

Plant community light efficiency: measuring light response as a function of both photosynthesis irradiance curves and leaf traits

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Full Time independent research

Summer 2014

Abstract

Light response is a unique plant trait that is caused by a species level adaptation to a particular light environment and leaf morphology. By ignoring individuals and focusing on communities as a whole, I was better able to understand how irradiance levels shape plant life. I measured some key characteristics of light responses: dark respiration, maximum rate of photosynthesis, and light compensation point as functions of light environment, reduced light environment, and leaf traits. The leaf area of the dominant species has a strong relationship to light compensation point and the maximum rate of photosynthesis of the community. Leaf mass per area had a negative correlation to dark respiration rates. The association between the leaf traits and light response characteristics demonstrated how communities respond to differences in irradiance levels.

Introduction

In changing landscapes, newly dominated by trees or buildings, shade tolerance is an important factor in determining the composition of the understory. Studies have focused on individual species mechanisms to shade tolerance, but there has not been many looking at the community-level production and light efficiency in induced shade. Studying shade tolerant communities and the effects of novel shade on intolerant communities will provide insight on the physiological mechanisms that permit or inhibit communities to thrive in the understory.

Phenotypic plasticity is the activation or methylation of specific genes from stressors in the environment that alter the phenotype. These specific genes affect the phenotype of the individual to potentially increase their fitness. Environmental cues that are more important to fitness are likely to induce a highly plastic response. In this case, the importance of irradiance to plant metabolism has evolved a high phenotypic plasticity response to light changes (Delagrange et al. 2004, Sultan 2000).

When some species are exposed to low light it stimulates the shade avoidance syndrome (SAS) which causes carbon to be sent to the stem for elongation at the expense of root and leaf development (Smith 1992). Herbaceous species that do not have the morphological capabilities to grow above these superior competitors must occupy the shaded understory niche. In this niche, low irradiance is commonly the limiting component (Chen et al. 1996). These species have developed proteins that inhibit SAS (Sesa et al. 2005), preventing allocation of carbon to their stem where it would not provide them increased fitness canopy. Instead, through natural selection these plants have evolved to have low trait values of leaf mass per area (LMA), stomatal density, and root to shoot ratio in shaded environments (Valladares 2008). These traits suggest that shade tolerant plants invest more energy into synthesis of broad thin leaves to capture the limited irradiance through the canopy. They have also evolved physiologically to have low dark respiration rates and fluorescence (Valladares 2008). Low dark respiration rates conserve nutrients within the plant when the plant is in an environment without irradiance. Individuals under certain canopy structures may encounter very low irradiance levels throughout the day depending on their location. By having low dark respiration rates, they will not lose a significant amount of carbon through respiration. Low fluorescence reduces the amount of light being reflected. This trait would increase fitness in an environment where the irradiance levels are high and the water is limited because it would reduce photo inhibition and the loss of carbon. It is also advantageous to have low fluorescence in environments where there is low irradiance so they can capture all the available sunlight. The most significant consequence of shade tolerant plant adaptations are lowered light compensation points (LCP) and increased rates of photosynthesis at lower light levels (Givnish 1988). These traits support the theory that shade

tolerance evolved to minimize the loss of CO₂ instead of maximizing carbon gain (Craine & Reich 2005, Walters & Reich 2000). This relates to the lack of photosynthetic active radiation (PAR) present. A shade intolerant species would have higher respiration rates under low PAR. Conversely, shade tolerant species will have much lower respiration rates and be able to photosynthesize in low irradiance environments where intolerant species might still be respiring. The Photosynthesis irradiance (PI) curve (figure 1) is the relationship between the irradiance level and the rate of photosynthesis or respiration. It can be used to assess the individual adaptation to a particular light environment and to predict how the individual will respond to a particular irradiance level. To my knowledge, this is the first study to measure the PI curves of entire communities and not just one individual. In order to make statements about the entire community light response, PI curves of individuals cannot be used. They have a narrow inference space. By measuring the entire community, I am controlling for interspecific and intraspecific variation in light response and seeing how the community responds as a whole. The photosynthesis irradiance (PI) curve is essential to analyzing sun and shade adaptation of an individual (Bjorkman 1981). There are four points on the PI curve that can be used to determine the characteristics of the plant: the light compensation point (Fig. 1-A), initial slope (Fig 1-B), photosynthesis maximum (P_{max})(Fig.1-C), and light saturation point(Fig.1 D). The LCP, found at the x intercept, is the minimal PAR required by the plant to absorb more carbon dioxide than it is releasing. The initial slope is known as the photosynthetic efficiency. It is the rate of photosynthesis at a low PAR. Shade tolerant species will have a higher efficiency at a lower PAR than intolerant species and reach maximum photosynthesis (P_{max}) sooner. The P_{max} is the point where increased PAR will not increase the rate of photosynthesis, it is also known as the light saturation point. A tradeoff exists between performing a high rate of photosynthesis at a low rate and having a high P_{max}.

Questions

How do light response curves of meadow communities differ from understory communities? How plastic is the response of the meadow communities to decreased PAR? How do the traits of the dominant species drive the differences in light response curve characteristics between communities?

Hypotheses

The light response curves of the understory communities will have lower light compensation points, lower respiration rates in complete darkness, and lower P_{max}. The dominant species in the understory communities will have lower LMA than the dominant of the meadow communities. The artificially shaded community will shift the characteristics of its light response curve towards the characteristics of a shade tolerant community.

Methods

Study site

The study was located at Rocky Mountain Biological Laboratory in Gothic, Colorado (30°57' N, 106°59' W, 2900 m elevation). There will be two distinct areas within the study site: the open meadow and inside the aspen stand.

Light Treatment groups

In this study, there were three distinct groups: two meadow and one aspen understory. Each group was composed of five .5x.5 m plots. The two meadow group transects ran parallel to each

other down a slope. At the completion of the initial measurements, one meadow group was artificially shaded using a shade cloth that allows 70% of ambient light to pass through. The other meadow group was not shaded and was used as a control for seasonal change between the three week period between measurements. The understory group was located in an adjacent aspen forest. The groups were labeled as the

Carbon flux vs irradiance measurements

Before the manipulation of the artificial shade group, an initial PI curve will be calculated for all plots using data from carbon flux measurements with varying PAR. Each CO₂ concentration measurement included the PAR it was taken at. I used a PAR sensor connected to a data logger to measure the internal light conditions of the tent ecosystem so that I can compare this to my ambient measure. Ambient CO₂ will be measured using a Li-Cor 7500 infra red gas analyzer for thirty seconds. The tent will be placed over the plot and the rate of change of carbon dioxide concentration in the tent which represented an overall uptake to the ecosystem (photosynthesis) or a release to the atmosphere (respiration) will be measured for 60 seconds. After the measurement, the tent will be removed and the plot will be allowed to return to ambient levels of CO₂. During this time period, an additional layer of tent material will be placed over the tent to decrease internal PAR. The carbon flux will again be measured for 60 seconds. This process of adding darkening fabrics will repeat until the tent internal environment is completely dark. For each plot there will be measurements at five decreasing light levels and one at complete darkness. I used a reflective blanket to reduce the temperature that the darkening tarp would cause inside the tent ecosystem. Each measurement will only be done with no cloud cover in order to promote consistent PAR levels between light level layers between plots.

