Characterization of the Competitiveness of Autumn Olive in a Mature Forest

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Abstract

As a continuation of research done by Ritsema and Dornbos in 2006, the purpose of our research was to quantify the physiological competitiveness of Autumn Olive, a non-native, invasive shrub, in a mature forest habitat. In order to evaluate the invasion of AO, we quantitatively mapped the infestation level of Autumn Olive using a GIS. We then used this to identify variables that might enable land practitioners to identify and protect environments at risk of invasion. Habitats at highest risk were identified as those with degraded soils, those eroded, acidic, or sandy. We also measured AO's photosynthetic and water use efficiencies, and stomatal conductance across a broad range of light intensities in comparison with four native species. As its rapid invasion may predict, greater photosynthetic efficiencies were recorded for AO. Our final experiment assessed the efficacy of four methods of removal of AO from a heavily infested site within a mature forest location. Through understanding of Autumn Olive's competitive advantages, preventing its spread, and employing the most efficient method of removal, we hope to take one step toward maintaining a healthier, restored natural world.

Introduction

Autumn Olive (*Elaeagnus umbellate* Thunb.) is a shrub native to Asia and invasive in the United States, posing a particular threat to the Midwest. Also known as Oleaster or Japanese Silverberry, Autumn Olive (AO) was brought to the United States in 1830 and commercially propagated in 1963. AO was originally used to recover mine spoils, prevent erosion, or serve as a natural barrier for wildlife cultivation or simply for ornamental sake. Today, AO has spread to what is predicted by the Illinois Department of Conservation to be almost every county in the Midwest (Vegetation Management Guideline Autumn Olive 2005).

Motivation for our invasive species research was driven by concern for the overall health and productivity of natural ecosystems. Invasion of a non-native reduces the biodiversity of the plant community which in turn affects all biotic members of the ecosystem. Also, a reduction in the biodiversity in a habitat potentially correlates to reduced productivity and thus reduced carbon sequestration (Dr. Leah Knapp, Olivet College; personal communication). Optimizing carbon fixation rates of plant communities represents a major method of addressing the rapid rise in atmospheric carbon dioxide concentration along with reducing emissions, potentially reducing negative impacts on the environment, particularly those associated with global warming. Consequently, something as seemingly non-threatening as invasion of a non-native species represents one important element in the development of a global crisis. Like many non-native, invasive species, Autumn Olive has presented itself as one such element due to its apparent competitive advantages; however, through informed land management consisting of preventative measures and efficient removal, one element of such a threat can be disarmed.

Part of AO's capacity for invasion includes its recently discovered physiological strength for tolerance in both shaded and sunny habitats. At Pierce Cedar Creek Institute in Barry County, AO has been observed in high density in both open meadow and mature, upland forest. Research done by Ritsema and Dornbos in 2006 quantified AO's photosynthetic strength in both habitats. They found AO to fix carbon faster than any of the native species in the meadow. Likewise, similar trends were found for AO in the forest at photosynthetic active radiation (PAR) over 600 µmol/m^2/s (Ritsema and Dornbos, 2007[MI Academy abstract]).

As a continuation of this previous research, we sought to further quantify AO seedling competitiveness in comparison with four native tree seedlings attempting to recruit a mature forest canopy. We thus divided the project into three experiments. In the first experiment plant communities throughout the PCCI land area were characterized by AO infestation level. These geographic areas were characterized by soil, light, and canopy characteristics, and physiological performance of several species in each location. These factors were then analyzed to determine which most significantly correlated to the presence of AO in order to predict habitats at high risk of its invasion. The second experiment was a single location from which we were able to compare light and water use efficiencies, stomatal conductance, and chlorophyll content of AO seedlings in comparison to Beech, Black Oak, Black Cherry, and Red Maple seedlings. Our third and final experiment compared the efficacy of four methods for removal of AO and restoration of the natural forest habitat.

Methods

Characterizing communities

Using a Thales Mobile Mapper Global Positioning System, the upland forest of Pierce Cedar Creek was classified into communities according to the density of Autumn Olive present. Communities were classified as having a density of AO being high, moderate, low, or none. These classifications were quantitatively determined according to the distance of one AO plant to another. AO within ten paces, or approximately 20 feet, of another were determined to be high; 10-20 paces (or about 20-40 feet) was called moderate; more than 20 paces apart but having AO present in the habitat was called low; and no AO present was called none.

Following classification, the data was analyzed using ArcView GIS 9.1 to determine the spread of AO via comparison to the study done at PCCI by Travis and Wilterding in 2005. Using these data, groupings of each infestation level were identified for the property and the community epicenters of high, moderate, low, or none density were mapped. Three replicates of the four community types were identified and flagged using GPS system. Each of these community replicates was characterized as follows: Leaf Area Index (LAI), soil moisture, soil pH, soil composition, and soil type, as well as light and water use efficiency of AO, Beech, and White Ash. Only Beech and Ash were used in the communities classified as having no AO present.

Again using the TPS-1 gas exchange meter (PP Systems, Inc.) CO_2 uptake, leaf temperature, leaf transpiration, and quantum light flux (of the auxiliary light) for two replicates of Autumn Olive, Beech, and White Ash were measured at each community site. The PAR corresponding to one quarter of full ambient light was selected for comparison of light use efficiency in each community. A complete set of measurements were collected on two different days.

Soil samples were taken removing a column of soil using a soil probe. Six columns were collected in a circular fashion at a radius of approximately 20 m from the epicenter of each community site. These samples were then sent to A & L Great Lakes Laboratories, Inc. for testing.

LAI was also measured using a Nikon camera with a mounted fish-eye lens and analyzed using a Gap Light Analyzer version 2.0 software program to quantify pixel darkness. Three pictures were taken in a triangular fashion around the outside of each community site.

Using the Statistix 7.0 software program, data was analyzed to compare the significant differences between variables and treatments according to their means square values, probability of significance, and standard deviations accounting for error and variability.

