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THE IMPACT OF GLOBAL ENVIRONMENTAL CHANGES ON AN EXOTIC INVASIVE SPECIES, *ALLIARIA PETIOLATA* (GARLIC MUSTARD)

A Thesis

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of

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by

Scott J. Collins

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For my family and friends that supported me throughout the process.

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ABSTRACT

Collins, Scott J. M.S., Purdue University, May 2016. The Impact of Global Environmental Changes on an Exotic Invasive Species, *Alliaria petiolata* (Garlic Mustard). Major Professor: Xianzhong Wang.

Invasive exotic species have caused severe ecological and economic damages to many communities in the United States and elsewhere. It is therefore important to improve our understanding of how global environmental changes will affect the invasiveness and severity of these invasive species. Over the last century, anthropogenic activities have caused multiple environmental changes. Previous studies have generally focused on the impact of the increasing atmospheric CO_2 level on the physiology and growth of invasive species. With atmospheric nitrogen (N) deposition on the rise over the past decades, it is essential to recognize how an increase in soil N will affect the invasiveness of some exotic species. To determine the impact of increased atmospheric N deposition and drought stress on invasive species, I studied the impact of different levels of N on *Alliaria petiolata* (garlic mustard), an exotic invasive species. In addition, I examined the interactive effects of N deposition and drought stress on garlic mustard. Multiple morphological measurements were used to analyze the growth rate at varying levels of N and soil moisture. The study on N deposition on plant growth will improve our understanding of the invasiveness of garlic mustard. The changes in precipitation patterns must also be examined to foresee if plants in increased atmospheric N conditions

can overcome drought stress conditions. I found an increase in plant growth and photosynthetic rate at higher levels of N. Plants with adequate water displayed a continued increase from the lowest level to the highest level of N. Increases in drought stressed plants plateaued at an intermediate N level of 20 kg ha^{-1}. My results demonstrated that during drought stress garlic mustard does not benefit from an increase in N above a certain level. These results are important to take into consideration when we analyze the spreading of invasive weeds due to global environmental changes, including increased atmospheric N deposition and regional drought, in order to apply the optimal management strategies for controlling invasive species.

INTRODUCTION

Invasive plants are those that reproduce in large quantities and, therefore, have the ability to spread over vast distances. (Richardson, Pysek et al. 2000). For a plant species to become invasive, the species must overcome dispersal barriers and biotic and abiotic barriers (Lonsdale 1999; Richardson, Pysek et al. 2000). Weeds are plants that are cultivated where they are not desired and have known negative economic and ecological effects (Vitousek, D'Antonio et al. 1997; Richardson, Pysek et al. 2000). Invasive plant species negatively affect ecosystems and agriculture all over the world (Callaway and Aschehoug 2000). Normally these invasive plants are spread by human activities, whether it is intentional or unintentional (Vitousek, D'Antonio et al. 1997), such as transporting a kudzu vine in a haystack without knowledge of its presence (Ken Cote, Indiana Department of Natural Resources, personal communication). Up to 25% of plant species found in North America are non-native species (Meekins and McCarthy 1999). These invasive plant species can greatly alter community structure and overall composition of their adopted ecosystems (Coblentz 1990; D'Antonio and Vitousek 1992). Many invasive plant species outcompete the native plant species, which leads to the native species being greatly reduced or crowded out (D'Antonio and Vitousek 1992; Lonsdale 1999). This competition has led to the addition of about 42% of the species listed as threatened or endangered under the Endangered Species Act (Wilcove, Rothstein et al. 1998; Pimentel, Zuniga et al. 2005).

In the Midwestern United States, one of the most important ecosystems is the hardwood forest. Hardwood forests have a rich diversity of plant species and communities. Hardwood forests are extremely important economically because of the vast lumber industry. Invasive species are the key culprit to decreasing biodiversity in hardwood forests (Vitousek, D'Antonio et al. 1997; Nuzzo 1999). The composition of hardwood forests has been greatly altered by the introduction of invasive species (Vitousek, D'Antonio et al. 1997; Nuzzo 1999; Morrison, Lubchansky et al. 2007). Invasive species can hinder the regeneration of hardwood forest species by negatively affecting the seeds and seedlings of hardwood species. The alteration of hardwood forests has the potential to hinder a 17 billion dollar (Indiana DNR, 2006) economic impact in Indiana. The introduction of invasive species has caused an enormous decline in production output in the lumber industry.

An example of an invasive species that affects the hardwood forests is *Pueraria lobata* (kudzu). Kudzu is a climbing, semi-woody, perennial vine that is native to Japan and China (Blaustein 2001). Kudzu was promoted by the Soil Conservation Service (SCS) in the late 1930s through early 1940s as a way to reduce soil erosion (Alderman and Alderman 2001). Kudzu is capable of climbing up and covering trees and other plant species (Alderman and Alderman 2001). The covered plant species are shaded from the sun by kudzu and eventually smothered. Kudzu grows so expansively that its incredible weight can uproot mature trees (Alderman and Alderman 2001). Kudzu covers so much area that it causes great damage to ecosystem diversity by not only smothering species, but also by not allowing any other plants to germinate and grow where the vines carpet the soil (Blaustein 2001). The thick layering of kudzu prevents regeneration and growth of hardwood forests (Blaustein 2001). Kudzu is estimated to cause more than half a billion dollars' worth of economic loss when decline in forest productivity is considered (Blaustein 2001). Kudzu is difficult to eradicate due to its rapid spread and lack of natural predators in the United States. Biannual treatments for ten years are required for a chance of complete eradication of a site (Ken Cote, Indiana Department of Natural Resources, personal communication). Kudzu is not the only invasive species that has negative effects on the hardwood forests in the Midwestern United States.

Lonicera japonica (Japanese honeysuckle) seriously affects the Midwestern hardwood forests. Brought to the United States from China in 1806 by a gardener (Schierenbeck 2004), honeysuckle has proven to be an extremely invasive exotic species. Currently, Japanese honeysuckle is found in 42 states (Schierenbeck 2004). Japanese honeysuckle is able to grow into the understory and shade out species that are lower to the ground, greatly diminishing the number of forest floor annuals (Schierenbeck 2004). Additionally, Japanese honeysuckle has the ability to climb with the support of a host and can climb to a height of up to 15 meters (Williams, Timmins et al. 2001). Honeysuckle reaches maturity and flowers two years after germination (Leatherman 1955). The seeds are dispersed by birds and mammals (Handley 1945; Williams and Karl 1996) and have a 47% viability after six months (Hidayati, Baskin et al. 2000). Japanese honeysuckle can survive extreme forest fires and recover at enormously successful rates (Barden and Matthews 1980; Faulkner, Clebsch et al. 1989). (Schwegman and Anderson 1986) demonstrated that post-fire coverage levels can be as high as four times the coverage levels before the prescribed burning. These species are just two examples of how exotic invasive species can alter a hardwood forest community.

Environmental changes can increase the threat posed by invasive plant species. Many studies have demonstrated that increased carbon dioxide levels increase growth rates of invasive species, such as kudzu (Sasek and Strain 1988). There are several other environmental changes that have intensified in the past decades. One of these environmental changes is the continual increase in atmospheric nitrogen (N) deposition or in other words the transfer of N from the atmosphere into the soil. Uneven distribution of atmospheric N will have the potential to cause extreme damage to community structure in many ecosystems.

Environmental changes are not the only cause for species to become invasive. Disturbances in hardwood forests may increase the spread of invasive species that can rapidly colonize a disturbed area (Vitousek, D'Antonio et al. 1997; Zavaleta 2000). One of the most prominent reasons why invasive species are able to outcompete native species is that they have few or no natural predators in non-native ecosystems (Callaway and Aschehoug 2000). Furthermore, many invasive plant species have a competitive advantage over native plant species because native plant species have not evolved to compete against some of the strategies the non-native species employ. For example, some invasive plants have allelopathic capabilities to which native plants have not adapted an effective response. Other characteristics of invasive species are seeds that germinate quickly, extended flowering periods, and the ability to reproduce vegetatively. Invasive plant species can also affect agricultural systems and other human-managed lands, causing immense cost and economic losses (Vitousek, D'Antonio et al. 1997). In the

Midwest, weedy species can greatly hinder the production of soybean, a billion dollar industry crop (USDA 2016). Invasive species cause damage to all ecosystems they overrun. One of the most important ecosystems in the Midwest is the hardwood forest. It is important to understand how environmental changes, such as increased atmospheric N will affect the growth and spreading of invasive exotic weedy species.

Figure 1. Garlic mustard in its second year of growth in central Indiana

One of the most widespread exotic invasive species in the United States is *Alliaria petiolata* (M. Bieb.) Cavara and Grande (garlic mustard) (Figure 1). Garlic mustard is a highly invasive species with a biennial life cycle (Bauer, Anderson et al. 2010). The species is native to Eurasia, and was first found in the United States in 1868 in Long Island, New York (Bauer, Anderson et al. 2010). Garlic Mustard can be identified by its heart-shaped leaves and the garlic odor it produces when any part of the plant is crushed (Cavers, Heagy et al. 1979) . Garlic Mustard has a two-year life cycle;

the first year of the garlic mustard life cycle is in the form of a rosette. These rosettes can be found in great densities along the forest floor. The second year, the plant blooms in the spring and early summer. Garlic mustard is capable of producing up to 103,000 seeds per m^2 of ground area that these plants cover (Cavers, Heagy et al. 1979; Nuzzo 1993). These seeds can remain viable for up to 4 years in the soil (Baskin and Baskin 1992; Nuzzo 2000). There are up to 69 different insects that feed on garlic mustard in its native habitats while none of these insects are found in the United States (Szentesi 1991). The lack of natural predators is a key contributor to why garlic mustard is such a successful invasive species (Szentesi 1991). Many different allelopathic chemicals have been found in garlic mustard that may contribute to its success as an invasive species (Vaughn and Berhow 1999; Stinson, Kaufman et al. 2007). These secondary compounds negatively affect the mutualistic relationship between mycorrhizal fungi and native plant roots (Haribal and Renwick 1998; Roberts and Anderson 2001; Stinson, Campbell et al. 2006; Cipollini and Gruner 2007; Callaway, Cipollini et al. 2008; Lind and Parker 2010). Allylisothiocyanate (AITC) is a glucosinolate commonly found in garlic mustard tissue; this is the product of the hydrolysis of sinigrin (Vaughn and Berhow 1999). AITC is a known anti-fungal compound (Olivier, Vaughn et al. 1999). Arbuscular mycorrhizal fungi (AMF) are recognized as a beneficial fungus. Many native plant species rely on the mutualistic relationship for many necessary nutrients, such as water and minerals (Brundrett and Kendrick 1988). It has been demonstrated that garlic mustard allelochemicals are most readily detected when the adult plants are senescing (Cantor, Hale et al. 2011). AITC was detected at biologically relevant levels that can negatively impact the germination of AMF spores (Cantor, Hale et al. 2011). Adult senescence is at the same time that peak AMF association with native plant species is occurring (Brundrett and Kendrick 1990). AMF is not the only fungus that many plant species rely on for mutualistic relationships. It has been demonstrated that increased garlic mustard density has a negative effect on the amount of ectomycorrhizae associated with *Quercus rubra* (northern red oak) seedlings (Castellano and Gorchov 2012)**.** Garlic mustard has been demonstrated to have negative impacts on seed germination rates in *Geum laciniatum* and *Geum urbanum* (Prati and Bossdorf 2004). The ability to upset the relationships between soil microbials and native plant species has the potential to severely change the composition of a plant community (Gupta, Satyanarayana et al. 2000). This will hinder the native species' natural functions and allow the invasive species to spread. The spread of this highly exotic invasive species will have important negative impacts on hardwood forest community structure and agricultural production. Once garlic mustard establishes in a forest, it may fluctuate in density and coverage, but it is there to stay (Nuzzo 1999). There is a lot we do not understand about how garlic mustard will react to environmental changes, such as increased atmospheric N deposition and drought stress. I will do this by examining how soil N levels and drought stress impacted garlic mustard.

Anthropogenic activities have caused and exacerbated many environmental changes. Increased atmospheric N deposition is one of these changes. Nitrogen is one of the limiting nutrients for plant production worldwide (Vitousek and Howarth 1991; Vitousek, Aber et al. 1997; Clark and Tilman 2008). Improper treatment of animal waste, use of N fertilizers, burning of fossil fuels, and cultivation of N fixating plant species have caused a significant increase in atmospheric N deposition (Galloway, Schindler et al.

1995; Liu, Zhang et al. 2013). In China there has been an increase in N deposition from 13.2 to 21.1 kg ha^{-1} N from the 1980s to the 2000s (Liu, Zhang et al. 2013). These levels are higher than any atmospheric N deposition evident in the United States and rivals even the highest levels seen in Europe (Erisman, Domburg et al. 2005; Holland, Braswell et al. 2005) Although atmospheric N deposition rates have nearly doubled, deposition rates are expected to continue to increase in the coming years (Vitousek, Aber et al. 1997; Galloway, Townsend et al. 2008) A primary reason for increased N deposition in the atmosphere is that less than half of the N in fertilizers used in China is actually used by the crops; the rest is lost to the environment (Liu, Zhang et al. 2013). Perhaps unsurprisingly, emissions of NH_3 have doubled from the 1980s to the 2000s while use of N fertilizer and number of domestic animals has consequently doubled (Liu, Zhang et al. 2013). The burning of fossil fuels transfers N to the atmosphere and accounts for over 20 Tg yr^{-1} of fixed N emitted into the atmosphere (Vitousek, Aber et al. 1997). Leguminous plant species (soybeans and kudzu) have a symbiotic relationship with N-fixating microorganisms in their roots. It is estimated that N fixation accounts for 40 Tg yr^{-1} (Vitousek, Aber et al. 1997). Anthropogenic activity has doubled the transfer of N from the atmosphere and made it available in pools across the globe for biological use (Vitousek, Aber et al. 1997). Nitrogen has not spread evenly over the Earth's surface and the increase is more prominent in some areas than others (Wright and van Breemen 1995). With the projected increase in N availability, one would expect to see a growth increase in many plant species (Vitousek and Howarth 1991). Adding a limiting nutrient to an ecosystem can dramatically affect the community structure (Vitousek, Aber et al. 1997; Aber, McDowell et al. 1998). Increased amounts of N typically lead to a decrease in biological diversity because species will react differently to the alteration in resource availability (Tilman 1987; Aber, Magill et al. 1995; Clark and Tilman 2008). It is important to note that all ecosystems do not respond to elevated N the same way. It will be important to understand how the increase in atmospheric N deposition affects particular plant species so that their spread and ecological impact can be understood. Increased N deposition is not the only environmental change of interest; unevenness in distribution of precipitation will lead to regions of drought. Understanding how drought stress will affect the spread of exotic invasive plant species will be extremely important.