Creating the PI curves

The six unique light levels and carbon flux measurements created six coordinates of irradiance and linear NEE. With these six points I was able to fit a quadratic line using Microsoft Excel.

Light compensation point

The light compensation point is the area where the plant community stops respiring and begins to photosynthesize. This point is indicative of tolerance to low light levels as well as good predictor of a species ability to survive under a canopy (Givnish, 1988). A low light compensation point allows the plant community to begin photosynthesis at a lower irradiance level. The artificially shaded meadow group will address if this trait is highly plastic. To find the light compensation point, I used the equation of the quadratic curve. The light compensation point will always have an irradiance level of 0, it will be the x intercept of the line. The equation can be solved by assigning $y = 0$.

Maximum rate of photosynthesis (Pmax)

The Pmax of the PI curve is the section of the line when it levels off at a light level that causes highest rate of photosynthesis. In this experiment, the Pmax will not be calculated as the photosynthetic rate at the light saturation point. Most of the calculated PI curves do not have this characteristic light saturation point. Instead, these lines are linear or exponential. In either case, an alternate method had to be used to calculate Pmax. I used the highest linear NEE out of the six measurements as the Pmax.

Leaf Traits

In each plot, five leaves were sampled from the dominant species after the late season measurements. Dominance was determined by visually estimating the species with the most biomass. Each leaf was measured for wet weight and scanned for leaf surface area. Then they were put into an oven at 65°C for at least twenty four hours to dry. After drying, I recorded the dry mass and calculated the leaf dry mass per area (LMA).

Data analysis

Shade and time

I performed a MANOVA repeated measured analysis to determine the effects of shade, time, and the cross effect of shade and time. I compared the early season pre-manipulation calculations from the two meadow groups of light compensation point, dark respiration, and Pmax to the late season post manipulation calculations. The understory communities were excluded from the analysis due to only one measurement.

Leaf traits

I used a linear regression to determine how LMA and leaf area predict light compensation point, dark respiration, and Pmax. I also performed an ANOVA to determine the differences in LMA and leaf area between plots and treatments.

Results

Shade and time

Light compensation point significantly increased due to time ($F=0.9287423$, $p=0.0260$). The LCP did not change due to shading or the cross of shading and time (Table 1)(fig 2). Dark respiration rates (fig.3) and Pmax (fig.4) did not significantly change due to time, shading, or the cross of shading and time (Table 1).

Leaf traits

LCP had a positive relationship with leaf area ($F=94.8120$, $p<0.0001$)(fig. 5), but had no relationship with LMA ($F=2.7528$, $p=0.1021$). Dark respiration decreased as LMA increased ($F=13.2601$, $p=0.0005$)(fig.6). Dark respiration had no correlation with leaf area (Table 2). Pmax significantly decreased with increasing leaf area ($F=18.7247$, $p<0.0001$)(fig.7). Pmax had no relationship with LMA (Table 2)

Discussion

How do meadow communities differ from understory communities?

The novelty in measuring community wide PI curves produced results that contradicted what was expected to be found between shade adapted communities and sun adapted communities. I hypothesized that the sun and shade communities to have similar PI curves to figure 8. As in the classical economic theory (Bjorkman et al 1972) the meadow communities should have had higher rates of Pmax, dark respiration, and LCP. I found that while the meadow communities did have higher rates of both Pmax and dark respiration, it had a lower LCP than the understory group. Since the understory group has survived in low irradiance levels for years, I assumed that it would take less light for them to begin photosynthesizing. However, four out of five plots (fig. 31,32,34,35) never reached the point of photosynthesis under my light levels. This could be a result of the irradiance levels not being high enough, but that would go against the idea of understory community survivorship in low irradiance, instead it is possible that an environmental

factor caused this. One factor to be looked at in future studies could be the role of soil moisture and respiration.

How plastic is the response of meadow communities to decreased PAR?

The factor of shading was not significant, but shade plot 3 (fig.33) showed significant response. It shifted its dark respiration point towards what I would expect a shade plant to look like. The dark respiration rate before the shading was $-17.113 \text{ umol CO}_2 / \text{m}^2 \text{ s}^{-1}$. After the shading it was $-7.043758798 \text{ umol CO}_2 / \text{m}^2 \text{ s}^{-1}$. This plot shifted about $+10 \text{ umol CO}_2 / \text{m}^2 \text{ s}^{-1}$ while the average shift was around $+3 \text{ umol CO}_2 / \text{m}^2 \text{ s}^{-1}$. This is a great example of a major community response in a short amount of time. I cannot say that this was solely done through a plastic response to the decreased irradiance because the shading treatment was not statistically significant throughout the treatment group. It was not a product of time or the cross between time and shade. This particular plot is evidence that a highly plastic response to become more shade tolerant is possible. On a group scale, I do not think there was enough time for a plastic response like shade plot 3. While there is one example of a rapid response, phenotypic plasticity is usually stronger in juvenile plants so that they may change their phenotype while they are still developing to have the highest fitness in that particular light environment (West-Eberhard, 1989). My study could have more accurately tested community plasticity if it was a long term study. If the shade structures were up long enough for the plants to grow new leaves that could have a greater plastic response than the mature leaves, there could have been a larger shift in the community PI curves.

How do the leaf traits of the dominant species drive the differences in PI curve characteristics between communities?

The most surprising result was that the LCP was positively related to leaf area. This result went against everything I thought about shade tolerance and adaption. It contradicts the idea that plants are creating wider and longer leaves in order to capture a higher percentage of the limited irradiance coming through the canopy so that they can stop losing carbon and start photosynthesizing. This relationship could be a result of the two *Ligusticum poreri* dominated plots that did not respire. Since their area is about eight times larger than any other dominant plant and they did not photosynthesize, it was a statistically heavy weight that could have caused this seemingly hypocritical result.

The inverse linear relationship between dark respiration levels and LMA is supported by a study done by Reich et al (1997). One of explanation of this trend could be that plants in higher irradiance environments have higher LMA (Givnish, 1979). In that case, there would be a correlation between high LMA and increasing dark respiration rates. This would an unfair assumption based off the idea that sun adapted plants also have higher darker respiration rates due to their physiology. In my study, there was no significant differences in LMA between groups ($F=0.1312$, $p=0.7182$) (fig. 9) so I am confident that LMA is a good predictor of dark respiration levels across communities.