Study site

The study site was located in a 230 m^2 area on a sloping hillside of an Oak-Beech forest. The site was located approximately ten meters west of a walking trail at Pierce Cedar Creek Institute. The hillside was characterized as having a two percent slope and a Coloma loamy sand soil type. Five replicates of Autumn Olive and four native species—Beech, Black Oak, Black Cherry, and Red Maple—were tagged for analysis. The selected replicates were all classified as juveniles with a height less than 1.5 m and implying an age of less than three years.

Irradiance was controlled using the auxiliary light source of a Flight LT lamp associated with the portable TPS-1 gas exchange meter (PP Systems, Inc.). Light levels were obtained using a combination of metal and plastic mesh filters that yielded Photosynthetic Active Radiation (PAR) of approximately (1)1000, (2)475, (3)200, and (4)60 µmol of photons $m^{-2}s^{-1}$. The goal of these levels was to mimic ambient light at full amount along with approximately half, a quarter, and at very low levels, reflecting the irradiance available in the deep forest.

Under these light levels, measurements of CO_2 uptake, leaf temperature, leaf transpiration, stomatal conductance, and quantum light flux (of the auxiliary light) were recorded using the TPS-1 gas exchange meter. Data for all 25 plants were taken within a one day period on five different days. Following these treatments, two replicated days of further measurements were taken of the 25 plants under lower light levels in effort to focus the photosynthetic activity at levels characteristic of the deep forest. Actual photosynthetic active radiation (PAR) levels were measured by the quantum light flux of the gas exchange meter as approximately 40, 30, 15 or 0 µmol of photons $m^{-2}s^{-1}$ (accounting for light levels 5 and 6). Although some light could be seen visually to reach the leaf, the reading of 0 of photons $m^{-2}s^{-1}$ was attributed to insensitivity of the quantum light flux meter at such low light levels. Data was also taken for CO_2 uptake under the control of no available light (7). Using these measurements, light and water use efficiency, identified as two of the primary limiting factors in competition and survival in plants, were calculated.

To further quantify the physiological strengths of Autumn Olive, chlorophyll content and natural quantum light flux were also measured for each replicate plant at this study site. Chlorophyll content was measured using a Minolta Chlorophyll Meter SPAD-502 for all 25 plants plus 5 replicates of white ash for comparison. Readings were taken of the top and bottom of two leaves on each replicate. Quantum light flux was also measured using a Li-Cor LI-191SA Line Quantum Sensor. The meter-long quantum sensor was held above each plant to measure the average ambient light coming through the canopy, accounting for sun flecks.

Removal and Restoration

An area of the Oak-Beech forest classified as a high density community was used to quantitatively compare the efficacy of four methods for removal of AO. Two concentrations of Glyphomate (glyphosate at 20.5% and 41%) as well as Crossbow (34.4% 2, 4-D and 16.5% triclopyr) were applied in the same fashion. AO plants of approximately 3-5 cm in diameter were randomly selected as a Completely Randomized Design with 25 replicates. The plants were cut at the base and immediately treated by saturating the surface of the stump with the herbicide using a sponge brush. The treated stumps were then marked with flagging to enable their relocation for re-growth assessment. The final method was insertion of copper tacks into the base of adult AO plants. Two copper plated tacks were nailed into the plant at least deep enough to break into the cambium layer. Finally, 25 plants were flagged as control plants to assess normal attrition rates.

Results and Discussion

Characterizing communities

The first hopes of characterizing community habitats according to the density of AO present was to quantify the spread of AO across PCCI since the property was surveyed by Travis and Wilterding in 2005. Due to the different methods of community surveying, the validity of the results may be weakened although the overall importance of the experiment is still present. For our survey, we used the classification method explained earlier and added all of the data points taken, seen in Figure 2, which were attempted to be recorded to evenly cover the forested area. We then found percentage of communities recorded as none, low, moderate or high. We then converted Travis and Wilterding's data so that our results could apply to the earlier survey. In their study, all of PCCI was surveyed as opposed to only the upland forest in our study. We therefore went through charts in the final write up for Travis and Wilterding, deleting areas of surveyed wetland and meadow habitat. The classification system used by Travis and Wilterding, as seen in Figure 1, was also converted. In their key absent became none, less than 25% became low, 26-50% became moderate and 50-100% density became high. Table 1 was then developed from the results.

Analysis of these results indicate that AO has apparently spread over the last two years both by increasing in frequency in already infested areas and by colonizing new territory. Areas classified in 2005 as moderate have become high; lows have become areas of moderate density. North of Cloverdale Rd. we see an increase in the ‘high’ density by 38% and by 21% south of Cloverdale Rd. This marks spread of AO by an increase in frequency. We also see some areas of no AO present in 2005 now invaded. This spreading is marked by a 12.5% decrease in the ‘none’ density north of Cloverdale Rd. and by 15% south of Cloverdale Rd. since 2005. Particular interest is due in the location of our study site and the nearby area of the removal experiment. Today the surrounding area is characterized by a very high density; in 2005 Travis and Wilterding recorded the area as none or low density. This only helps to emphasize Autumn Olive’s potential to spread even in a mature forest community.

Community factors were then analyzed using step-wise regression to identify factors significantly correlated to the presence of and recruitment by AO. Most significant factors related to the quality and composition of the soil. Soils with lower percent organic matter, relating to a lower cation exchange capacity (CEC) were closely associated with higher densities of AO. Likewise, parts per million of potassium and percent base saturation of calcium were inversely related to the presence of AO. Also, though not identified as a significant factor, lower pH’s were associated with higher AO density. This correlation is worth noting as AO was observed in and around pine forest communities at the Wege Nature Conservancy in Lowell, MI (personal communication).