The change of precipitation patterns is another environmental change that is of immense importance (Saxe, Cannell et al. 2001; Salinger 2005). Some areas will receive additional precipitation while others will receive less (Rind, Goldberg et al. 1990). Periods of regional drought will also become more prevalent (Rind, Goldberg et al. 1990; Saxe, Cannell et al. 2001; Schär, Vidale et al. 2004; Salinger 2005; Bréda, Huc et al. 2006). One cause of increased drought will be the ability of the atmosphere to hold greater quantities of water due to the increasing temperatures (Rind, Goldberg et al. 1990). The use of general circulation models has led to the conclusion that the Midwest will experience amplified drought frequency (Xie, Eheart et al. 2008). This expectation seems controversial since there is expected to be an increase in rainfall, but this can be explained by the change in rainfall frequency (Xie, Eheart et al. 2008). Although there will be more precipitation, the change in frequency will cause increased rainfall in a short period and then long stretches with none. It is important to understand how ecosystems will respond to changes in precipitation levels and patterns. With composition of vegetation expected to change more rapidly (Pastor and Post 1988; Overpeck, Bartlein et al. 1991), regional drought will change the dynamics of diversity in an ecosystem (Rind, Goldberg et al. 1990). The largest impact extreme drought may have on an ecosystem is by increasing the occurrence and the magnitude of other anthropogenic environmental changes (Archaux and Wolters 2006). Some species will be able to respond to more extreme conditions while others will not (LeBlanc 1998). The same ectomycorrhizals affected by garlic mustard's secondary compounds are extremely important for trees when dealing with drought conditions (Coners and Leuschner 2002). The mycorrhizae association with the fine root tips is the most important part of the water and mineral uptake in hardwood forest's trees (Coners and Leuschner 2002). If these mycorrhizae are not available to aid during drought stress, there is immense potential for a remarkable change in community structure. Drought stress has the potential to cause intense natural selection for drought tolerant plant species (Archaux and Wolters 2006). In Europe, the decline in oak populations has been directly associated to the increased occurrence of drought (Landmann 1993; Thomas, Blank et al. 2002). It has also been demonstrated that drought is one of the factors that helps other plant species outcompete oak (Finsinger, Tinner et al. 2006). Drought is extremely influential for seedling growth in many hardwood forests (Osmond, Austin et al. 1987). If garlic mustard is able to tolerate drought stress, then it may gain an advantage over oak species in hardwood forests in the Midwest. It will be critical to determine how other environmental changes, such as increased N deposition, will affect weedy species ability to deal with drought stress. Long periods of drought will be directly linked with other environmental changes, such as increased atmospheric N deposition (Gordon, Woodin et al. 1999; Fuhrer 2003). The interaction between these environmental changes will be critical in understanding the possible impact that exotic invasive species will have.

Studies have focused on increasing CO_2 levels and how it will affect invasive species' growth and spreading. With increasing atmospheric N deposition, it will be important to see the effect increased N has on invasive species. I hypothesize that garlic mustard growth and overall invasiveness should increase with the addition of a limiting nutrient like N. I believe drought stress will slow the garlic mustard's growth and possibly even kill it at low N levels. However, I believe the addition of increased levels of N will allow the garlic mustard to survive drought stress and even increase photosynthetic rate and morphological characteristics above those from the low N well-watered treatments.

This study will have extreme importance for the investigation of environmental changes and the spread of invasive weedy species. With the increase in atmospheric N, it will be incredibly significant to understand how increased atmospheric N will affect garlic mustard and how increased N will interact with changing precipitation patterns. Understanding how increased atmospheric N will affect garlic mustard will provide a greater knowledge of the hardwood forest ecosystem's composition in the future.

MATERIALS AND METHODS

Collection of Plants

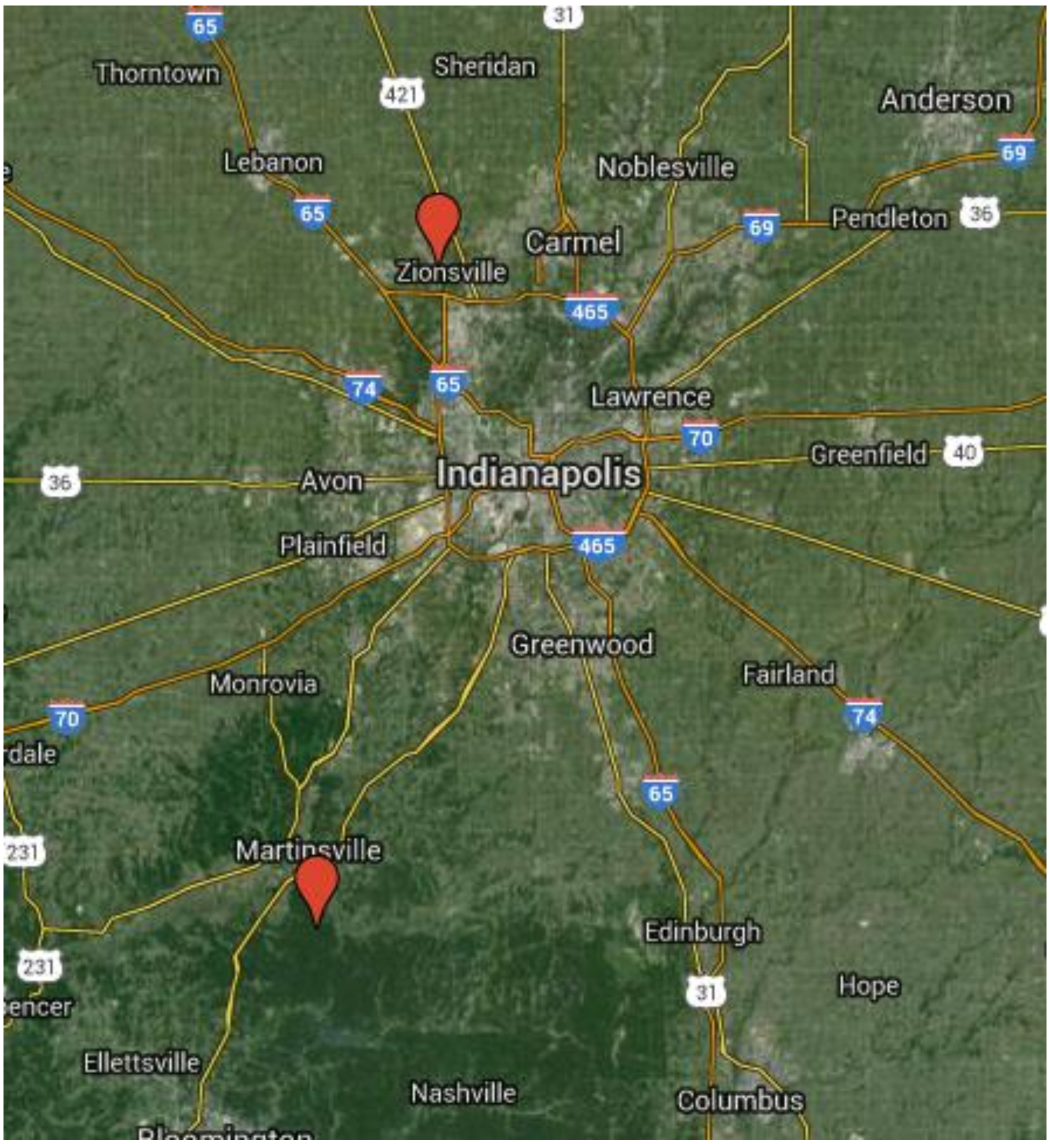

Figure 2. Morgan County (39.359, -86.418) and Zionsville (39.957, -86.274) plant collection sites in Indiana, United States.

Garlic mustard is found throughout Indiana. Garlic mustard was collected twice from the same site in Morgan County, Indiana (Figure 2). Only plants in their first year of growth were collected.

Fifty plants were collected on May 6, 2015. Garlic mustard was collected in a field and along the road (Catholic Cemetery Road). The plants were transported in plastic tubs lined with wet paper towels to keep the plants from drying out. They were transplanted the same day at the IUPUI greenhouse. All of the plants were transplanted to Promix HP soil (Premier Horticulture Inc., Quakertown, PA, USA) in late June at the suggestion of Dawn Bauman, the IUPUI greenhouse director.

Thirty plants were collected on July 1, 2015. All of these plants were collected along the road (Catholic Cemetery Road). They were transported in a plastic tub lined with moist paper towels. They were transplanted the same day at IUPUI's greenhouse in Promix HP.

A third set of plants was collected on September 26, 2015. These plants were collected off of Bloor Lane in Zionsville, Indiana. Transportation method was the same as the other collections and plants were transplanted the same day into Promix HP soil in the IUPUI greenhouse.

Growth in the Greenhouse

Forty garlic mustard plants were transplanted into fresh Promix HP medium on September 26, 2015. Promix HP is extremely low in soil nutrients so it was the best choice as the medium to allow nutrient manipulation. The garlic mustard plants were placed in the southeastern corner of the IUPUI greenhouse. The pots were randomly arranged along the benches. They were randomly rearranged every week to make sure location in the greenhouse did not affect the growth rate. The plants were separated into four N levels consisting of ten pots each. These groups were split into groups of five with half receiving adequate water and the other receiving minimal water to simulate drought stress conditions. An effort was made to evenly distribute into the treatment groups by size and maturity. Well-watered plants were watered every third day to allow for wet and dry cycles. The drought stress plants received water every six days after displaying signs of drought stress. Observations were made daily to see if plants were showing visible symptomatic signs of drought stress (leaves and stems drooping over the edge of the pot). Plants were treated for spider-mites and thrips. Every pot was treated with Peter's fertilizer equivalent to 5 kg ha^{-1} N. Next, each plant was treated with ammonium nitrate to simulate one deposition level of 5, 10, 20, or 40 kg ha^{-1} N. N treatments were performed every three weeks to replenish the N taken up by the plants or leached from the soil. Peter's fertilizer was added at levels equivalent to 5 kg ha^{-1} N every six weeks and coincided with the N treatments. Morphological and physiological measurements were taken periodically. Crown diameter (data not included), open leaf count, stem and leaf length, and youngest mature leaf area were taken at weekly intervals to monitor growth. Leaves were counted only if they had completely opened by the weekly data collection. The height of the plant was measured from where the stem meets the crown to the tip of the largest leaf. The leaf area of the youngest mature leaf (leaf that had expanded completed, but showed no sign of senescence) was measured in a non-destructive procedure. The leaf was laid flat on a sheet of paper and methodically traced. The leaf tracings were run through a LI-COR 3100 Area Meter (Lincoln, Nebraska, USA). Photosynthetic rate, leaf conductance, and intercellular CO_2 concentration (Ci) were measured at weekly intervals, using Li-6400 portable photosynthesis system (Li-Cor, Lincoln, Nebraska, USA). The youngest mature leaf was measured to represent the plant as a whole. Measurements were made at the same time each day and measured at 1000 μmol photo m^{-2} s^{-1}. Each plant was measured once over the course of two days due to the amount of time it took to take the measurements within the allotted time of day. Light response curves were also created to measure the light saturated photosynthetic point and light saturation point (Figure 3). The curves were created by starting at an irradiance of 1500 μmol m^{-2} s^{-1} and gradually decreasing to 0 μmol m^{-2} s^{-1} taking measurements every five minutes. The light saturated photosynthetic rate is the rate of photosynthesis where an increase in light no longer results in an increased photosynthetic rate. Light saturation point is the light level at which the light saturated photosynthetic rate is reached. The LI-COR's Li-6400 light response curve program was used to create the light curves (Figure 3). Light saturated photosynthetic rate and light saturation point were calculated using Baly's equation (Baly 1935). Physiological measurements were made when the drought stressed plants showed signs of experiencing stress. This typically occurred around three to four days after a round of watering. Healthy well-watered leaves did not droop and were rather rigid. The leaves would lose their rigid state and fold in many places under drought stress.