Pmax was negatively correlated with leaf area. Leaf area in the understory was significantly larger than the meadow community ($F=28.4174$, $p<0.0001$)(fig. 10). All the leaves that were sampled were from the dominant specie. This shows that a high leaf area is needed to thrive in the understory. This correlation also matches the theory that shade plants have adapted to survive in low irradiance as a tradeoff for Pmax.

Bjorkman, O. (1981). Responses to different quantum flux densities. In 'Physiological Plant Ecology. I. Responses to the Physical Environment'. (Eds O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler.) *Encycl. Plant Physiol. New Ser.*, Vol. 12A, pp. 57-107. (Springer-Verlag: New York.)

Bjorkman, O., M.M. Ludlow, and P.A. Morrow. 1972. Photosynthetic performance of two rainforest species in their native habitat and analysis of their gas exchange. *Carnegie Institute of Washington Year Book* 71:94–102.

Chalker, B. E., W. C. Dunlap, and J. K. Oliver. P-I curves for *Acropora digitifera* from a depth of 1m and *A. divaricata* from a depth of 40m (after Chalker et al., 1983). Digital image. *Reefkeeping.com*. N.p., n.d. Web. 13 Aug. 2014. <<http://reefkeeping.com/issues/2007-01/atj/index.php>>

Chen, H. Y. H., Klinka, K., and Kayahara, G. J. 1996. Effects of light on growth, crown architecture, and specific leaf area for naturally established *Pinus contorta* var *latifolia* and *Pseudotsuga menziesii* var *glauca* saplings. *Can. J. For. Res.* 26:1149–1157.

Craine JM, Reich PB. 2005. Leaf-level light compensation points in shade-tolerant woody seedlings. *New Phytol.* 166:710–13

Delagrange S, Messier C, Lechowicz MJ, Dizengremel P. 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiol.* 22:775–84

Givnish, T. J. 1979. On the adaptive significance of leaf form. In O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven [eds.], *Topics in plant population biology*, 375–407. Columbia University Press, New York, New York, USA.

Givnish TJ. 1988. Adaptation to sun and shade: a whole-plant perspective. *Aust. J. Plant Phys.* 15:63–92

Morris, Tom E. (2009). [Photosynthetic irradiance curve]. [Graph]. Retrieved from http://morriscourse.com/elements_of_ecology/chapter_6.htm

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* 94: 13 730–13 734.

Sessa, G. et al. (2005) A dynamic balance between gene activation and repression regulates the shade avoidance response in *Arabidopsis*. *Genes Dev.* 19, 2811–2815

Smith, H. (1992) The ecological functions of the phytochrome family. Clues to a transgenic programme of crop improvement. *Photochem. Photobiol.* 56, 815–822

Sultan SE. 2000. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.* 5:537–42

Valladares, F., & Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, 39(1), 237.

Walters MB, Reich PB. 2000. Trade-offs in low-light CO₂ exchange: a component of variation in shade tolerance among cold temperate tree seedlings. *Funct. Ecol.* 14:155–65

West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* 20:249–278

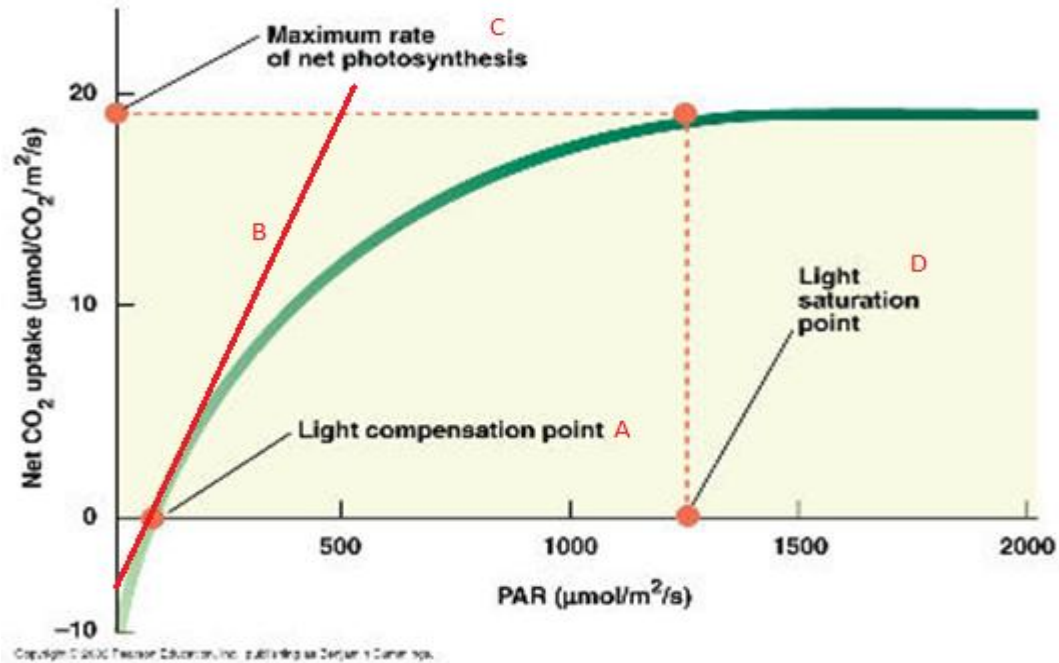


Figure 1 (Photosynthetic irradiance curve with main points of interest)(Morris, 2009)

	Time	Shade	Time x Shade
LCP	F=0.9287423, p=0.0260*	F=0.013393, p=0.7518	F=0.0512524, p=0.5399
Dark respiration	F=0.0959358, p=0.4065	F=0.1677497, p=0.2801	F=0.0083796, p=0.8022
Pmax	F=0.0154174, p=0.7345	F=0.2006913, p=0.2408	F=0.0005044, p=0.9509

Table 1 (Statistical results of treatments on PI curve characteristics)

	LMA	Leaf area
LCP	F=2.7528, p=0.1021	F=94.8120, p<0.0001*
Dark respiration	F=13.2601, p=0.0005*	F=1.1768, p=0.2816
Pmax	F=0.8305, p=0.3651	F=18.7247, p<0.0001*

Table 2 (Statistical results of leaf traits on PI curve characteristics)