All of these factors regarding soil quality collectively point at degraded soils as the most significant characteristic of a forest habitat for the spread of AO. Less organic matter, less CEC, and less available potassium and calcium are all indicative of sandy soils. The pH factor then expands this to the general title of degraded soils. Degraded soils are commonly composed of sandy soil textures through which organic matter is rapidly drained. Due to the weaker negative charge associated with the less surface area of the sand particles, these types of soils are unable to hold water, organic matter, or nutrients. These soils, according to D'Antonio will lower the resistance of the native species to non-native invasion and increase the disturbance of the habitat (Dr. Carla M. D'Antonio, University of California Santa Barbara. Eminent Ecologist seminar, 2007). Like many invasive species, AO has been observed to thrive in such disturbed habitats (Vegetation Management Guideline Autumn Olive 2005).

Though this correlation was observed in the forested areas, we have observed that the relationship may be consistent with observation of other habitats as well. Examples of such degraded soils and disturbed habitats may include mining spoils, edges of highways, or highly eroded or chemically treated soils. Also the increasing threat from pollution including acid rain may play a role in the spread of AO now and in the future.

Study Site

After general quantification of the invasion of AO and the contributing factors, the second experiment provided more intricate analysis of AO's physiological advantages. CO_2 uptake rate, as an assessment of net photosynthesis rate, is indicative of the basal growth rate of each plant and species. Across the seven light levels used, AO demonstrated a CO_2 uptake rate significantly higher than for any of the native species for the highest five light levels. (See Table 3)   It is also understandable that the lowest light levels (6 and 7) could be associated with lower CO_2 uptake as AO would likely employ a higher rate of respiration associated with its usual faster nitrogen fixation. However, as it is the higher light levels that are vital in driving seedling survivability, these low light levels are of less importance.

Autumn Olive's capacity for higher CO_2 uptake at a given PAR indicates greater light use efficiency (as shown in Figure 8) across the full spectrum of light intensities available within the mature forest canopy. Some advantage concerning light use of AO was hypothesized due to its high density in the deep, upland forest where light is a limiting factor. One sought distinction was whether AO was actually capable of a faster rate of photosynthesis or it simply out competed native species for colonization in the available sunflecks made by gaps in the forest canopy. Measurement of the quantum light flux for each replicate helped to rule out the latter possibility. (See Table 6) Measured ambient light flux data was not higher for AO, suggesting that AO does not necessarily colonize in sun flecks. As a result, we concluded that the capability of greater light use efficiency was AO's advantage over the limiting factor of light availability in the forest. How AO possesses such an advantage was the next focus of our research.

Measured chlorophyll content of the replicates in part supported an explanation for these higher rates of photosynthesis characteristic of AO. As shown in Table 4, AO measured significantly higher chlorophyll content on both the top and bottom surfaces than any of the native species.   Chlorophyll use efficiency (CUE), which was calculated as the quotient of CO_2 uptake rate divided by the chlorophyll content of individual plants, was greater for AO than any of the native tree seedlings evaluated. Chlorophyll use efficiency was calculated for CO_2 uptake rates at light levels 1 (1000 μmol/m^2/s) and 4 (60 μmol/m^2/s). The differences between CUE values of the different species was statistically significant with AO being much more efficient at light level 1, however the CUE differences at the lower light level 4 did not show statistical significance. This observed difference is hypothesized to be due to the different levels of available photosynthetic enzymes in each species, which is the capacity of the leaf to process increasing light levels effectively. At low light levels it is understandable for CUE to be similar among species as the rate of photosynthesis is more limited by the available light than by the enzymes available within the plant; thus we see less margin in the efficiency of the use of chlorophyll among species. Though we still see differences in the rates of photosynthesis due to the concentration of chlorophyll present, the use efficiency of this chlorophyll is more similar. However, at high light levels, the surplus of available light places the photosynthetic rate determining step on the availability of photosynthetic enzymes, in particular Rubisco, to efficiently use the energy molecules produced during the light reactions, or, inability of the plants' photocenters to process available light into energy molecules.

Consequently, with hopes of further analysis, we hypothesize that it is the greater availability and concentration of enzymes such as Rubisco or membrane proteins of the electron transport system, working along with the greater chlorophyll content that gives AO its potential for faster photosynthesis and thus faster growth. The potential for greater concentration of Rubisco or membrane proteins in the leaves of AO could link to its nitrogen fixation capability. More available nitrogen to the plant allows for greater production of proteins such as enzymes like Rubisco. A post-experiment leaf collection was done for the purpose of testing the leaves of AO and the native plants for their protein content. Likewise, final soil samples were pulled close to and away from AO contributed to the same goal of characterizing AO's nitrogen fixation capabilities.

Also from the data taken by the gas exchange meter, we see that the efficiency of the stomatal conductance was also higher for AO. Shown in Figure 9, AO was able to take in more CO_2 than the native species for the same dilation of the stomates. Though AO does show higher efficiency of stomatal conductance, the large error bars subtract from the strength of the advantageous finding. Curiously though, while more efficient stomatal conductance would imply less water lost for the CO_2 taken in, AO actually showed lower water use efficiency than the natives. As shown in Table 8, transpiration for AO is higher than the natives. Therefore, water use efficiency, or the amount of CO_2 taken in for the amount of water lost is lower for AO than the native species.

Despite this disadvantage of high transpiration, we have observed AO thriving in very dry, sandy soils. The ability to compete in these habitats implies that AO may have a more extensive root system than the native species. The ability of the root system to reach available, surrounding water may compensate for the lower water use efficiency by the leaves.

Comments

Future Analysis

In preparation for future analysis, further soil sampling and leaf sampling was done. The final soil sampling was done in effort to measure the available nitrogen in the soil close to the base of an AO and away in order to quantify the nitrogen fixation capabilities of Autumn Olive. Five replicates of soil samples both close to and away from AO were collected for testing. Also 10 cm^2 leaf material was collected from each replicate seedling (plus White Ash) at the study site were collected with plans to more specifically analyze the chlorophyll and protein content of the leaves of Autumn Olive as a result of its nitrogen fixing capabilities in comparison to the natives.