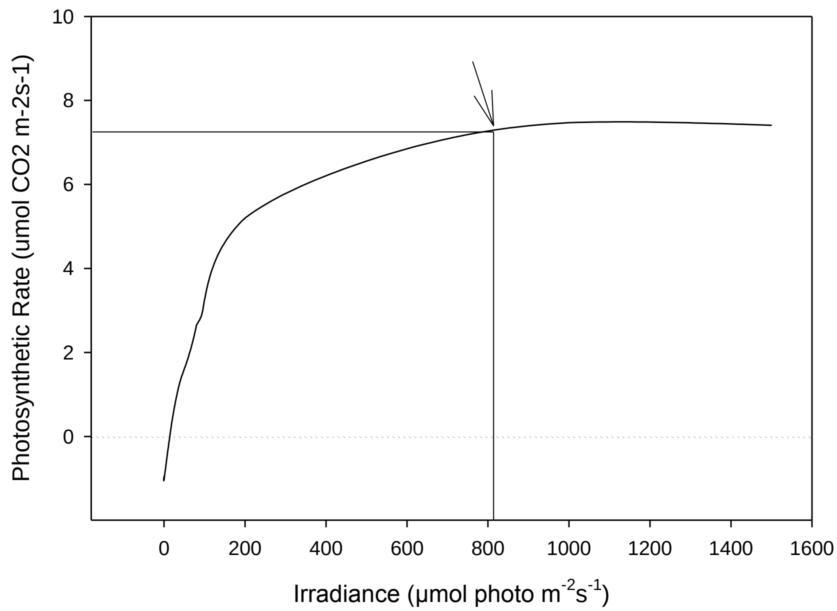

Figure 3. Photosynthetic response curve used to obtain the light saturation point and light saturated photosynthetic rate. The arrow represents the light saturation point and light saturated photosynthetic rate. This is where an increase in irradiance does not increase the photosynthetic rate.

Statistical analysis

A t-test was performed for each treatment against all seven other treatments to determine a statistical significance. T-tests were performed using the SigmaPlot 10.0 software (Systat Software Inc. in San Jose, California).

RESULTS

Physiology

Photosynthetic Rate

Photosynthetic rate measurements were taken of all plants in every treatment group with leaves large enough to fit the Li-6400 portable photosynthesis system's 2x3 cm leaf chamber. Five sets of measurements were made over the course of the experiment. The results are provided in Figures 4 through 8. In the first two measurements, photosynthetic rate is higher in well-watered plants at every level besides 20 kg ha^{-1} N. During the last three measurements photosynthetic rate was higher in the well-watered plants at the 20 and 40 kg ha^{-1} N. Figure 9 represents the average of all the measurement points made from all five sets of measurements. The well-watered plants exhibit an increase in photosynthetic rate at each increasing N level (Figure 9). The average values of the well-watered plants were 3.846, 4.137, 5.297, and 7.298 μmol CO_2 m^{-2} s^{-1} matching the 5, 10, 20 and 40 kg ha^{-1} N, respectively. The drought stressed plants demonstrate a smaller increase in photosynthetic rate and display a leveling off at the 20 kg ha^{-1}. The average values of the drought stressed plants were 3.634, 4.058, 5.571, and 5.123

μmol CO_2 m^{-2} s^{-1} matching the 5, 10, 20 and 40 kg ha^{-1} N, respectively.

Thephotosynthetic rates of well-watered plants ranged from 3.846 μmol CO_2 m^{-2} s^{-1} to7.298 μmol CO_2 m^{-2} s^{-1}. The drought stressed plants photosynthetic rates ranged from 3.634 μmol CO_2 m^{-2} s^{-1} to 5.571 μmol CO_2 m^{-2} s^{-1}. P values from the t-tests for all sets of measurements are provided in tables 1-6.

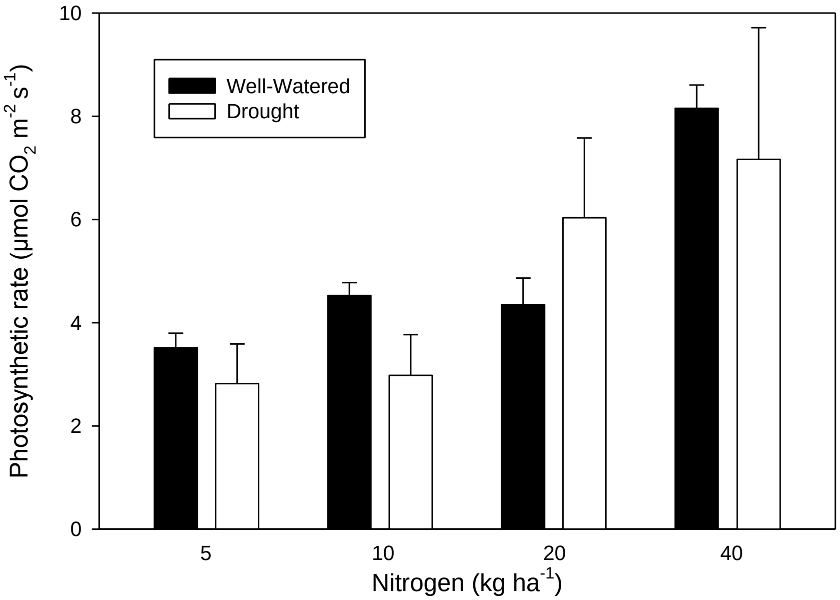

Figure 4. Photosynthetic rates in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on November 24-25, 2015. n=2-5. Error bars represent one standard error.

Table 1. P values from the t-test on photosynthetic rates in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on November 24-25, 2015. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.078	0.316	0.002	0.544	0.643	0.339	0.349
10 WW	0.078	------	0.773	0.001	0.102	0.134	0.450	0.362
20 WW	0.316	0.773	------	0.002	0.173	0.219	0.411	0.340
40 WW	0.002	0.001	0.002	------	0.001	0.001	0.187	0.612
5 D	0.544	0.349	0.173	0.001	------	0.893	0.158	0.178
10 D	0.643	0.134	0.219	0.001	0.893	------	0.177	0.192
20 D	0.339	0.450	0.411	0.187	0.158	0.177	------	0.704
40 D	0.349	0.362	0.340	0.612	0.178	0.192	0.704	------

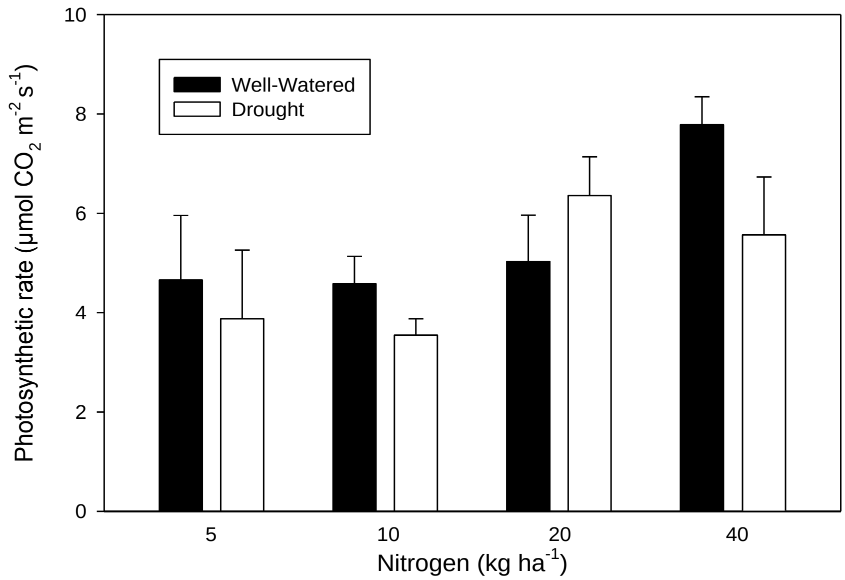

Figure 5. Photosynthetic rates in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on December 8-10, 2015. n=2-5. Error bars represent one standard error.

Table 2. P values from the t-test on photosynthetic rates in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on December 8-10, 2015. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.953	0.824	0.044	0.727	0.372	0.296	0.660
10 WW	0.953	------	0.698	0.009	0.662	0.185	0.147	0.528
20 WW	0.824	0.698	------	0.035	0.527	0.208	0.323	0.749
40 WW	0.044	0.009	0.035	------	0.021	0.002	0.172	0.109
5 D	0.727	0.662	0.527	0.021	------	0.828	0.155	0.391
10 D	0.372	0.185	0.208	0.002	0.828	------	0.033	0.211
20 D	0.296	0.147	0.323	0.172	0.154	0.033	------	0.594
40 D	0.660	0.528	0.749	0.109	0.391	0.211	0.594	------

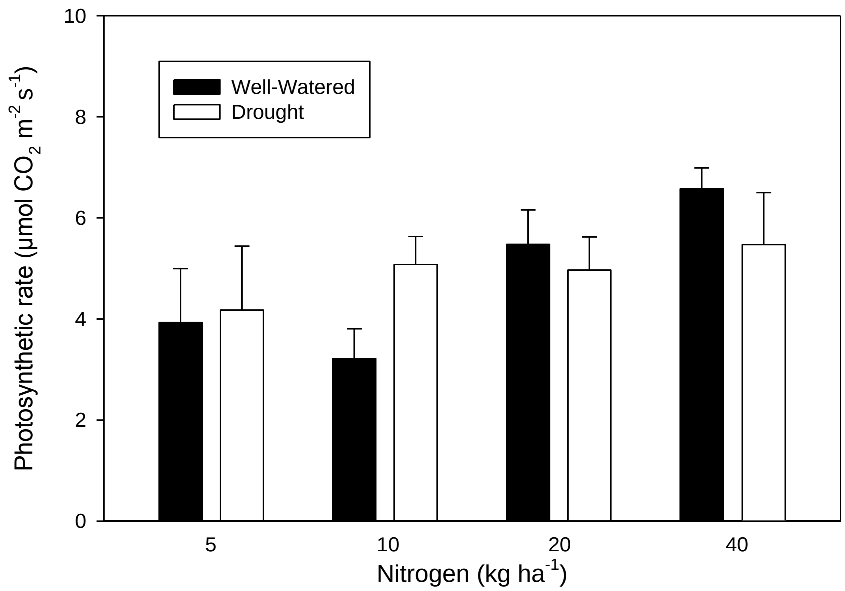

Figure 6. Photosynthetic rates in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on December 24-27, 2015. n=2-5. Error bars represent one standard error.

Table 3. P values from the t-test on photosynthetic rates in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on December 24-27, 2015. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.562	0.283	0.031	0.901	0.361	0.427	0.393
10 WW	0.562	------	0.066	0.003	0.530	0.083	0.114	0.130
20 WW	0.283	0.066	------	0.189	0.417	0.673	0.620	0.997
40 WW	0.031	0.003	0.189	------	0.067	0.070	0.067	0.281
5 D	0.901	0.530	0.417	0.067	------	0.550	0.572	0.472
10 D	0.361	0.083	0.673	0.070	0.550	------	0.908	0.753
20 D	0.427	0.114	0.620	0.067	0.572	0.908	------	0.682
40 D	0.393	0.130	0.997	0.281	0.472	0.753	0.682	------

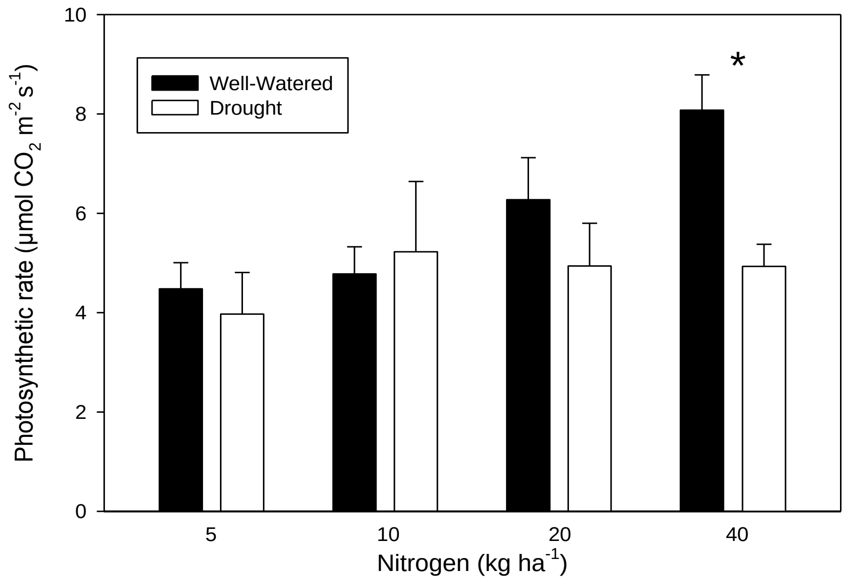

Figure 7. Photosynthetic rates in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on January 6-11, 2016. n=2-5. *P < 0.05 and **P < 0.01 for comparing water levels. Error bars represent one standard error.

Table 4. P values from the t-test on photosynthetic rates in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on January 6-11, 2016. n=2-5 WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.734	0.220	0.032	0.687	0.716	0.723	0.564
10 WW	0.734	------	0.212	0.018	0.463	0.783	0.884	0.841
20 WW	0.220	0.212	------	0.161	0.125	0.560	0.331	0.233
40 WW	0.032	0.018	0.161	------	0.011	0.088	0.033	0.020
5 D	0.687	0.463	0.125	0.011	------	0.487	0.465	0.369
10 D	0.716	0.783	0.560	0.088	0.487	------	0.871	0.852
20 D	0.723	0.884	0.331	0.033	0.465	0.871	------	0.994
40 D	0.564	0.841	0.233	0.020	0.369	0.852	0.994	------

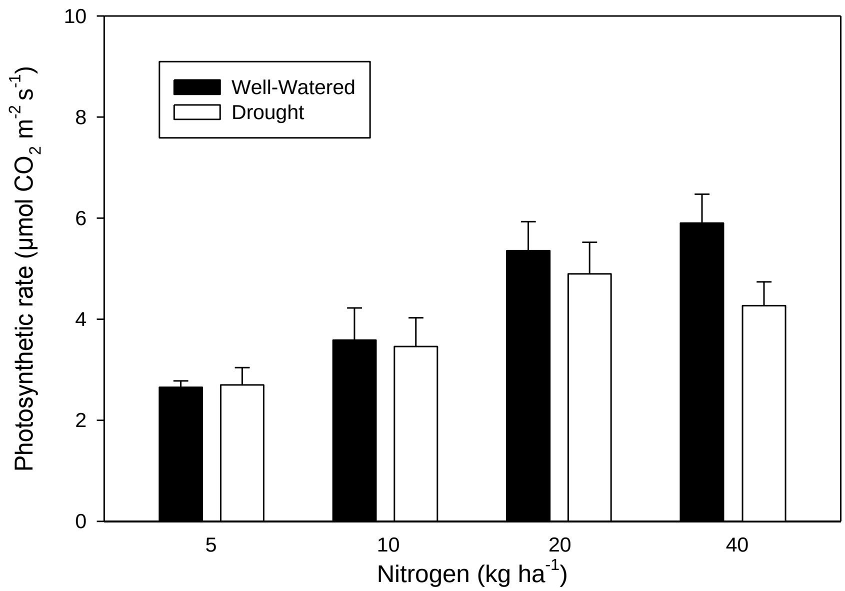

Figure 8. Photosynthetic rates in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on January 20-22, 2016. n=2-5. Error bars represent one standard error.