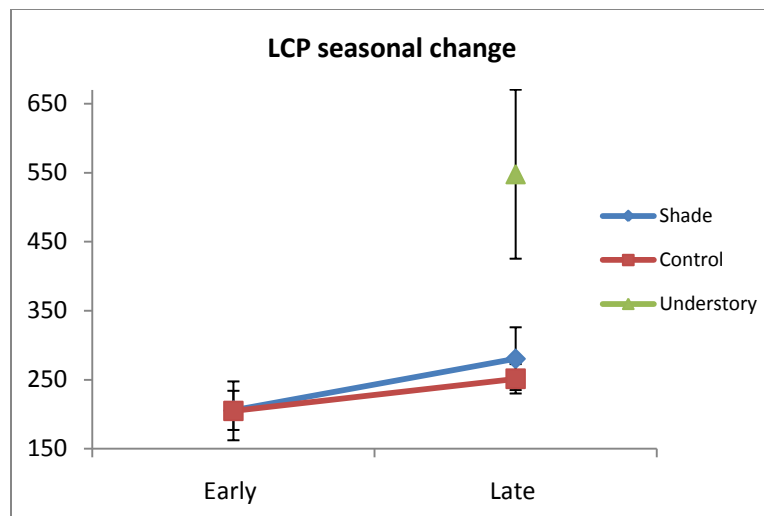


Figure 2 (Seasonal change of LCP)

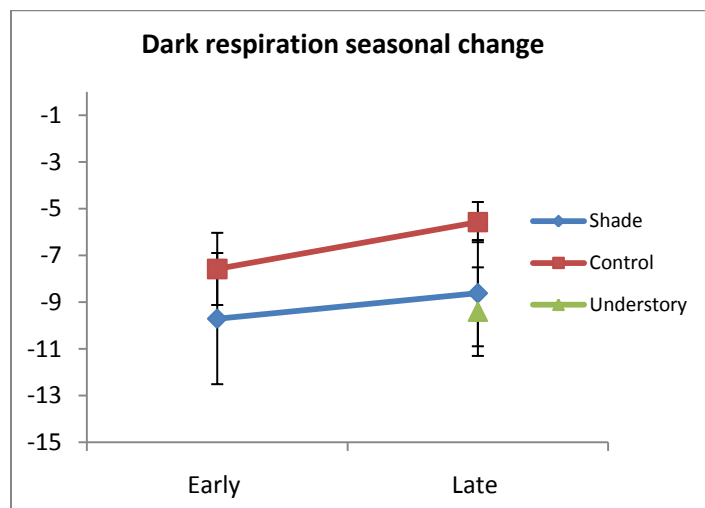


Figure 3 (Seasonal change of dark respiration)

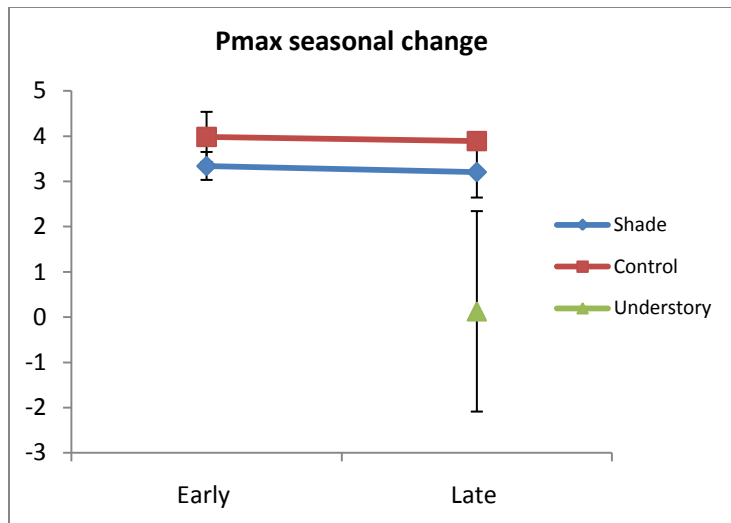


Figure 4 (Seasonal change of Pmax)

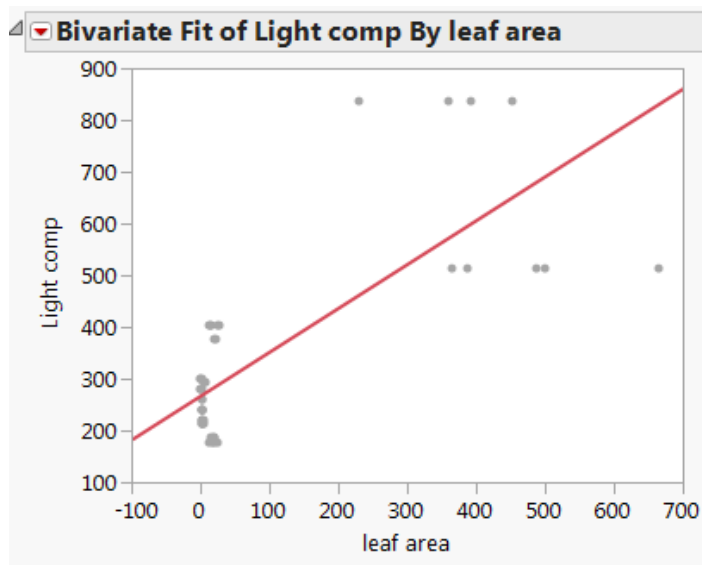


Figure 5 (Relationship of leaf area to LCP)

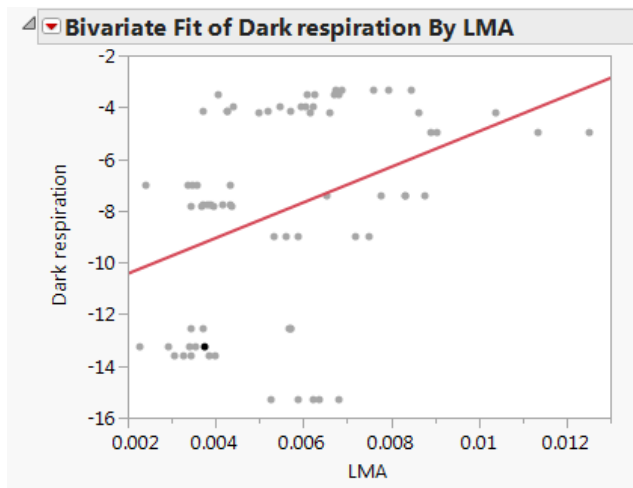


Figure 6 (Relationship between LMA and dark respiration)