Additional Variables

Other variables deserve consideration in their potential to influence our research at PCCI. One important variable was rainfall. According to the National Weather Service, Barry County, like many in southwest Michigan suffered a level 1 drought this summer. Level 1 indicates "a moderate drought. Damage to vegetation and a high fire risk. Streams… reservoirs and wells are low." However, these dry conditions only emphasize AO's ability to compete in disturbed environments and the strength of its extensive root system.

Another observed variable for consideration was a fungal pathogen that began parasitizing juvenile Black Oak plants. What appeared as juveniles with healthy leaves at the beginning of the summer became shredded and scarred by the end.

Conclusion

From the community experiment and the study site, we were able to quantify the competitiveness of Autumn Olive seedlings in comparison to native species to recruit a mature forest. Characterizing communities helped us to evaluate the spread of AO in the forest habitat over two years time. This experiment also indicated the strong correlation between high AO density in an environment and soils of poor quality, in particular sandy soils. Knowing that AO is more likely to thrive in degraded soils helps biologists watch habitats of high risk. Identified areas of high risk may help prevent the spread of AO in the future, which is a strong factor in the battle of restoration.

From the study site, the research as a continuation of the project done the previous year by Ritsema and Dornbos, confirmed the trend found by Ritsema. Autumn Olive is capable of a faster rate of photosynthesis for the given light availability. This means that AO has higher light use efficiency than the native plants with which it competes. It also has greater chlorophyll content and what was observed to be greater chlorophyll use efficiency at PAR. This CUE is hypothesized to be due to greater Rubisco content in the leaves as a result of AO's capability to fix nitrogen. Also data from the study site implied that AO must employ a more extensive root system than native species to thrive in such a dry environment despite its lower water use efficiency.

Although the final experiment on removal and restoration cannot be analyzed presently, future analysis will be valuable in comparison of the efficacy of herbicides and removal methods for restoring natural areas and fighting the spread of Autumn Olive.

Acknowledgements

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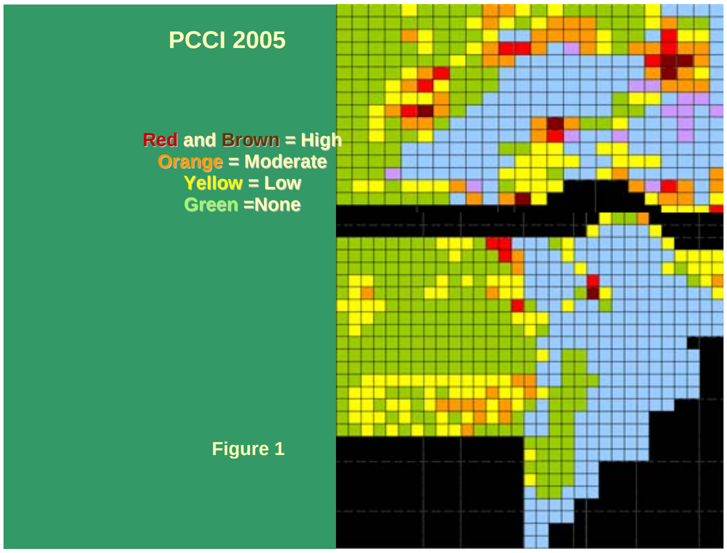
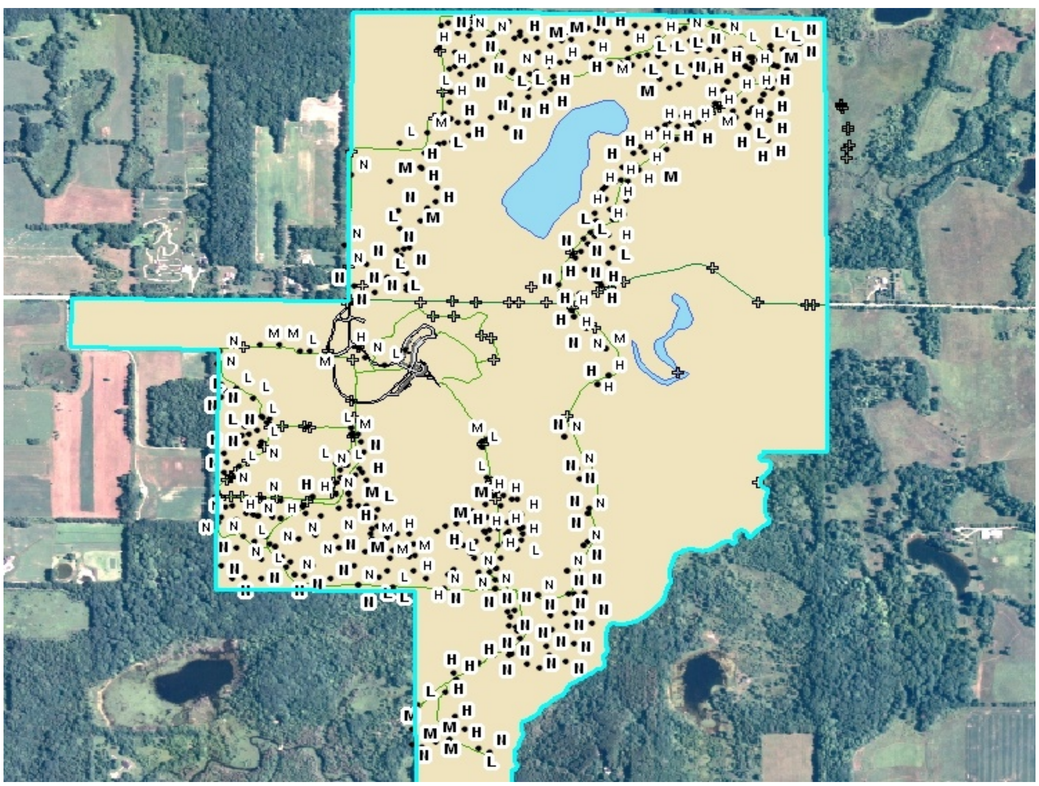

