for removal and control. Should water become less readily available, the relative cost of continued proliferation could increase. While the findings discussed here indicate that Japanese knotweed utilizes water under varied moisture conditions and has significant impacts on water supply, further assessment is required.

Conclusion

In this current era of climate change and population growth, invasive species may further stress environments due to increased opportunities (Walther et al., 2009) and create greater environmental and economic costs (Pimentel et al., 2005). Taken together, the greenhouse and field studies paint a picture of an invasive plant that will continue to efficiently use a large amount of water across a wide range of water regimes. When placed in a water-saturated area, such as a riparian region, Japanese knotweed will potentially transpire vast amounts of water, reducing streamflow and output. Under arid conditions, Japanese knotweed will still transpire water, utilizing limited resources. Based on the findings from this research, Japanese knotweed may impact water yield in both riparian and disturbed sites. It may do so via relatively high transpiration rates facilitated by efficient hydraulic architecture and a high leaf area index coupled with an intrinsic ability to thrive under a variety of water supply regimes

Because our greenhouse plants exhibited similar morphology to dry site plants, it may be that water-use habits and amounts were less than would have been detected had greenhouse conditions mirrored wet site conditions. This being the case, the true transpiration potential of Japanese knotweed was most likely underestimated. However, the amount used and conditions under which the greenhouse plants continued to use water made clear that this invasive will use water if any is available, and continue to transpire, albeit at a reduced rate, under stress.

Observed growth in dry field sites and continued function under drought treatment in our study indicates that Japanese knotweed may be able to adjust to conditions of water stress in ways that impart some drought tolerance. The implications of this are that should our area be subject to drought stress, the presence of Japanese knotweed could place further demands on our water supply. Continued transpiration by a prolific invader could prove disadvantageous to our ecosystems and communities.

The question of whether a change in vegetation from native to exotic species will impact the water cycle remains of particular interest. Alterations in vegetation can impact deep soil drainage and runoff, key factors in determining water yield (Wilcox & Thurow, 2006.) In riparian corridors, such changes may impact stream flow in the event that native plants are replaced by invasives with a fundamentally different evapotranspiration profiles (Wilcox & Thurow, 2006). Climate change models for Japanese knotweed in Great Britain indicate that increases in carbon dioxide may allow range expansion to higher altitudes and regions where current growth is patchy (Beerling & Woodward, 1994). Japanese knotweed is present in overwhelming abundance in riparian and roadside areas of the mid-Atlantic region, yet has not received the degree of inquiry accorded invasives such as *Tamarisk* in the Southeast. Studies carried out in arid regions are largely inconclusive, yet have led to governmental policy change and funding allocation. The water profile of the northeast region is largely ignored excepting the occasional drought. In the future, the priority level of this issue may increase. A proactive approach to assessing the impact of Japanese knotweed on our water budget may serve to prevent future complications.

Results from the greenhouse study and field study demonstrated that Japanese knotweed will continue to use water even in arid conditions. While it grows taller and displays greater leaf area under wet conditions, it will draw water from the ground and transpire even when subject to drought treatments and can thrive under dry conditions.

Physiological adjustments, altered hydraulic conductivity, and varied morphology may allow for continued function and explain such diverse range expansion. The ecological implications of such use may create a situation analogous to that of *Tamarisk* in the southeast should a drought or drier climate conditions strike the mid-Atlantic region.

The ability of Japanese knotweed to extract water across a range of moisture conditions and vary both morphology and physiology to do so may render it a necessary area of concern in terms of water resource management. Vegetation plays a key role in local hydrology and ecosystem function and composition. The presence of a prolific invader capable of intercepting and utilizing vast quantities of water poses a threat to both ecosystem balance and water supply. In an urban area such as the North Jersey region, under drought conditions, the threat extends to our human population. Greater understanding of the nature and extent of water-use by Japanese knotweed would aid in determining its viability as a target for water resource management.

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