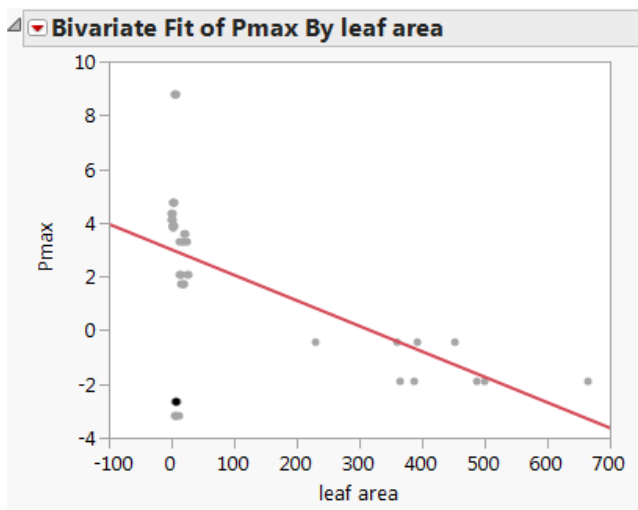


Figure 7 (Relationship between leaf area and Pmax)

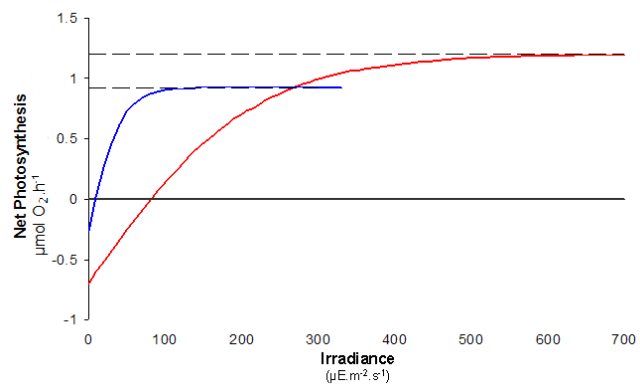


Figure 8 (PI curve comparison of shade adapted (blue) and sun adapted (red) species)(Chalker et al 2014)

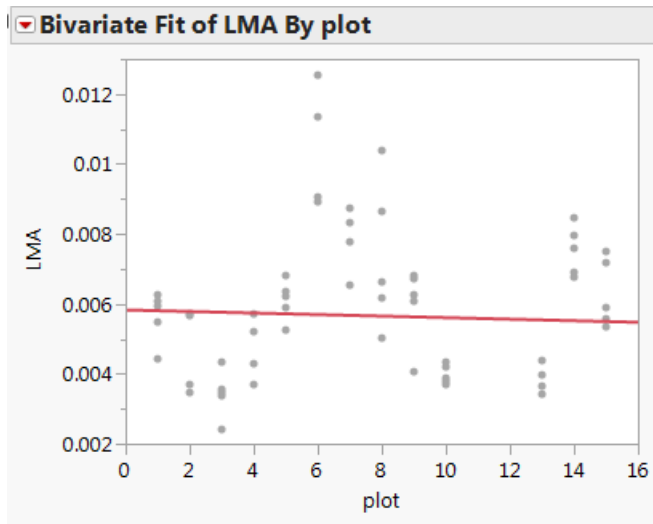


Figure 9 (No variation of LMA between plots)

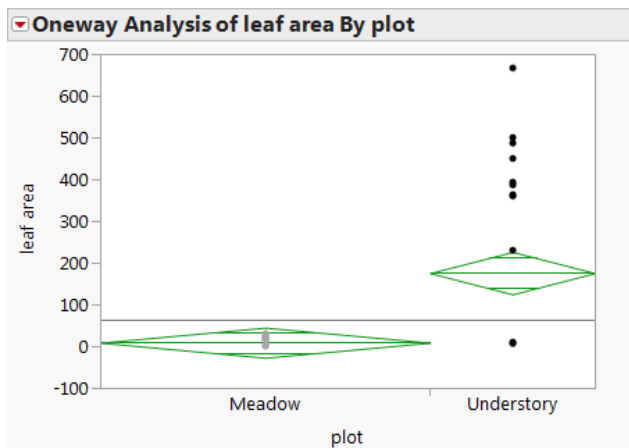


Figure 10 (Comparison of leaf area between meadow and understory groups)

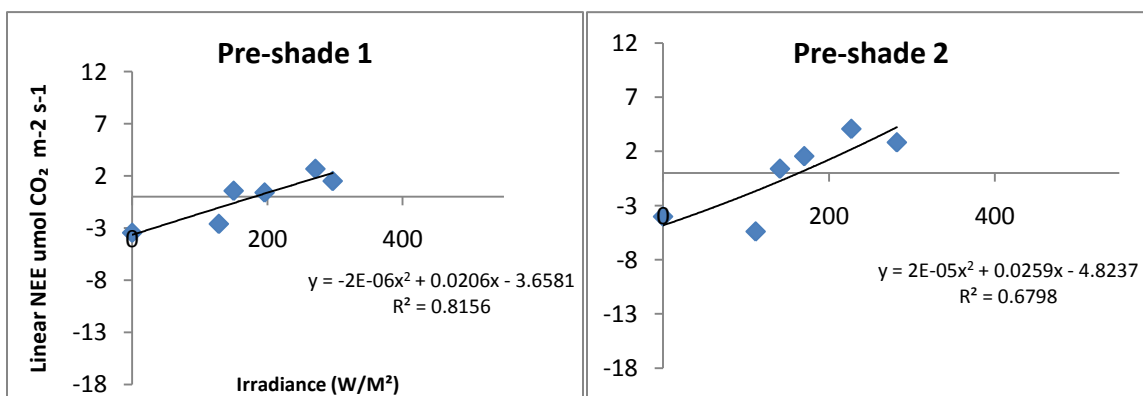


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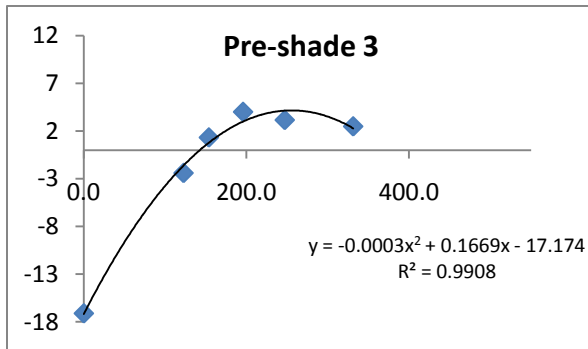


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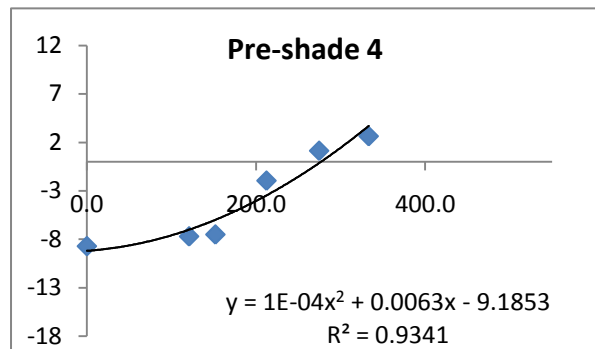