PCCI 2005
Red and Brown = High
Orange = Moderate
Yellow = Low
Green =None
Figure 1



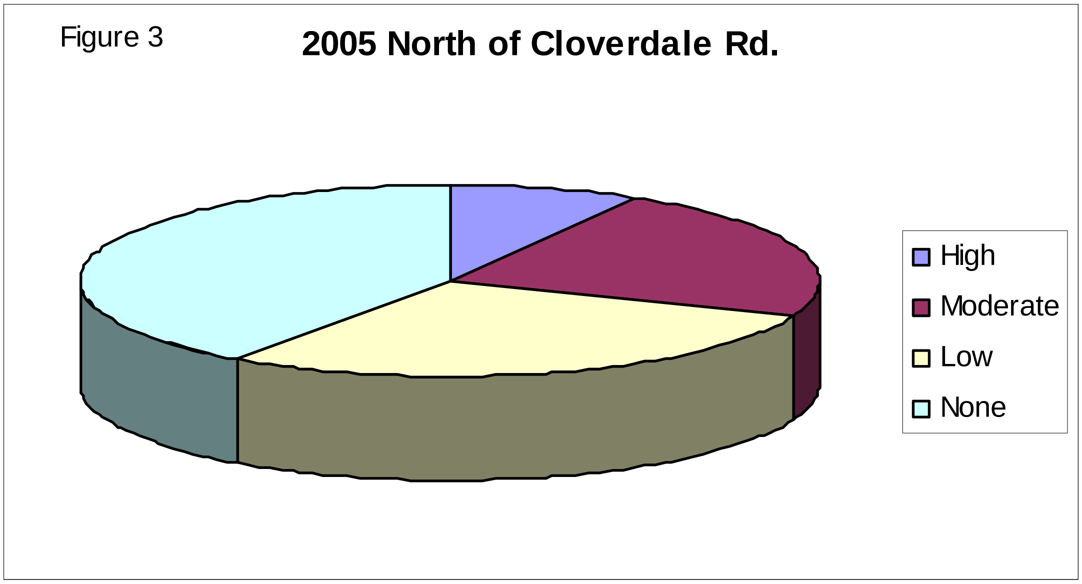


Figure 3
2005 North of Cloverdale Rd.
High
Moderate
Low
None

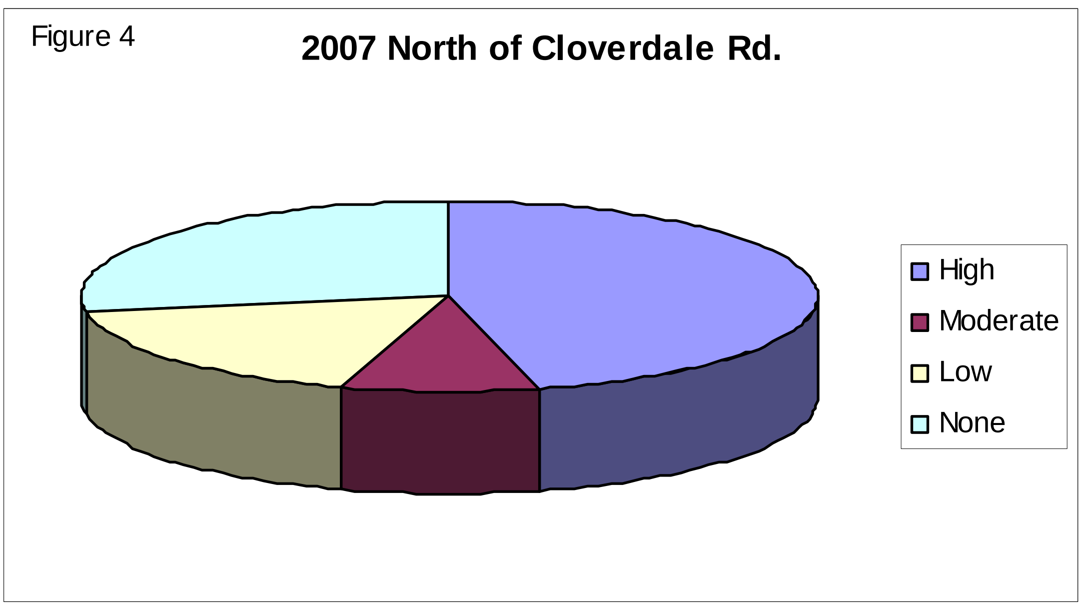
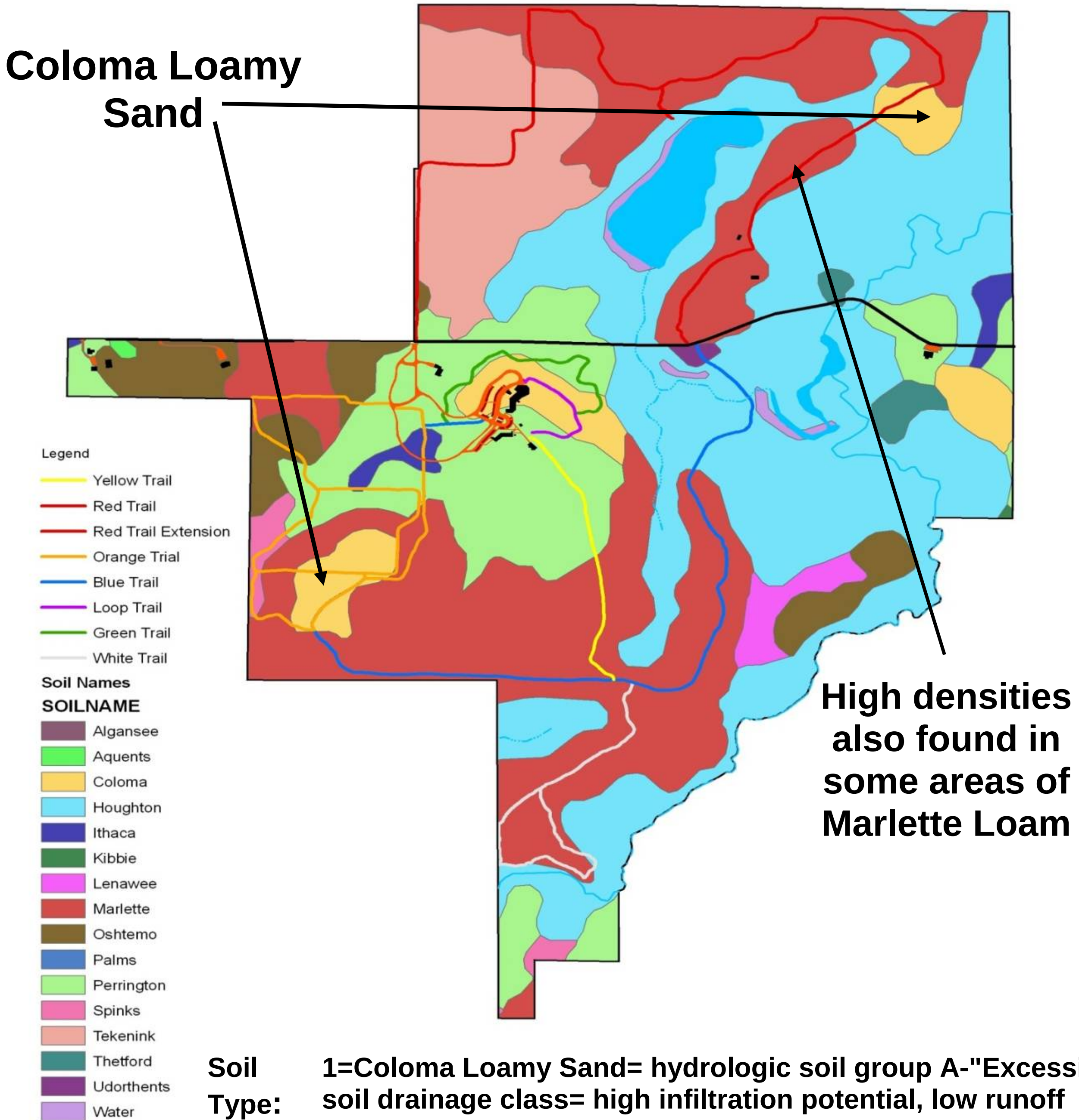