Table 5. P values from the t-test on photosynthetic rates in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on January 20-22, 2016. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.341	0.036	0.020	0.913	0.355	0.076	0.079
10 WW	0.341	------	0.108	0.041	0.377	0.889	0.211	0.438
20 WW	0.036	0.108	------	0.554	0.043	0.079	0.623	0.216
40 WW	0.020	0.041	0.554	------	0.022	0.031	0.275	0.099
5 D	0.913	0.377	0.043	0.022	------	0.399	0.084	0.335
10 D	0.355	0.889	0.079	0.031	0.399	------	0.164	0.335
20 D	0.076	0.211	0.623	0.275	0.084	0.164	------	0.489
40 D	0.079	0.438	0.216	0.099	0.335	0.335	0.489	------

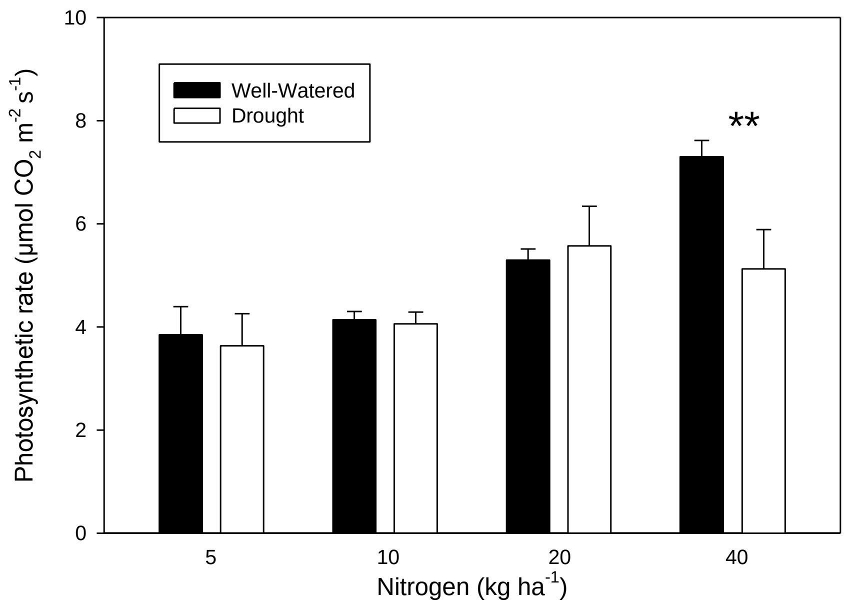

Figure 9. Average photosynthetic rates from the five sets of measurements in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels measured from November 2015 to January 2016. n=10-25. *P < 0.05 and **P < 0.01 for comparisons between water levels. Error bars represent one standard error.

Table 6. P values from the t-test on average photosynthetic rates in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels measured from November 2015 to January 2016. n=10-25. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.508	0.007	<0.001	0.643	0.712	0.016	0.046
10 WW	0.508	------	0.009	<0.001	0.261	0.867	0.015	0.044
20 WW	0.007	0.009	------	<0.001	0.003	0.022	0.760	0.780
40 WW	<0.00	<0.001	<0.001	------	<0.00	<0.00	0.001	0.003
5 D	0.643	0.261	0.003	<0.001	------	0.407	0.004	0.014
10 D	0.712	0.867	0.022	<0.001	0.407	------	0.021	0.051
20 D	0.016	0.015	0.760	0.001	0.004	0.021	------	0.976
40 D	0.046	0.044	0.780	0.003	0.014	0.051	0.976	------

Stomatal Conductance

Conductance measurements were taken of all plants in every treatment group with leaves large enough to fit the Li-6400 portable photosynthesis system's 2x3 cm leaf chamber. Five sets of measurements were made over the course of the experiment. The results are provided in Figures 10-14. Stomatal conductance was higher in well-watered plants than in drought stressed plants at every N level for each set of measurements. The well-watered plants displayed an increase in conductance at each increasing N level (Figure 15). The average values of the well-watered plants were 0.0769, 0.1128, 0.1357, and 0.1440 mol H_2O m^{-2} s^{-1} matching the 5, 10, 20 and 40 kg ha^{-1} N, respectively. The drought stressed plants have a smaller increase in conductance and demonstrate a plateau at the 20 kg ha^{-1}. The average values of the drought stressed plants were 0.0556, 0.0582, 0.1022, and 0.0734 mol H_2O m^{-2} s^{-1} matching the 5, 10, 20 and 40 kg ha^{-1} N, respectively. The conductance of well-watered plants ranged from 0.0769 mol H_2O m^{-2} s^{-1} to 0.1440 mol H_2O m^{-2} s^{-1}. The conductance of drought stressed leaves ranged from 0.0556 mol H_2O m^{-2} s^{-1} to 0.1022 mol H_2O m^{-2} s^{-1}. P values for all sets of measurements are provided in tables 7-12.

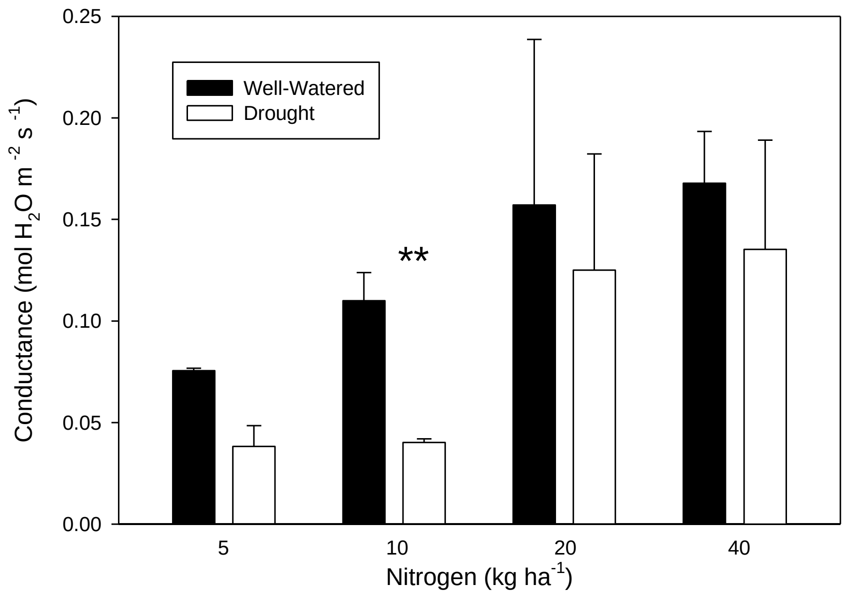

Figure 10. Stomatal conductance in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on November 24-25, 2015. n=2-5. *P < 0.05 and **P < 0.01 for comparisons between water levels. Error bars represent one standard error.

Table 7. P values from the t-test on stomatal conductance in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on November 24-25, 2015. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.149	0.495	0.083	0.066	0.001	0.595	0.453
10 WW	0.149	------	0.600	0.154	0.014	0.007	0.836	0.672
20 WW	0.495	0.600	------	0.880	0.222	0.225	0.752	0.834
40 WW	0.083	0.154	0.880	------	0.010	0.010	0.484	0.553
5 D	0.066	0.014	0.222	0.010	------	0.863	0.260	0.151
10 D	0.001	0.007	0.225	0.010	0.863	------	0.266	0.152
20 D	0.595	0.836	0.752	0.484	0.260	0.266	------	0.905
40 D	0.453	0.672	0.834	0.553	0.151	0.152	0.905	------

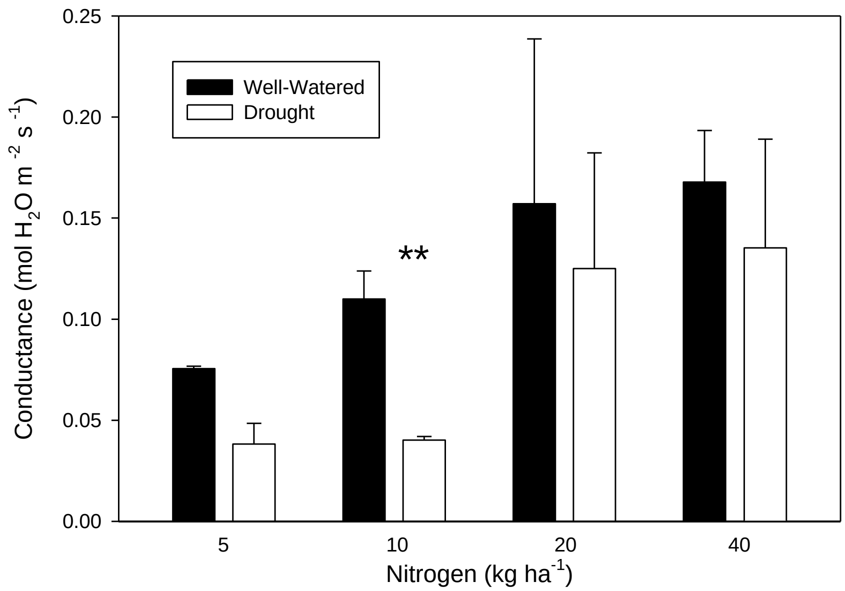

Figure 11. Stomatal conductance in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on December 8-10, 2015. n=2-5. Error bars represent one standard error.

Table 8. P values from the t-test on stomatal conductance in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on December 8-10, 2015. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.369	0.311	0.116	0.801	0.867	0.414	0.435
10 WW	0.369	------	0.872	0.139	0.210	0.187	0.533	0.773
20 WW	0.311	0.872	------	0.118	0.181	0.135	0.497	0.701
40 WW	0.116	0.139	0.118	------	0.045	0.047	0.570	0.196
5 D	0.801	0.210	0.181	0.045	------	0.881	0.259	0.258
10 D	0.867	0.187	0.135	0.047	0.881	------	0.273	0.274
20 D	0.414	0.533	0.497	0.570	0.259	0.273	------	0.632
40 D	0.435	0.773	0.701	0.196	0.258	0.274	0.632	------

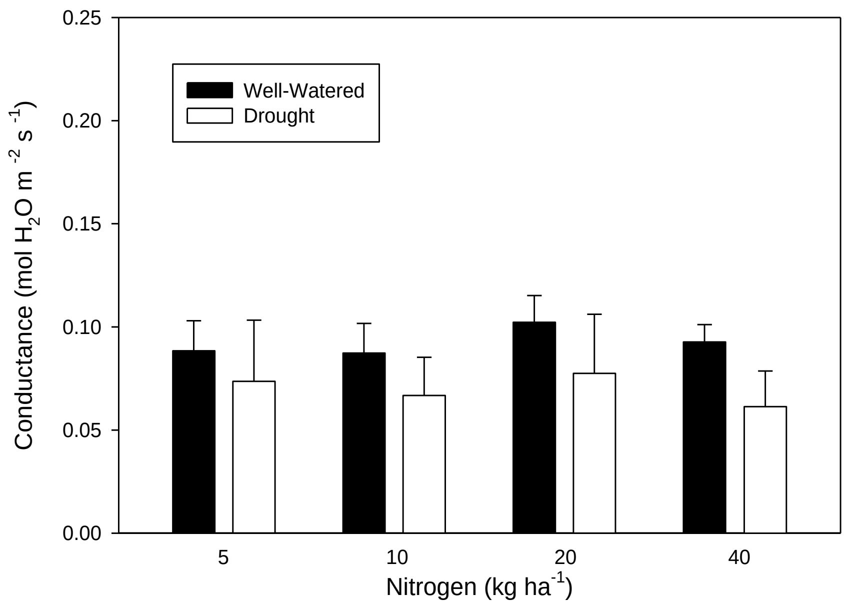

Figure 12. Stomatal conductance in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on December 24-27, 2015. n=2-5. Error bars represent one standard error.