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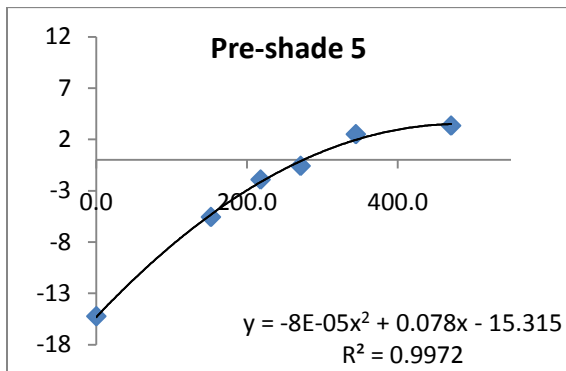


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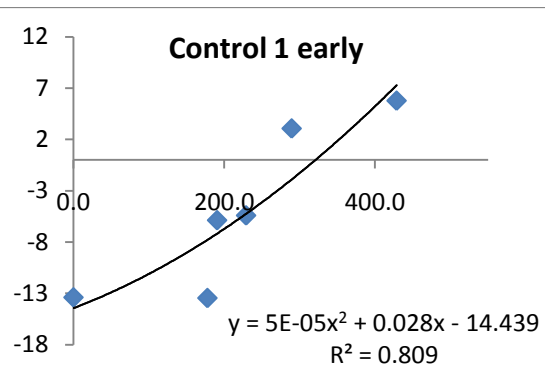


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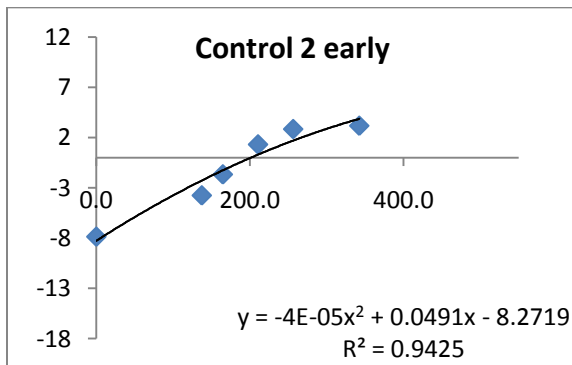


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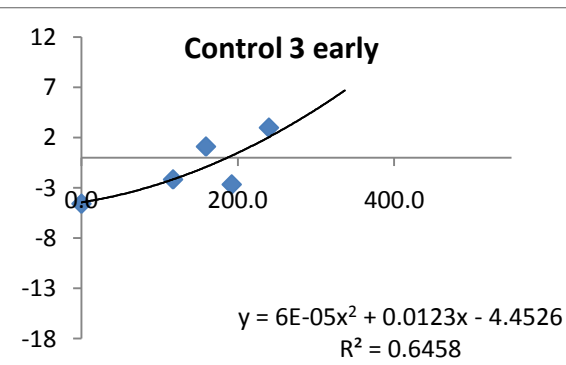


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Figure 18

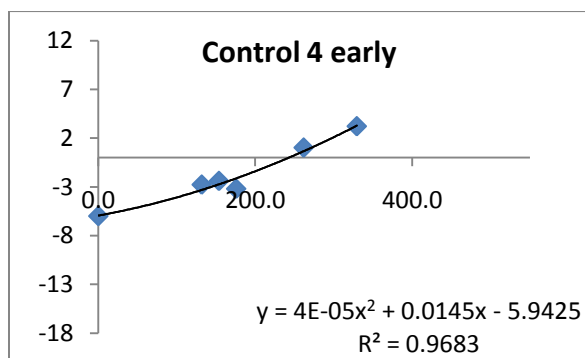


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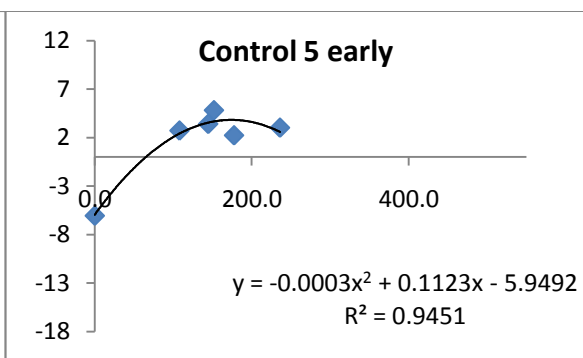


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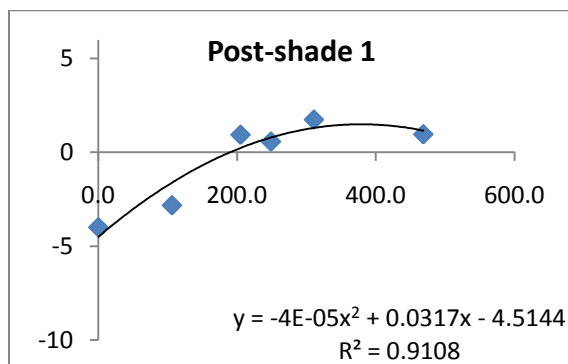


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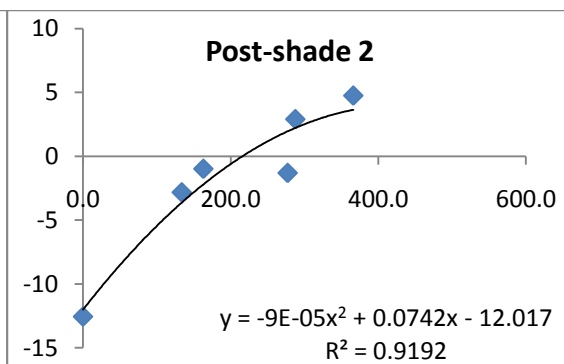


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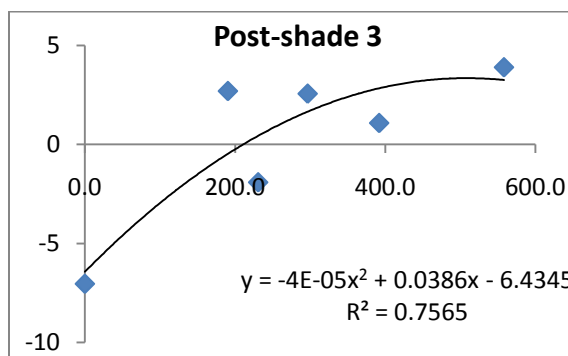


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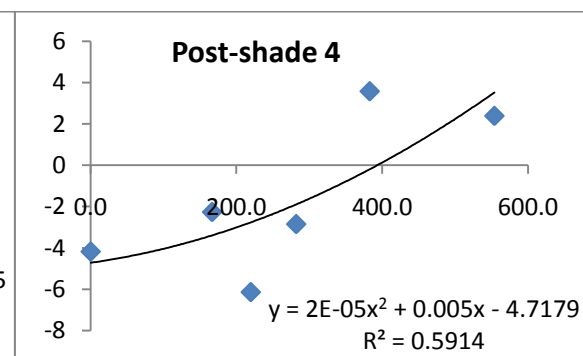