Figure 4
2007 North of Cloverdale Rd.
High
Moderate
Low
None



Soil Type:

1=Coloma Loamy Sand= hydrologic soil group A-"Excessive" soil drainage class= high infiltration potential, low runoff potential

2=Marlette Loam= hydrologic soil group B-"Well" soil drainage class= not hydric soil type

Figure 6

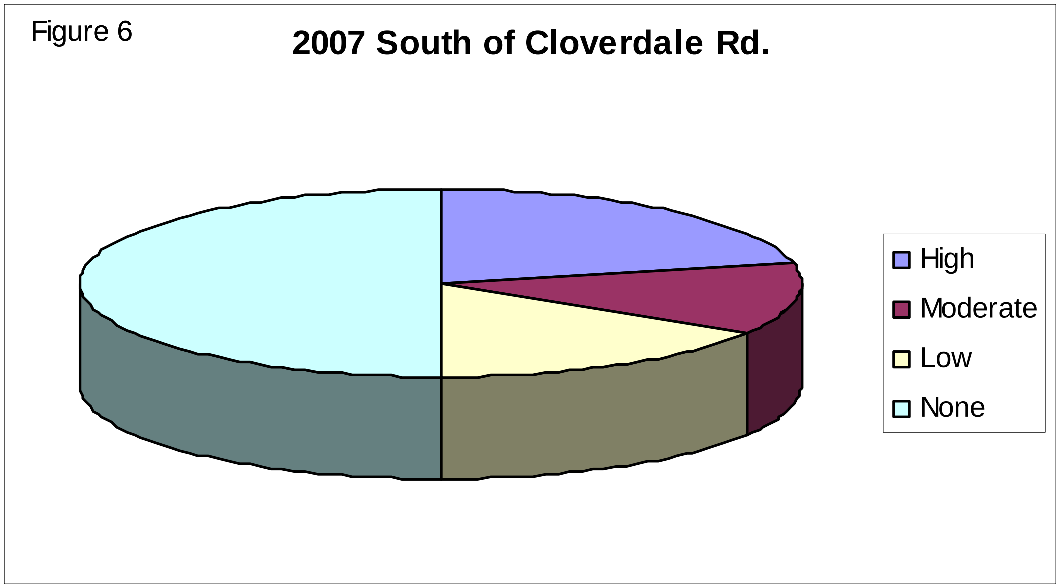
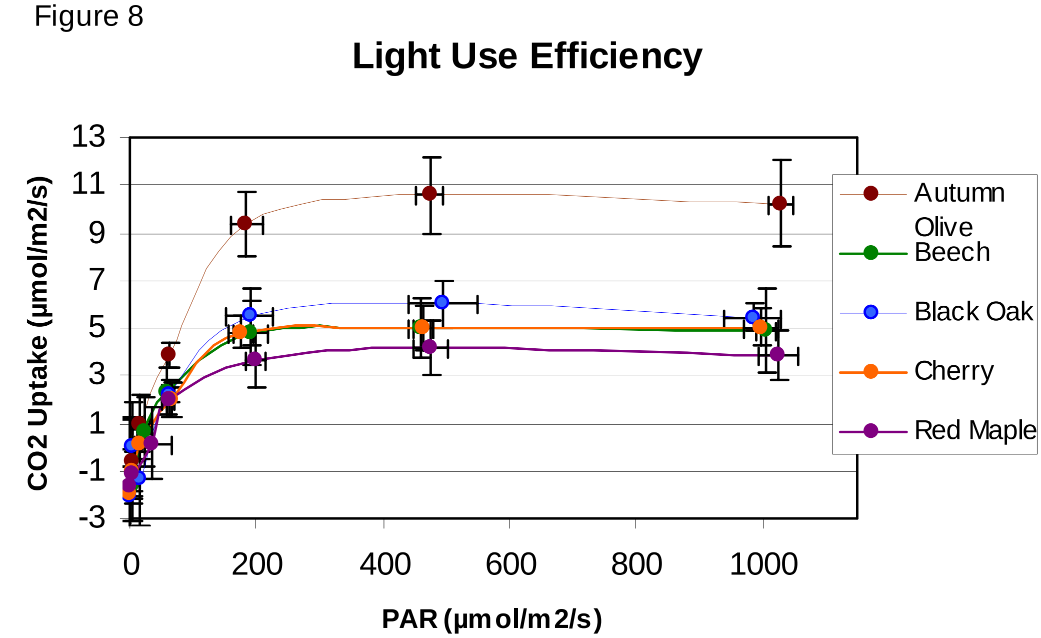