Table 9. P values from the t-test on stomatal conductance in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on December 24-27, 2015. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.962	0.537	0.803	0.735	0.469	0.815	0.355
10 WW	0.962	------	0.482	0.741	0.699	0.430	0.795	0.312
20 WW	0.537	0.482	------	0.538	0.426	0.190	0.517	0.130
40 WW	0.803	0.741	0.538	------	0.465	0.192	0.590	0.114
5 D	0.735	0.699	0.426	0.465	------	0.854	0.931	0.739
10 D	0.469	0.430	0.190	0.192	0.854	------	0.786	0.841
20 D	0.815	0.795	0.517	0.590	0.931	0.786	------	0.681
40 D	0.355	0.312	0.130	0.114	0.739	0.841	0.681	------

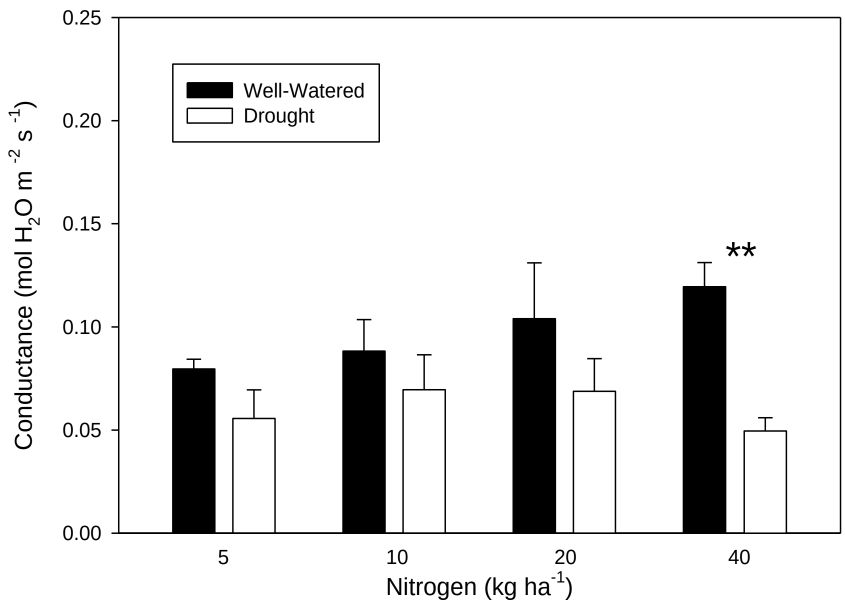

Figure 13. Stomatal conductance in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on January 6-11, 2016. n=2-5.*P < 0.05 and **P < 0.01 for comparisons between water levels. Error bars represent one standard error.

Table 10. P values from the t-test on stomatal conductance in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on January 6-11, 2016. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.697	0.536	0.0503	0.280	0.681	0.638	0.044
10 WW	0.697	------	0.638	0.089	0.190	0.459	0.428	0.081
20 WW	0.536	0.638	------	0.435	0.186	0.341	0.324	0.122
40 WW	0.0503	0.089	0.435	------	0.007	0.025	0.021	0.002
5 D	0.280	0.190	0.186	0.007	------	0.560	0.566	0.711
10 D	0.681	0.459	0.341	0.025	0.560	------	0.975	0.332
20 D	0.638	0.428	0.324	0.021	0.566	0.975	------	0.324
40 D	0.044	0.081	0.122	0.002	0.711	0.332	0.324	------

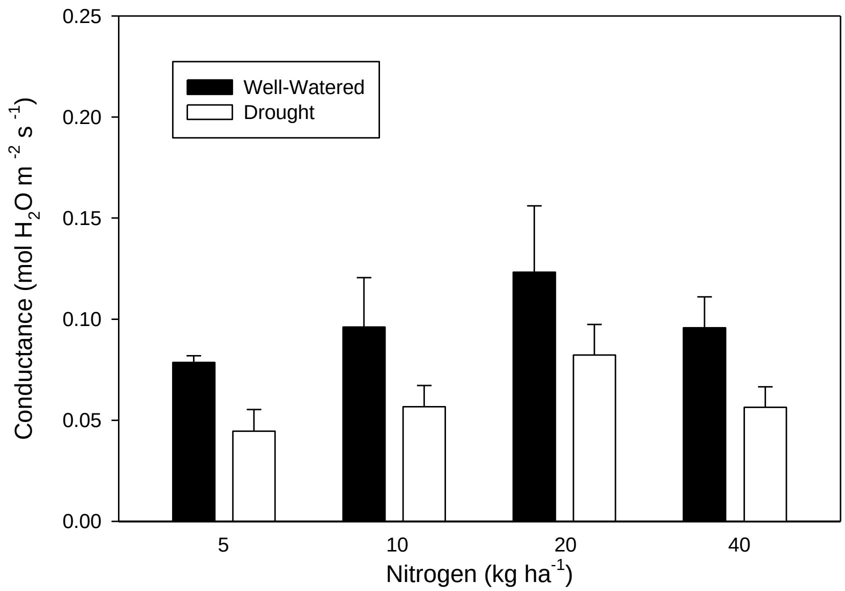

Figure 14. Stomatal conductance in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on January 20-22, 2016. n=2-5. Error bars represent one standard error.

Table 11. P values from the t-test on stomatal conductance in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on January 20-22, 2016. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.620	0.370	0.534	0.094	0.210	0.880	0.194
10 WW	0.620	------	0.543	0.990	0.212	0.213	0.633	0.209
20 WW	0.370	0.543	------	0.415	0.166	0.125	0.266	0.123
40 WW	0.534	0.990	0.415	------	0.109	0.123	0.557	0.120
5 D	0.094	0.212	0.166	0.109	------	0.500	0.186	0.498
10 D	0.210	0.213	0.125	0.123	0.500	------	0.256	0.987
20 D	0.880	0.633	0.266	0.557	0.186	0.256	------	0.249
40 D	0.194	0.209	0.123	0.120	0.498	0.987	0.249	------

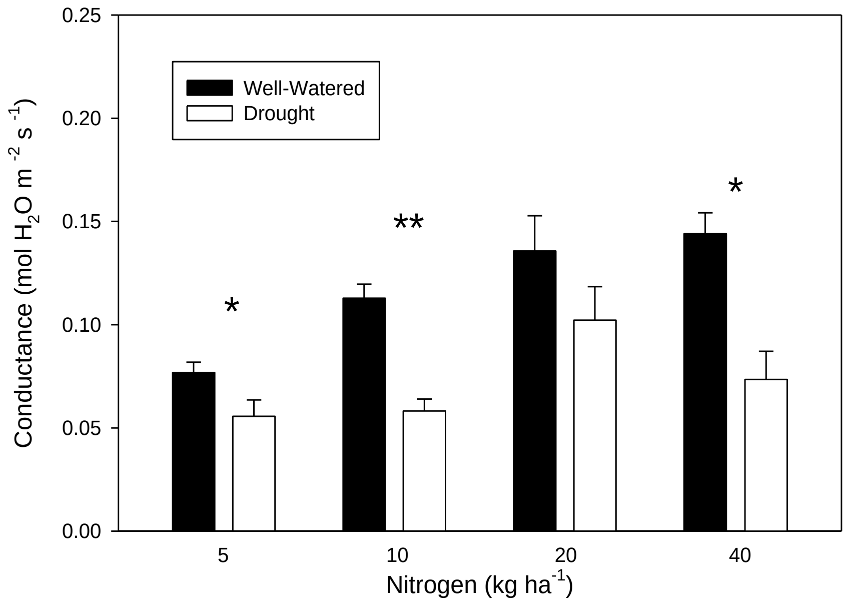

Figure 15. Average stomatal conductance from the five sets of measurements in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels measured from November 2015 to January 2016. n=2-5. .*$P < 0.05$ and **$P < 0.01$ for comparisons between water levels. Error bars represent one standard error.

Table 12. P values from the t-test on average stomatal conductance in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels measured from November 2015 to January 2016. n=10-25. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.078	0.092	0.005	0.036	0.033	0.379	0.797
10 WW	0.078	------	0.275	0.028	0.001	<0.00	0.869	0.426
20 WW	0.092	0.275	------	0.525	0.004	0.004	0.472	0.139
40 WW	0.005	0.028	0.525	------	<0.00	<0.00	0.118	0.011
5 D	0.036	0.001	0.004	<0.001	------	0.661	0.039	0.103
10 D	0.033	<0.001	0.004	<0.001	0.661	------	0.048	0.136
20 D	0.379	0.869	0.472	0.118	0.039	0.048	------	0.471
40 D	0.797	0.426	0.139	0.011	0.103	0.136	0.471	------

Intercellular CO_2 Concentration

Intercellular CO_2 concentration (Ci) measurements were taken of all plants in every treatment group with leaves large enough to fit the Li-6400 portable photosynthesis system's 2x3 cm leaf chamber. Five sets of measurements were made over the course of the experiment. The results are displayed in Figures 16 through 20. Ci levels were higher in the well-watered plants than the drought stressed plants at every N level except for 5 kg ha^{-1} in the second round of measurements (Figure 17). Figure 21 represents the average of all the measurement points made from all five sets of measurements. Ci decreases steadily as N levels increase in both the well-watered plants and the drought stressed plants. The well-watered plant averages were greater at every N level. The average values of the well-watered plants were 302.45, 314.43, 299.03, and 282.20 µmol CO_2 mol^{-1} matching the 5, 10, 20 and 40 kg ha^{-1} N, respectively. The average values of the drought stressed plants were 269.78, 267.57, 268.76, and 255.18 µmol CO_2 mol^{-1} matching the 5, 10, 20 and 40 kg ha^{-1} N, respectively. There were statistical differences for the averages at the 10 and 40 kg ha^{-1} N treatment groups between the well-watered and drought stressed plants. P values from the t-tests for all sets of measurements are provided in tables 13-18.

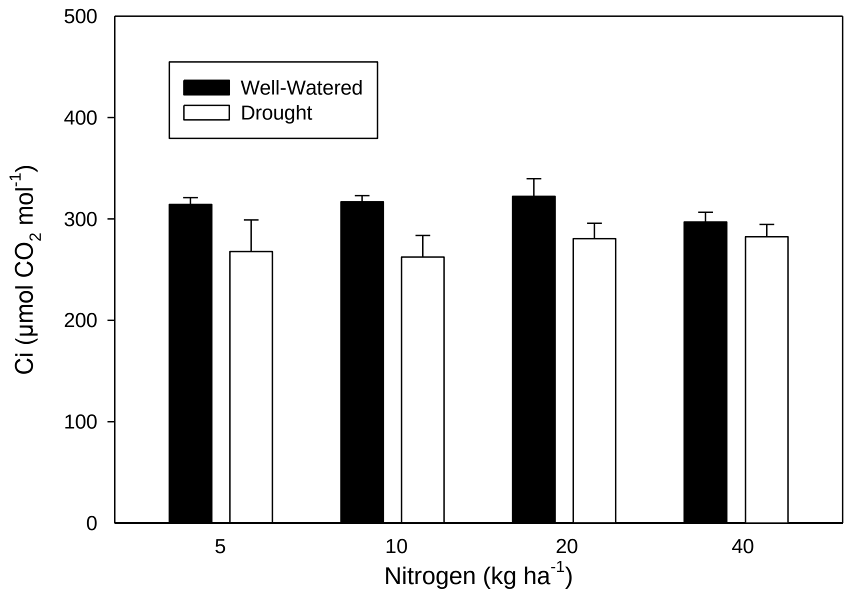

Figure 16. Intercellular CO_2 concentration in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on November 24-25, 2015. n=2-5. Error bars represent one standard error.

Table 13. P values from the t-test on Intercellular CO_2 concentration in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on November 24-25 2015. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.801	0.754	0.342	0.335	0.160	0.219	0.148
10 WW	0.801	------	0.788	0.194	0.198	0.069	0.110	0.064
20 WW	0.754	0.788	------	0.213	0.203	0.095	0.132	0.135
40 WW	0.342	0.194	0.213	------	0.309	0.137	0.374	0.388
5 D	0.335	0.198	0.203	0.309	------	0.891	0.706	0.687
10 D	0.160	0.069	0.095	0.137	0.891	------	0.505	0.460
20 D	0.219	0.110	0.132	0.374	0.706	0.505	------	0.933
40 D	0.148	0.064	0.135	0.388	0.687	0.460	0.933	------

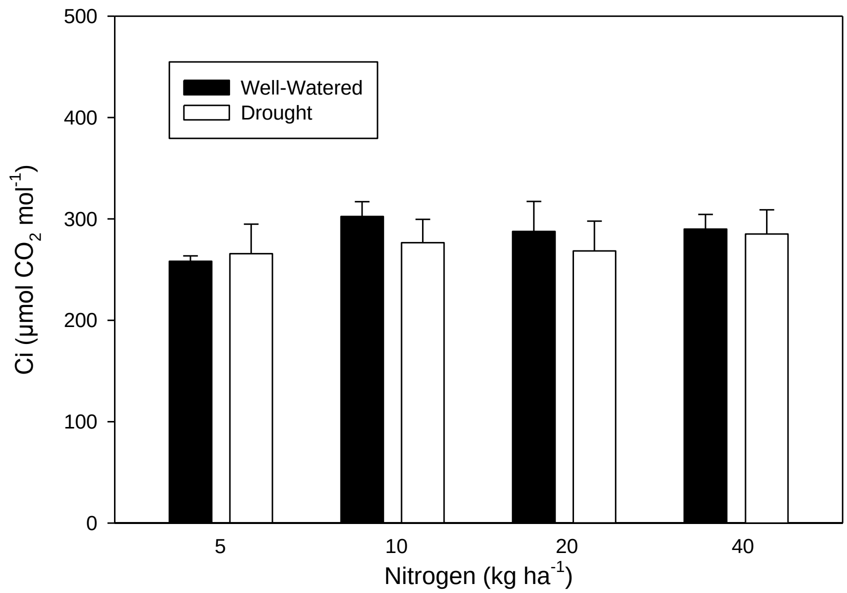

Figure 17. Intercellular CO_2 concentration in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on December 8-10, 2015. n=2-5. Error bars represent one standard error.