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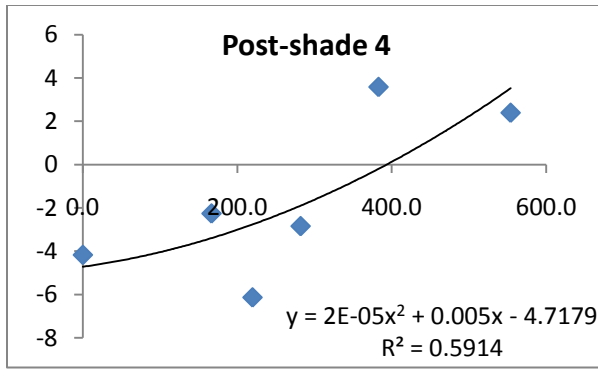


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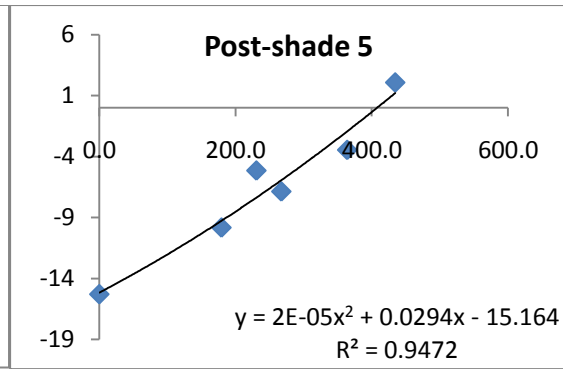


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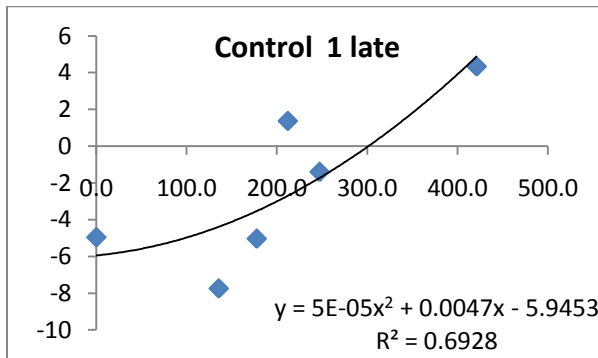


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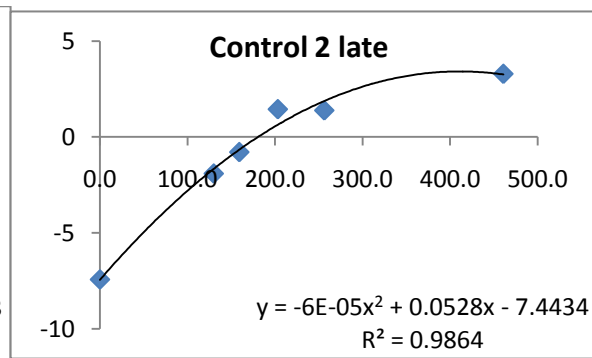


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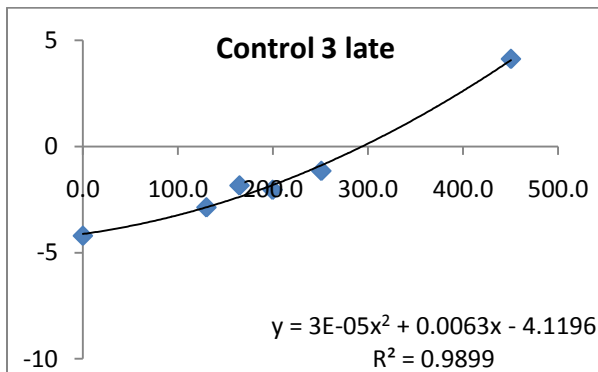


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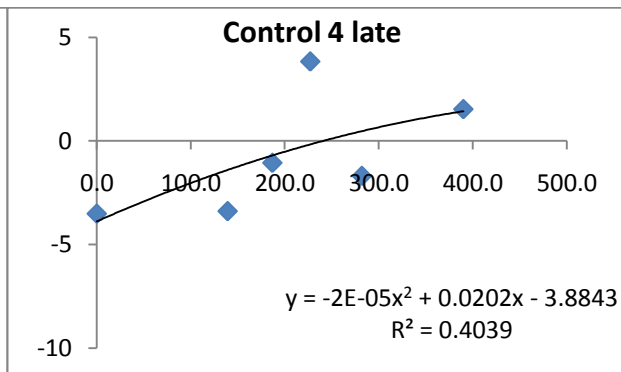


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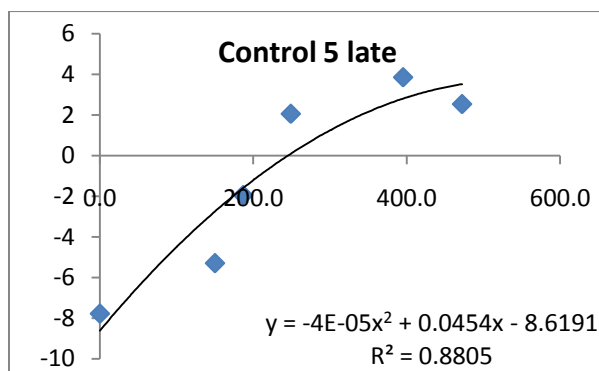


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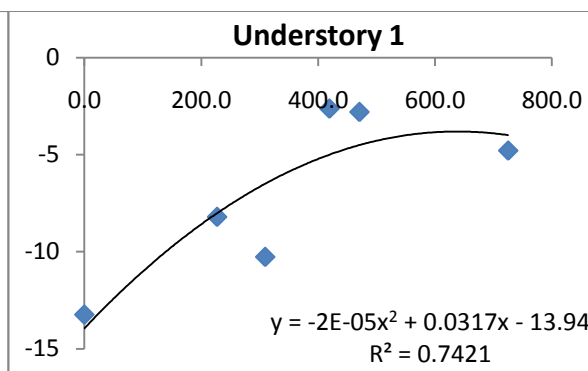