Figure 8



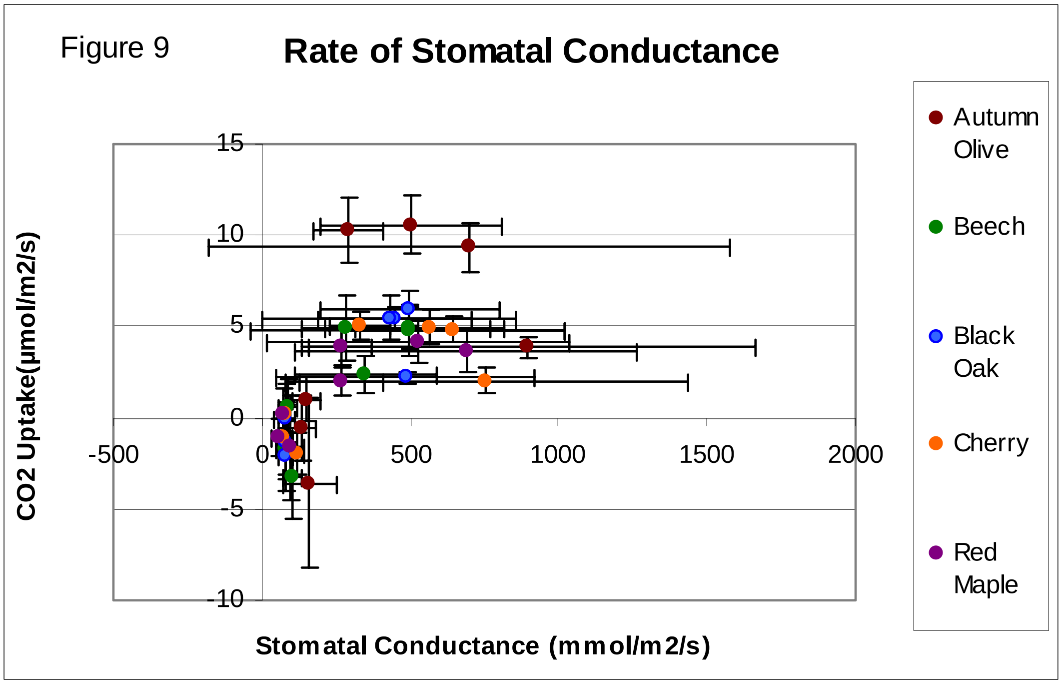


Figure 9
Rate of Stomatal Conductance
CO2 Uptake(µmol/m2/s)
Stomatal Conductance (mmol/m2/s)
15
10
5
0
-5
-10
-500
0
500
1000
1500
2000
Autumn Olive
Beech
Black Oak
Cherry
Red Maple

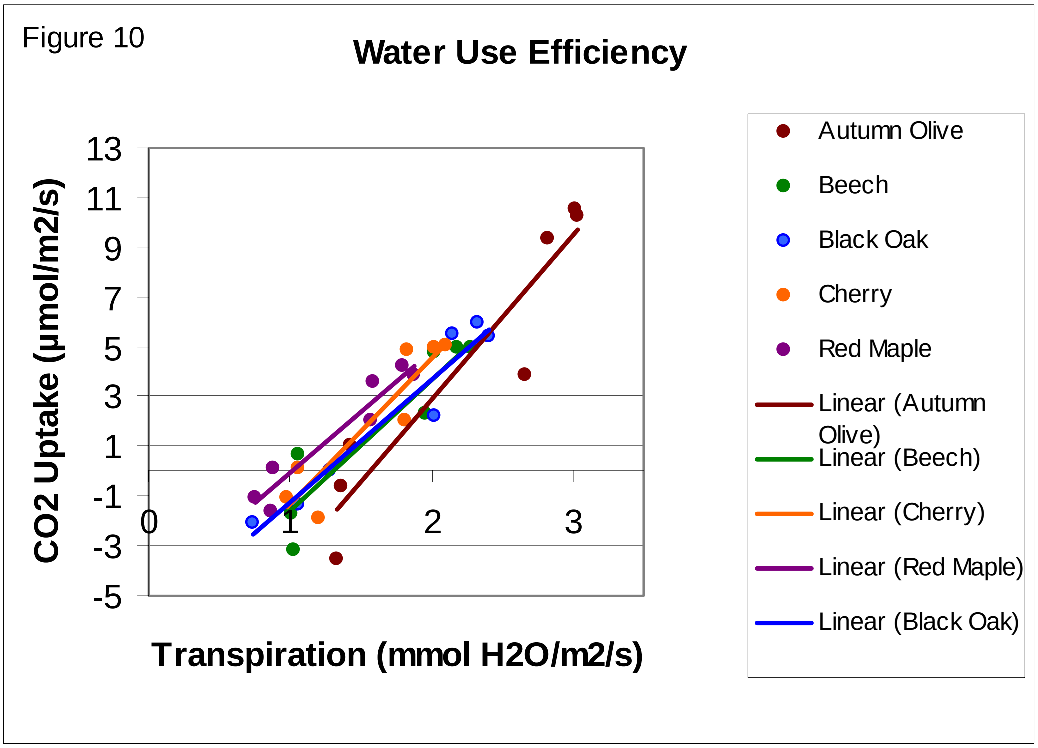


Figure 10
Water Use Efficiency
CO2 Uptake (µmol/m2/s)
Transpiration (mmol H2O/m2/s)
13
11
9
7
5
3
1
-1
-3
-5
0
1
2
3
Autumn Olive
Beech
Black Oak
Cherry
Red Maple
Linear (Autumn Olive)
Linear (Beech)
Linear (Cherry)
Linear (Red Maple)
Linear (Black Oak)