Table 14. P values from the t-test on Intercellular CO_2 concentration in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on December 8-10, 2015. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.105	0.499	0.250	0.857	0.585	0.830	0.496
10 WW	0.105	------	0.679	0.592	0.323	0.396	0.399	0.600
20 WW	0.499	0.679	------	0.941	0.624	0.781	0.670	0.949
40 WW	0.250	0.592	0.941	------	0.431	0.619	0.504	0.863
5 D	0.857	0.323	0.624	0.431	------	0.785	0.952	0.624
10 D	0.585	0.396	0.781	0.619	0.785	------	0.846	0.811
20 D	0.830	0.399	0.670	0.504	0.952	0.846	------	0.674
40 D	0.496	0.600	0.949	0.863	0.624	0.811	0.674	------

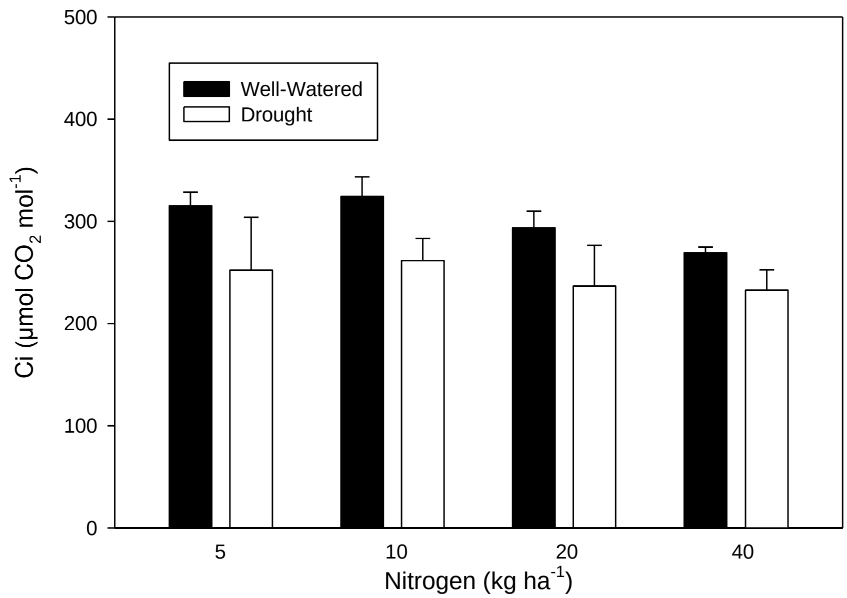

Figure 18. Intercellular CO_2 concentration in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on December 24-27, 2015. n=2-5. Error bars represent one standard error.

Table 15. P values from the t-test on Intercellular CO_2 concentration in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on December 24-27, 2015. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.756	0.422	0.011	0.419	0.168	0.262	0.058
10 WW	0.756	------	0.290	0.013	0.261	0.096	0.138	0.029
20 WW	0.422	0.290	------	0.131	0.487	0.301	0.297	0.077
40 WW	0.011	0.013	0.131	------	0.674	0.674	0.390	0.066
5 D	0.419	0.261	0.487	0.674	------	0.876	0.818	0.743
10 D	0.168	0.096	0.301	0.674	0.876	------	0.643	0.382
20 D	0.262	0.138	0.297	0.390	0.818	0.643	------	0.940
40 D	0.058	0.029	0.077	0.066	0.743	0.382	0.940	------

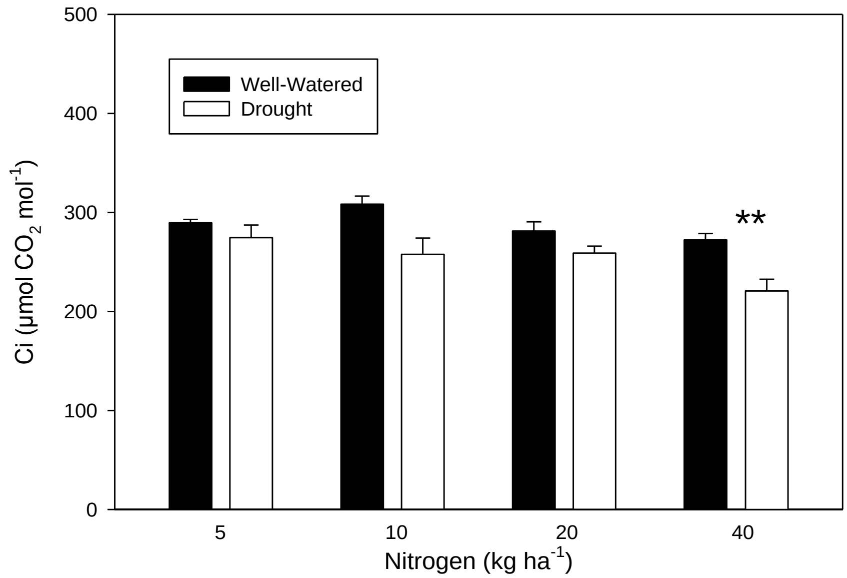

Figure 19. Intercellular CO_2 concentration in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on January 6-11, 2016. n=2-5. *P < 0.05 and **P < 0.01 for comparing water levels. Error bars represent one standard error.

Table 16. P values from the t-test on Intercellular CO_2 concentration in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on January 6-11, 2016. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.184	0.547	0.176	0.434	0.232	0.046	0.021
10 WW	0.184	------	0.094	0.014	0.090	0.051	0.01009	0.004
20 WW	0.547	0.094	------	0.446	0.695	0.281	0.129	0.016
40 WW	0.176	0.014	0.446	------	0.862	0.362	0.234	0.006
5 D	0.434	0.090	0.695	0.862	------	0.463	0.345	0.036
10 D	0.232	0.051	0.281	0.362	0.463	------	0.944	0.141
20 D	0.046	0.01009	0.129	0.234	0.345	0.944	------	0.049
40 D	0.021	0.004	0.016	0.006	0.036	0.141	0.049	------

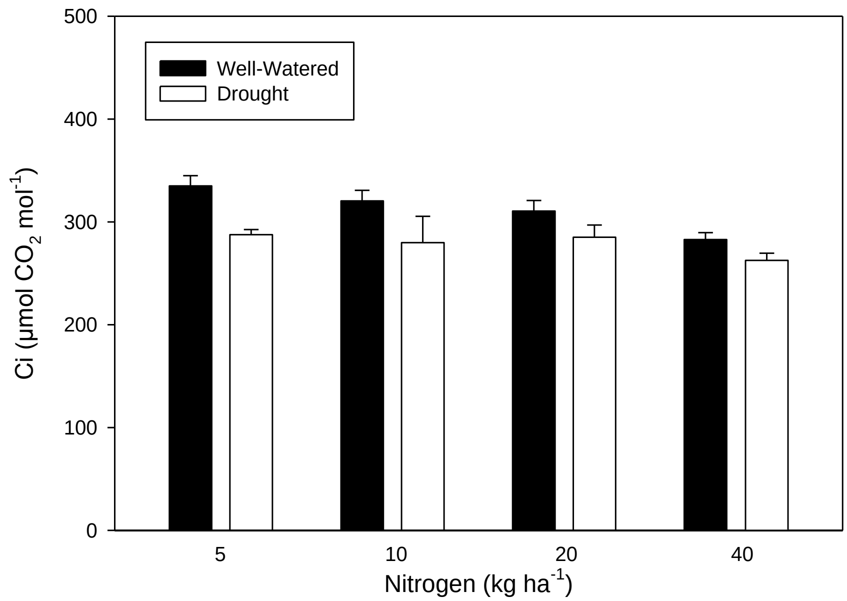

Figure 20. Intercellular CO_2 concentration in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels on January 20-22, 2016. n=2-5. Error bars represent one standard error.

Table 17. P values from the t-test on Intercellular CO_2 concentration in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels on January 20-22, 2016. n=2-5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.409	0.205	0.008	0.051	0.202	0.056	0.009
10 WW	0.409	------	0.537	0.018	0.099	0.216	0.084	0.009
20 WW	0.205	0.537	------	0.054	0.193	0.328	0.181	0.018
40 WW	0.008	0.018	0.054	------	0.698	0.891	0.861	0.095
5 D	0.051	0.099	0.193	0.698	------	0.832	0.901	0.085
10 D	0.202	0.216	0.328	0.891	0.832	------	0.844	0.549
20 D	0.056	0.084	0.181	0.861	0.901	0.844	------	0.195
40 D	0.009	0.0099	0.018	0.095	0.085	0.549	0.195	------

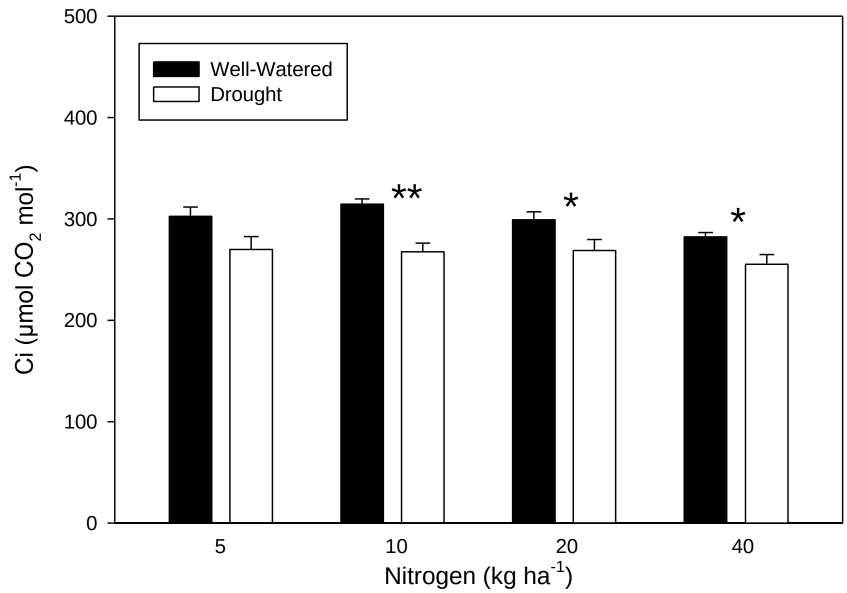

Figure 21. Average intercellular CO_2 concentration from the five sets of measurements in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels measured from November 2015 to January 2016. n=10-25.*P < 0.05 and **P < 0.01 for comparisons between water levels. Error bars represent one standard error.

Table 18. P values from the t-test on average intercellular CO_2 concentration in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels measured from November 2015 to January 2016. n=10-25. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.236	0.784	0.030	0.057	0.013	0.036	0.005
10 WW	0.236	------	0.116	<0.001	0.002	<0.001	0.001	<0.001
20 WW	0.784	0.116	------	0.049	0.047	0.012	0.027	0.003
40 WW	0.030	<0.001	0.049	------	0.216	0.098	0.141	0.015
5 D	0.057	0.002	0.047	0.216	------	0.964	0.907	0.486
10 D	0.013	<0.001	0.012	0.098	0.964	------	0.930	0.486
20 D	0.036	0.001	0.027	0.141	0.907	0.930	------	0.597
40 D	0.005	<0.001	0.003	0.015	0.486	0.486	0.597	------

Light Response Curves

The plants grown at the largest N levels had the highest photosynthetic rate at the light saturation point (Figure 22). The well-watered plants ranged from 3.913 to 7.277 μmol CO_2 m^{-2} s^{-1}. The drought stressed plants ranged from 4.937 to 6.16 μmol CO_2 m^{-2} s^{-1}. The plants grown at the greatest N levels had the largest light saturation point (Figure 23). The well-watered plants grown at 40 kg ha^{-1} N had a higher light saturation point than those grown under drought stress. The well-watered plants ranged from 297 to 575.5 μmol photon m^{-2} s^{-1}. The drought stressed plants ranged from 360 to 530 μmol photon m^{-2} s^{-1}. There is a statistically significant difference between the 5 kg ha^{-1} N and both the 20 and 40 kg ha^{-1} N. P values from the t-tests are provided in tables 19-20.

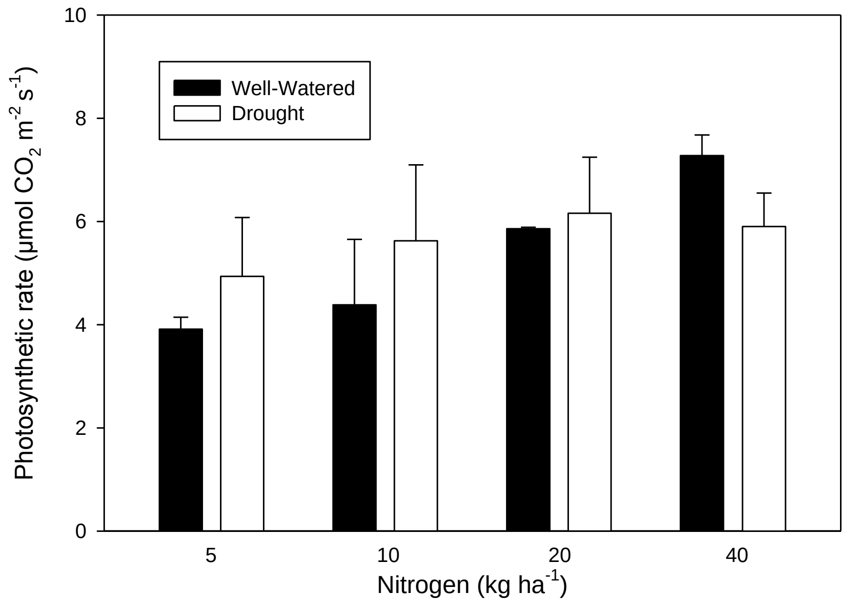

Figure 22. The light saturated photosynthetic rate in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels. Error bars represent one standard error.