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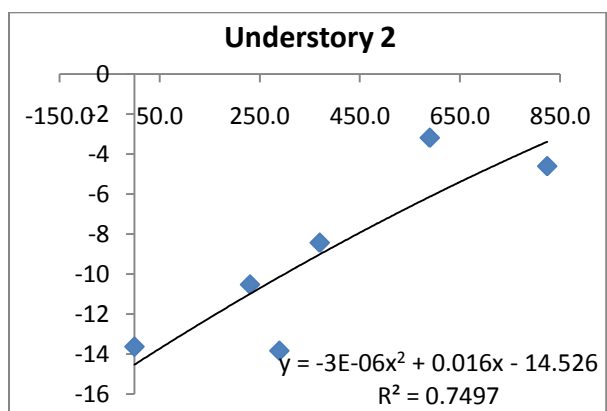


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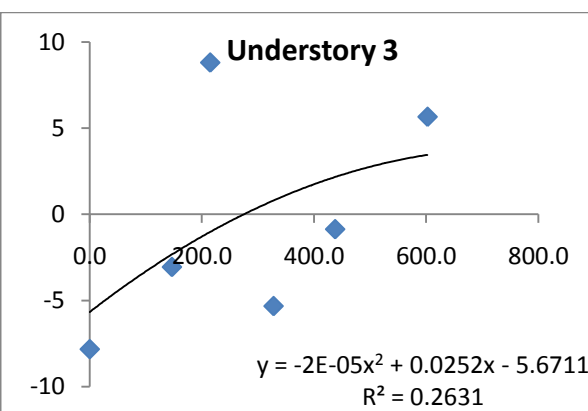


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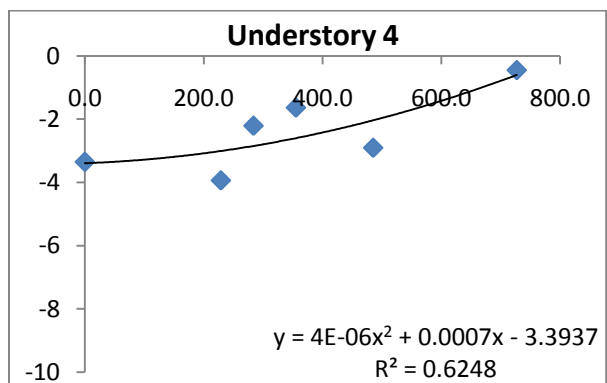


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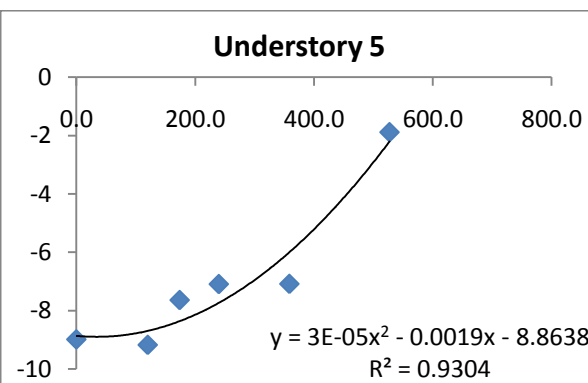
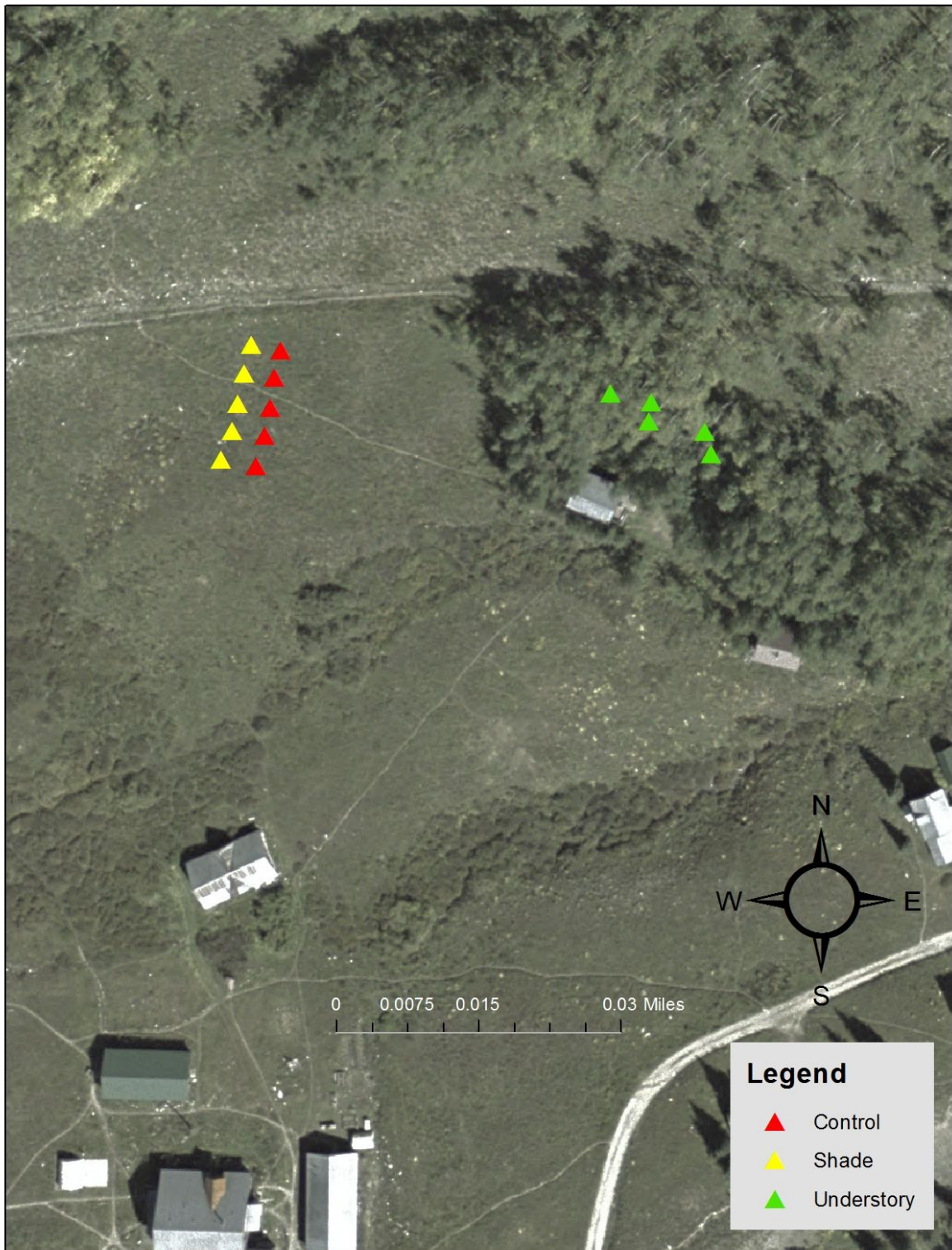


Figure 35



Rocky Mountain Biological Laboratory Gothic, CO. Site map