Table 1		Data from Travis and Wilterding 2005	
		North	South of Cloverdale Rd.
High	1.0%	8.30%	1.0%
Moderate	6.9%	22.80%	6.9%
Low	27.0%	28.60%	27.0%
None	65.2%	40.30%	65.2%
		Data from Edwards and Dornbos 2007	
		North	South of Cloverdale Rd.
High	21.80%	46.10%	21.80%
Moderate	12.0%	8.70%	12.0%
Low	16.20%	17.40%	16.20%
None	50.0%	27.80%	50.0%

Table 3	CO2 Uptake				
Light level	Autumn Olive	Beech	Black Oak	Black Cherry	Red Maple
1	10.24	4.92	5.46	5.048	3.88
2	10.56	4.98	6	4.98	4.2
3	9.36	4.76	5.48	4.84	3.62
4	3.86	2.34	2.2	2.02	2.02
5	1	0.64	-1.31	0.16	0.15
6	-0.58	-1.67	0.01	-1.03	-1.11
7	-3.56	-3.18	-2.06	-1.92	-1.62

Table 2 Step-wise regression

Community	Replicate	VWC	Distance(m)	LAI
High	1	4.7	9	1.637
High	2	7.8	2.5	1.427
High	3	4.5	28	1.7
Moderate	1	3.3	59	1.843
Moderate	2	11	50	2.55
Moderate	3	7.5	111	1.813
Low	1	7.8	68	1.643
Low	2	8.7	64	2.093
Low	3	3.2	45	2.493
None	1	12.5	25	2.55
None	2	10.8	17	1.563
None	3	4.2	45	1.613

Table 2 continued

pH	SoilType	Mg(ppm)	K(ppm)	Ca(ppm)	Soil %Organic Matter	CEC	Bray-P1(ppm)
5.3	2	35	51	100	1.2	2.1	60
5.6	1	55	65	150	1.8	2.6	28
5.1	1	25	32	100	1.4	2	58
5.9	2	85	91	450	3.1	4.4	6
5.8	2	125	93	550	2.6	5.2	14
5.6	2	70	86	250	2.5	3.3	6
5.7	2	110	67	550	3.4	5	20
6	2	135	64	750	3.6	6.2	17
5.9	2	135	100	800	4.2	6.6	13
6.4	2	140	100	1250	4.1	8.9	27
5.8	2	85	106	550	3	4.9	23
5.6	2	95	139	500	4	4.8	16

Table 2 continued

Percent Base Saturation			
%K	%Mg	%Ca	%H
6.2	13.7	23.6	56.5
6.5	17.8	29.1	46.6
4.1	10.5	25.1	60.3
5.3	16.1	51.2	27.3
4.6	19.9	52.6	22.9
6.8	17.9	38.4	36.9
3.1	18.2	54.7	23.9
2.6	18	60.1	19.2
3.9	17.1	60.8	18.2
2.9	13.1	70.4	13.5
5.5	14.4	55.8	24.3
7.4	16.3	51.6	24.8

Key: Soil Type

1=Coloma Loamy Sand= hydrologic soil group A-
"Excessive" soil drainage class=
high infiltration potential, low runoff potential

2=Marlettle Loam= hydrologic soil group B-
"Well" soil drainage class= not hydric soil type

Table 4 Chlorophyll content

	Autumn Olive	White Ash	Beech	Black Oak	Black Cherry	Red Maple
Top Surface	44.6	25.4	31.0	35.6	30.1	30.4
Bottom Surface	43.4	24.7	29.7	34.5	28.6	29.3

Table 5 Chlorophyll Use Efficiency

	Autumn Olive	Beech	Black Oak	Black Cherry	Red Maple
At light level 1	0.2637	0.2107	0.1953	0.2153	0.1754
At light level 4	0.1239	0.1232	0.1055	0.1256	0.1303

Table 6 Quantum Light Flux

Autumn Olive	White Ash	Beech	Black Oak	Black Cherry	Red Maple
24.658	20.282	46.002	17.478	20.154	15.948

Table 7 Stomatal Conductance

Light level	Autumn Olive	Beech	Black Oak	Black Cherry	Red Maple
1	290.04	283.88	447.24	331.52	264.76
2	503.56	494.28	496.4	566.24	527.76
3	700.28	493.24	430.64	642.04	689
4	896.8	350.12	483.6	757.48	268.88
5	147.7	86.1	79.5	78.3	71.8
6	133.8	80.1	79.2	75.4	58.6
7	158.4	102.4	81.4	117.6	94.6

Table 8 Transpiration

Light level	Autumn Olive	Beech	Black Oak	Black Cherry	Red Maple
1	3.0396	2.2744	2.4036	2.11	1.8768
2	3.0188	2.1852	2.3248	2.0204	1.7924
3	2.8184	2.018	2.1568	1.8312	1.5888
4	2.6652	1.9616	2.0284	1.8152	1.5792
5	1.429	1.054	1.053	1.057	0.88
6	1.363	1.018	1.28	0.979	0.762
7	1.334	1.028	0.744	1.21	0.866