Table 19. P values from the t-test on light saturated photosynthetic rate in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.751	0.013	0.018	0.471	0.370	0.180	0.102
10 WW	0.751	------	0.365	0.162	0.777	0.589	0.399	0.398
20 WW	0.013	0.365	------	0.071	0.504	0.888	0.807	0.953
40 WW	0.018	0.162	0.071	------	0.192	0.392	0.436	0.213
5 D	0.471	0.777	0.504	0.192	------	0.748	0.518	0.538
10 D	0.370	0.589	0.888	0.392	0.748	------	0.797	0.879
20 D	0.180	0.399	0.807	0.436	0.518	0.797	------	0.857
40 D	0.102	0.398	0.953	0.213	0.538	0.879	0.857	------

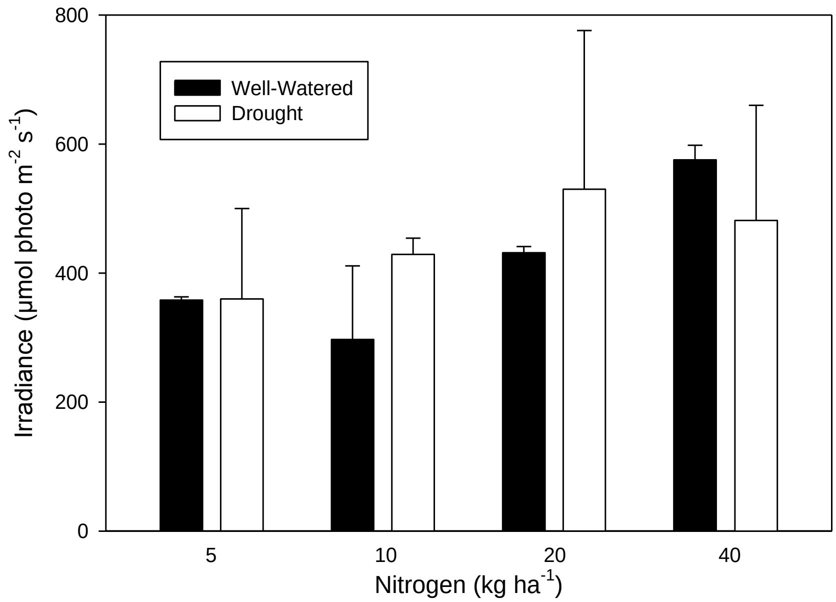

Figure 23. The light saturation point in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels. Error bars represent one standard error.

Table 20. P values from the t-test on light saturation point in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.646	0.021	0.011	0.990	0.108	0.557	0.561
10 WW	0.646	------	0.361	0.139	0.760	0.375	0.481	0.476
20 WW	0.021	0.361	------	0.028	0.661	0.934	0.728	0.806
40 WW	0.011	0.139	0.028	------	0.268	0.049	0.871	0.653
5 D	0.990	0.760	0.661	0.268	------	0.675	0.609	0.646
10 D	0.108	0.375	0.934	0.049	0.675	------	0.723	0.798
20 D	0.557	0.481	0.728	0.871	0.609	0.723	------	0.888
40 D	0.561	0.476	0.806	0.653	0.646	0.798	0.888	------

Morphology

Leaf Number and Area

The well-watered garlic mustard plants in the 20 and 40 kg ha^{-1} N treatment groups had the largest number of leaves per plant (Figure 24). The 20 kg ha^{-1} N treatment group had a peak at 15.2 leaves per plant (Figure 24) and averaged 14.4 leaves per plant (Figure 26). The 40 kg ha^{-1} N treatment group had a peak at 14.4 leaves per plant (Figure 24) and averaged 12.8 leaves per plant (Figure 26). The 40 kg ha^{-1} N treatment group had the highest increase in leaves over the course of the study.

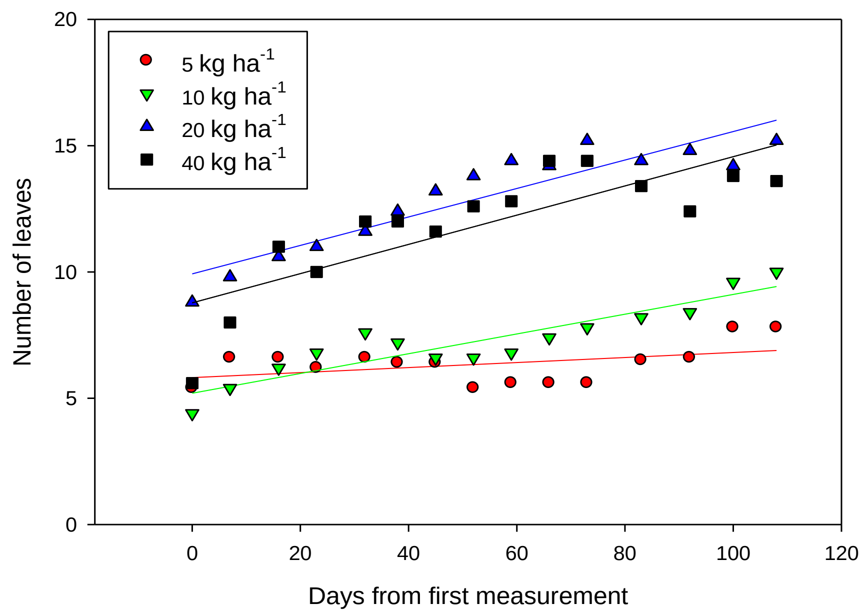

Figure 24. Average number of leaves per plant in well-watered garlic mustard plants grown at 5 (red symbols and line), 10 (green symbols and line), 20 (blue symbols and line) and 40 (black symbols and line) kg ha^{-1} N levels grown from September 2015 to January 2016. n=5.

The drought stressed garlic mustard plants in the 20 and 40 kg ha^{-1} N treatment groups had the largest number of leaves per plant (Figure 25). Although the difference in N treatments is smaller than it is in the well-watered plants. The regression lines exhibit a greater rate of leaf develop in the 20 and 40 kg ha^{-1} N. The 20 kg ha^{-1} N treatment group had a peak at 13.2 leaves per plant (Figure 25) and average averaged 11.5 leaves per plant (Figure 26). The 40 kg ha^{-1} N treatment group had a peak at 16.5 leaves per plant (Figure 25) and average averaged 9.7 leaves per plant (Figure 26). P values from the t-tests for average number of leaves (Figure 26) are provided in tables 21.

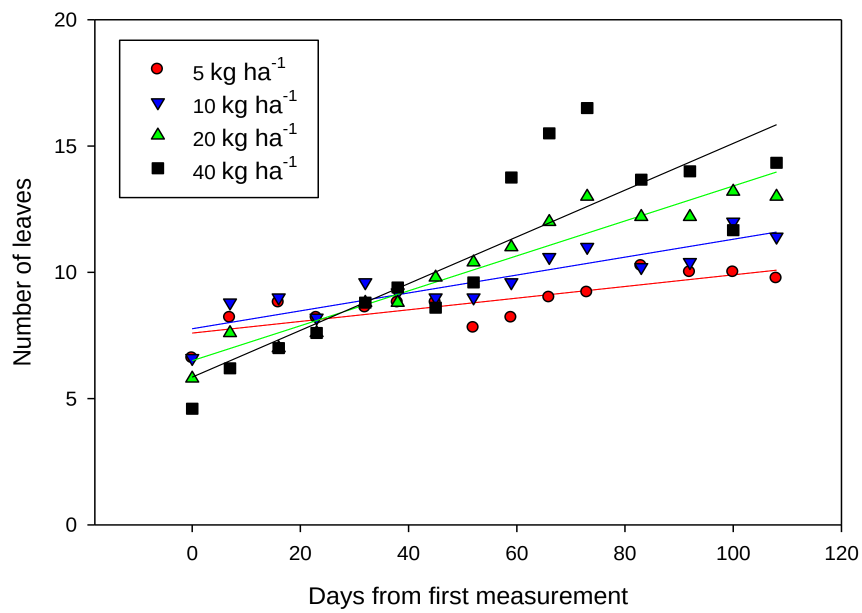

Figure 25. Average number of leaves per plant in drought stressed garlic mustard plants grown at 5 (red symbols and line), 10 (green symbols and line), 20 (blue symbols and line) and 40 (black symbols and line) kg ha^{-1} N levels grown from September 2015 to January 2016. n=5.

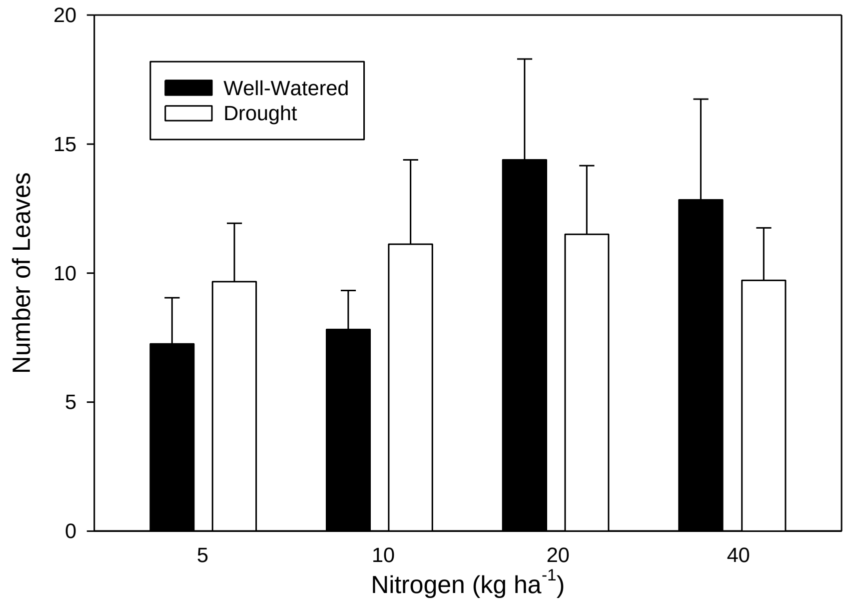

Figure 26. Average number of leaves per plant grown at 5, 10, 20 and 40 kg ha^{-1} N levels grown from September 2015 to January 2016. n=5. Error bars represent one standard error.

Table 21. P values from the t-test on average number of leaves per plant in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, 40 kg ha^{-1} levels grown from September 2015 to January 2016. n=5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.685	0.162	0.166	0.472	0.394	0.261	0.232
10 WW	0.685	------	0.215	0.230	0.674	0.528	0.372	0.349
20 WW	0.162	0.215	------	0.826	0.353	0.539	0.577	0.499
40 WW	0.166	0.230	0.826	------	0.415	0.650	0.705	0.609
5 D	0.472	0.674	0.353	0.415	------	0.773	0.639	0.674
10 D	0.394	0.528	0.539	0.650	0.773	------	0.905	0.971
20 D	0.261	0.372	0.577	0.705	0.639	0.905	------	0.914
40 D	0.232	0.349	0.499	0.609	0.674	0.971	0.914	------

The leaf area was on average higher in the 20 and 40 kg ha^{-1} N treatments for the well watered plants (Figure 27). An increase in leaf area over time is shown by the linear regression for 5 and 40 kg ha^{-1} N. 10 kg ha^{-1} N had the lowest leaf area in the drought stressed treatment groups (Figure 28). An increase in leaf area over time is shown by the linear regression for 5, 20 and 40 kg ha^{-1} N. There was not statistical difference between the N levels or drought and well-watered groups.

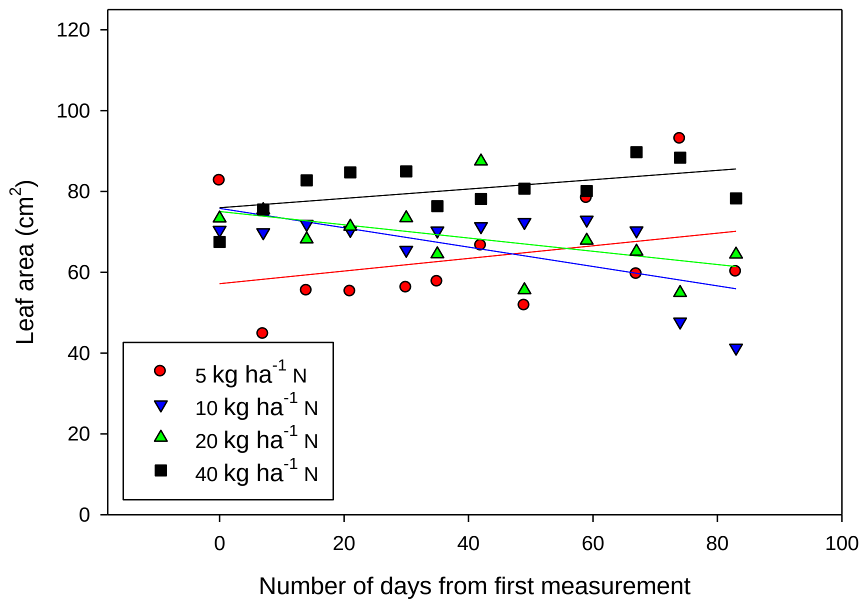

Figure 27. Leaf area of the youngest mature leaf in well-watered garlic mustard plants grown at 5 (red symbols and line), 10 (green symbols and line), 20 (blue symbols and line) and 40 (black symbols and line) kg ha^{-1} N levels grown from September 2015 to January 2016. n=5.

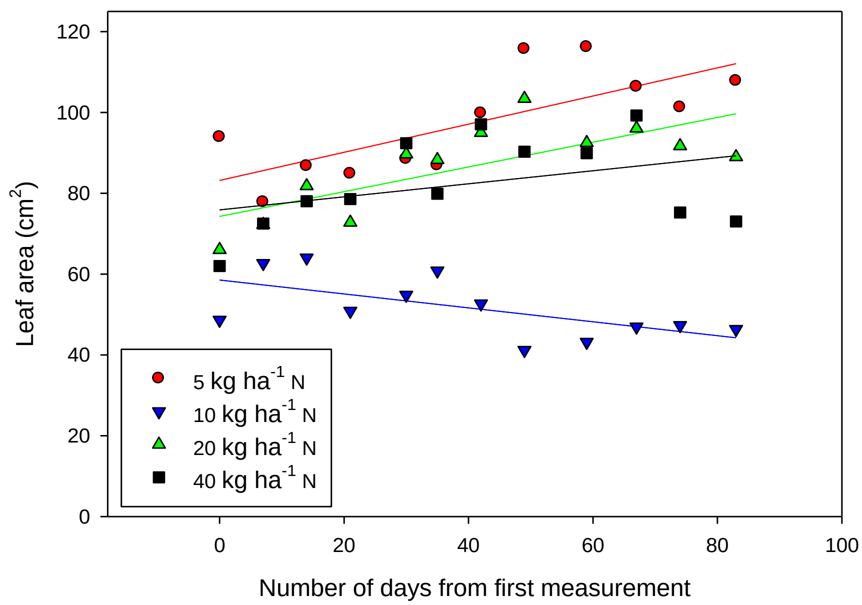

Figure 28. Leaf area of the youngest mature leaf in drought stressed garlic mustard plants grown at 5 (red symbols and line), 10 (green symbols and line), 20 (blue symbols and line) and 40 (black symbols and line) kg ha^{-1} N levels grown from September 2015 to January 2016. n=5.

Plant Height

The well-watered plants had an average growth rate of plant height of 1.18, 1.40, 2.38, and 3.62 cm matching the 5, 10, 20 and 40 kg ha^{-1} N, respectively (Figure 29). The drought plants had an average growth rate of plant height of 0.96, 1.64, 1.92, and 2.12 cm matching the 5, 10, 20 and 40 kg ha^{-1} N, respectively. The well-watered plants exhibit an increase in photosynthetic rate at each increasing N level. There is a statistically significant difference between the lowest two N treatments and the largest two treatments for the well-watered plants. The drought stressed plants demonstrate an increase in growth up until 20 kg ha^{-1} N and then level off at 40 kg ha^{-1} N .There is a statistical difference between the 5 kg ha^{-1} N treatment and the 20 and 40 kg ha^{-1} N treatments for the drought stressed plants. There were no statistical differences between the well-watered and drought stressed plants in the same N treatments. The total growth of well-watered plants ranged from 1.18 cm to 3.62 cm. The drought stressed plants total growth ranged from 0.96 cm to 2.12 cm. P values from the t-tests for all sets of measurements are provided in table 22.

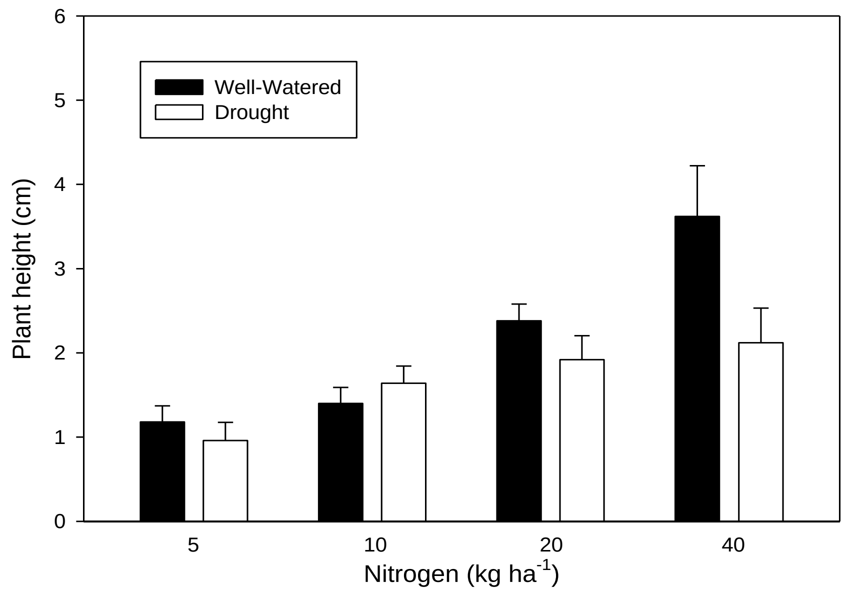

Figure 29. Total growth in plant height in well-watered (filled bars) and drought-stressed (open bars) garlic mustard plants grown at 5, 10, 20 and 40 kg ha^{-1} N levels from September 2015 to January, 2016. n= 5. Error bars represent one standard error.

Table 22. P values from the t-test on total growth in plant height in garlic mustard plants grown under well-watered and drought stressed conditions at N levels of 5, 10, 20, and 40 kg ha^{-1} levels grown from September 2015 to January 2016. n=5. WW= Well-watered plants. D= Drought stressed plants.

	5 WW	**10 WW**	**20 WW**	**40 WW**	**5 D**	**10 D**	**20 D**	**40 D**
5 WW	------	0.437	0.002	0.005	0.467	0.138	0.062	0.072
10 WW	0.437	------	0.007	0.008	0.164	0.414	0.166	0.150
20 WW	0.002	0.007	------	0.085	0.001	0.03	0.220	0.584
40 WW	0.005	0.008	0.085	------	0.003	0.014	0.034	0.073
5 D	0.467	0.164	0.001	0.003	------	0.051	0.027	0.037
10 D	0.138	0.414	0.03	0.014	0.051	------	0.446	0.327
20 D	0.062	0.166	0.220	0.034	0.027	0.446	------	0.700
40 D	0.072	0.150	0.584	0.073	0.037	0.327	0.700	------

DISCUSSION

Physiology

Garlic mustard plants grown at increasing N levels exhibited an increase in photosynthetic rate corresponding to N level increases. The well-watered plants responded with a steady increase in photosynthetic rate from 5 to 40 kg ha^{-1} N. The average photosynthetic rate increased 89.8% from the 5 to the 40 kg ha^{-1} N well-watered plants (Figure 9). The 40 kg ha^{-1} N treatment group was significantly higher than the 5 and 10 kg ha^{-1} N treatment group for every measurement (Table 1-6). The 20 kg ha^{-1} N treatment was significantly higher on average than the 5 and 10 kg ha^{-1} N (Table 6). However, the drought stress plants saw an increase in photosynthetic rate up to 20 kg ha^{-1} N and at the 40 kg ha^{-1} N the photosynthetic rate leveled off and even dropped slightly. There was a significant difference between the 40 kg ha^{-1} N in the well-watered and drought stressed plants (Figure 9). The well-watered 40 kg ha^{-1} N plant had a greater photosynthetic rate by 2.175 μmol CO_2 m^{-2} s^{-1} over the 40 kg ha^{-1} N drought stressed plants. This suggests that the plants were only able to utilize the increase in available N if they were not under drought stressed conditions. An increase in photosynthesis will lead to an increase in protein production for overall plant metabolism. Higher photosynthetic rates would be expected at ambient light levels for garlic mustard plants on the outskirts of a forested area in comparison to plants grown at full exposure in a greenhouse experiment (Dhillion and Anderson 1999).

Conductance, as expected, had a very similar pattern to photosynthetic rate. Higher stomatal conductance would be necessary to intake the CO_2 required for increased photosynthetic rates. The garlic mustard plants displayed an increased trend inconductance as N levels increased. Again, the well-watered plants demonstrated a steady increase for all N levels (Figure 15). The drought plants increased up to the 20 kg ha^{-1} N treatment and then reached a plateau.

Garlic mustard grown at higher N levels saw a decrease in internal CO_2 concentration (Ci). There was a significant difference between the two lowest N treatments and 40 kg ha^{-1} N well-watered plants. There is a statistical difference between the 10, 20, and 40 kg ha^{-1} N water treatments (Figure 21). The higher photosynthetic rates in the high N groups lead to low Ci values because the CO_2 is being used at a higher rate and less CO_2 is left in the tissues of the leaves.

The light saturation photosynthetic rate exhibits that higher photosynthetic rates are needed in order to reach the saturation point as the N level increases (Figure 22). There is a steady increase in light saturation photosynthetic rate between each N level. The 20 kg ha^{-1} N plants increased photosynthetic rate by 49.7% over the 5 kg ha^{-1} N plants. The 40 kg ha^{-1} N plants increased photosynthetic rate by 86% over the 5 kg ha^{-1} N plants. The differences between the 5 kg ha^{-1} N treatment and the 20 and 40 kg ha^{-1} N are significant. Increased N availability increases the maximum rate of photosynthesis garlic mustard can perform. The plants needed higher levels of light at increased N levels to achieve the light saturation point. The ability to receive necessary light levels are extremely important for the growth and usage of nutrients in garlic mustard plants (Meekins and McCarthy 2000). In most natural settings light levels should be sufficient to provide the necessary irradiance to reach the light saturation point, therefore allowing a higher rate of photosynthesis. An increase in light utilization efficiency aided by an increase in N would allow garlic mustard to photosynthesize at lower light levels. This will allow garlic mustard to perform photosynthesis for a longer period of time during the day. An increase in photosynthetic rate will help garlic mustard grow and spread at faster rates.

Morphology

Increase in biomass has been directly linked to an increase in nutrient availability (Meekins and McCarthy 2000). Addition of a key nutrient, such as, N would be expected to demonstrate a similar outcome. Garlic mustard increased the number of leaves as N levels increased in well-watered plants. The drought stressed plants did not display this pattern. The ability to increase the number of leaves indicates well-watered plants were able to take advantage of the extra N. An increase in leaves would be expected to correspond to an increase in water loss. Due to the need to preserve water, drought stressed plants were unable to utilize the extra N for production of leaves. The increase in leaves leads to an increase in total surface area, which means an increase in photosynthetic potential and, therefore, plant metabolism. When photosynthetic rates increase, garlic mustard is able to increase plant biomass.

Area of the youngest mature leaf fluctuated greatly. A new leaf reaching maturation and being smaller than the previous leaf caused a decrease in leaf area. Increases were seen when the youngest mature leaf died and a larger more mature leaf was measured. The youngest mature leaf was the smallest of the mature leaves. A plant with a large youngest mature leaf would have other mature leaves with even greater surface area. In the well-watered plants, 20 and 40 kg ha^{-1} N plants exhibit the highest leaf area. The plants with the greatest leaf area typically had the largest leaf number.

Garlic mustard demonstrated an increase in total growth from crown to leaf tip as N levels increased. The well-watered plants exhibited growth between each N level, while the drought stressed plants leveled off at the 20 kg ha^{-1} N. The increase in leaf number and area are expected to increase photosynthetic capabilities. An increase in photosynthesis will be directly linked with increased plant growth. Not all weed species benefit from N availability to the same extent (Blackshaw, Brandt et al. 2003). The ability to grow at an increased rate with an amplified amount of N will help garlic mustard spread and infest a forest community with increased atmospheric N deposition at a quicker rate.

Significance

The potential damage garlic mustard presents is amplified by an increase in atmospheric N deposition. Increasing N availability leads to a decrease in community diversity and dominance by a few species (Tilman 1987; Bobbink, Hicks et al. 2010). Garlic mustard has exhibited the ability to increase photosynthetic rates when N availability is increased. Garlic mustard has displayed an increase in leaf number and growth when provided with an increase in N. If garlic mustard benefits from continuing increases in atmospheric N deposition more than native species, then the negative impacts of garlic mustard will only increase. With changing precipitation patterns, it will be important to note if garlic mustard will have ample water supply to utilize an increase in N availability. Garlic mustard grows the most effectively in lowland areas and forest edges where water availability is high (Meekins and McCarthy 2001). However, garlic mustard does grow in drought stress conditions, but it is less effective in its growth and reproduction (Cavers, Heagy et al. 1979). Exotic invasive weeds, such as garlic mustard, cause extreme economic and ecological damage wherever they are established. Garlic mustard greatly decreases community diversity when present in an area and an increase in Shannon diversity occurs when it is removed (Stinson, Kaufman et al. 2007). A continual increase in atmospheric N deposition will increase the potential spread and growth rate of garlic mustard. This will only augment the damage garlic mustard will cause to the hardwood forests of Indiana and any area that it invades.

Future Study

Garlic mustard is an early season species. Will environmental changes such as increased N deposition and changes in precipitation patterns change garlic mustard's growing season? It will be important to know if these changes will allow garlic mustard to grow earlier or later in the season. It is possible that environmental changes will simply shift the growing period, but not extend it. This will be important to study because if garlic mustard is able to establish earlier in the season, it may have increased negative effects on the species that exit dormancy later in the season. A field study would be the next step in understanding the effects of environmental changes on garlic mustard and the ecological communities it inhabits. A possible study done in a hardwood forest would allow one to see the interactions between different species and how these interactions also affect the impact garlic mustard may have on a community. Variability in population density is a key factor in garlic mustard growth (Meekins and McCarthy 2000) and would be an important variable to study. This study would allow one to determine if garlic mustard benefits more from an increase in N availability than other invasive weeds.

CONCLUSION

As environmental changes continue to occur, it will be important to study how these changes will affect invasive plants. Management of invasive species will rely on the projected ability of invasive plants to grow in specific habitats (Luken and Mattimiro 1991). Many invasive species were introduced relatively recently, and we have not seen the extent of their spread. Little is known about many exotic invasive species. Continuing research on invasive species will be essential in combating their spread.

Garlic mustard has continued its spread across the United States since its introduction in the late 1800s. Increased N availability led to an increase in photosynthetic rate in garlic mustard. It is important to note that well-watered plants were capable of increasing photosynthetic rates between every N level while drought stressed plants leveled off after 20 kg ha^{-1} N. Garlic mustard was not able to utilize an increase in N past a certain point if it was under drought stressed conditions. This will be important in the future as precipitation patterns continue to change. The ability of garlic mustard to increase growth corresponded with the increase in photosynthetic rates. Plants grown at higher N levels displayed more growth than the plants grown at low N levels. Well-watered plants demonstrated more growth than drought stressed plants, and drought stressed plants continually displayed an inability to utilize N past a certain level. If atmospheric N continues to increase, then it can be expected that garlic mustard will increase growth and spread rates. If garlic mustard benefits more than native plant species, the potential for negative impacts to hardwood forests and the economy will increase.

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