Seasonal Photosynthetic Acclimation in *Alliaria petiolata* (garlic mustard) and

Competing Native Herbs

By

Joshua Booker

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Thesis Advisors:
      Professor David Ellsworth
      Professor Mark Hunter

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Abstract

Alliaria petiolata (garlic mustard) is a quickly spreading invasive plant that is tolerant of many different environmental conditions, including the seasonal fluctuating light conditions of an understory deciduous forest. *Alliaria*, along with native understory herbs, is able to acclimate to extreme changes in light level by altering physiological traits. An investigation into the plasticity of *Alliaria*'s photosynthetic capabilities revealed a much more flexible dark respiration rate (R_{dark}- the energy cost of maintenance) than that of competing native species. *Alliaria* reduced R_{dark} to very low levels under low light conditions, thus paying low maintenance costs. There were no significant differences in the plasticity of other photosynthetic traits between *Alliaria* and native species. The plastic R_{dark} of *Alliaria* may give it a competitive edge over native plants in understory habitats. Further studies are needed to explore the extent of *Alliaria*'s photosynthetic flexibility.

Introduction

By definition, invasive plants pose a serious threat to native ecosystems (Davis et al. 2000; Dhillion and Anderson 1999; Myers and Anderson 2003; Pattison et al. 1998). Many invasives have been shown to reduce the biodiversity of native plant species and disrupt normal ecosystem functions after colonizing an area (Davis et al. 2000; Daehler 2003; Pattison 1998; Davis et al. 2000). The success of control methods against these invasive species is dependent upon the amount of knowledge that scientists are able to acquire about the plant's natural history, physiology, and ecology. Therefore, it is crucial to gather information on invasives through extensive research studies, specifically information on what makes one particular species more successful than another. The study of plant ecophysiology, which seeks to understand physiological mechanisms behind ecological observations, provides an opportunity to gather these types of data.

One reason invasive plants are able to dominate large areas lies in their broad environmental tolerances (Zimdahl 1999; Myers and Anderson 2003; Davis et al. 2000; Myers and Anderson 2003; Zimdahl 1999).

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Garlic mustard (*Alliaria petiolata*) is a well-known example of a tolerant invasive. It is able to persist and out-compete native species in environments as diverse as wet or dry deciduous forests, roadsides, floodplains, riverbanks, savannas and urban areas (Rebek and O'Neil 2005). Specific studies of *Alliaria* have shown that this invasive plant has a plastic seed mass, a trait that is considered the most inflexible of all reproductive traits (Susko and Lovett-Doust 2000). Differing seed masses correlate to timing of germination and primary leaf production, allowing *Alliaria* to adjust its phenology more so than most plants (Susko and Lovett-Doust 2000). This finding suggests that *Alliaria* may have other flexible traits that contribute to its ability to adapt to a wide range of conditions.

Like many species, light is the most important resource for the propagation of *Alliaria*. Meekins and McCarthy's (2000) experiments with *Alliaria* demonstrate that changes in light affect~~ed~~ growth rate and biomass allocation significantly more so than nutrient additions or changes in population density. Other studies have shown that *Alliaria* needs some shade in its habitat in order to be successful (Dhillion and Anderson 1999). Examining how *Alliaria* is able to acquire light in its environment may provide some insight into controlling its rapidly spreading population.

A habitat with fluctuating resources is especially vulnerable to invasions due to the ability of many exotic plants to take advantage of differing conditions (Davis et al. 2000). In the understory of deciduous forests in southern Michigan, light availability changes drastically throughout the year as mature trees grow, and eventually drop, their leaves. *Alliaria* is able to exploit these changes in light by sprouting ~~out~~ sun-adapted leaves in the direct sunlight of early spring, before the canopy leafs out, and then

lowering its photosynthetic capabilities to shade-tolerant levels in the low light of summer, after the canopy is fully formed (Myers and Anderson 2003). While this competition strategy seems to be an important component of *Alliaria*'s success, only one study has examined it in any substantial detail (Myers and Anderson 2003).

Photosynthetic acclimation is not a strategy unique to *Alliaria*. Several native forest herbs have also shown an ability to adapt to lower light levels throughout the year (Myers and Anderson 2003; Rothstein and Zak 2001; Myers and Anderson 2003). In order to out-compete these species, *Alliaria* should show a higher propensity to acclimate to the changes in light and thus maximize its growth rate. This study aims to compare the photosynthetic acclimation to seasonal fluctuations in light of garlic mustard and native herbaceous species.

To measure photosynthetic acclimation, this study compares components of the plants' light response curves. Light response curves measure the rate of CO2 accumulation by plants against step changes in quantum flux density (light availability). They are useful tools for assessing the environmental limitations to a plant's photosynthetic processes at a particular point in time. The five components of the curve are the dark respiration rate (Rdark), the maximum net photosynthetic rate (Amax), the light compensation point (LCP), the saturation point, and the apparent quantum yield (Fig. 1A).

Rdark measures the rate of CO_2 production that results from cellular respiration and is represented by the y-intercept of the light response curve (it should be noted that Rdark is actually a negative number but is referred to throughout this paper as an absolute value). Amax is a measure of the maximum rate of CO_2 accumulation and is measured as

the maximum y-value of the light response curve. The light compensation point is the light level at which CO_2 production (respiration) equals CO_2 accumulation (photosynthesis), and is measured by the x-intercept of the light response curve. The saturation point can be described as the quantum flux density at 95% of the Amax. The apparent quantum yield is the efficiency at which the incident light is converted into fixed carbon, and it is measured as the initial slope of the light response curve. This parameter is usually constant among C_3 species, but can be partly determined by leaf absorbance (Lambers et al. 1998). Shade-adapted leaves generally have higher leaf absorbances in low light and sun-adapted leaves have higher leaf absorbances in high light environments (Poorter et al. 1995). Based on this knowledge, I do not expect *Alliaria* to necessarily show the greatest amount of seasonal acclimation in apparent quantum yield.

Not a parameter of the light response curve, Vcmax is nonetheless an important variable to consider when studying light acclimation in plants. Vcmax is the maximum rate of carboxylation, and is determined by the activity of the Rubisco enzyme in a leaf. It is therefore a useful indicator of enzyme levels in a leaf, which indicates sun or shade adaptation. As they become acclimated to the shade, I expect all of the study species to show a decline in Vcmax over time, and *Alliaria* to show the greatest relative decline.

 I define photosynthetic acclimation as the relative difference between initial spring measurements (open canopy) and summer measurements (closed canopy). All of the parameters of the light response curve except apparent quantum yield typically show a downward shift with a plant's acclimation to a lower light level (Fig. 1B).

My hypotheses are as follows: 1) All plants (native species and *Alliaria*) will show some photosynthetic acclimation to the seasonal change in light on the forest floor

and, 2) *Alliaria* will show the highest amount of acclimation in all parameters of the light response curve, except apparent quantum yield.

Materials and Methods

Species Background

In addition to *Alliaria*, three co-occurring perennial herbs native to the region were studied. *Podophyllum peltatum* (may apple; Berberidaceae) is a native rhizomatous perennial herb most common in moist woods and pastures (Newcomb 1977). Its distribution covers all of the eastern U.S. It reproduces by rhizomes in the understory of forests, sprouting out in early spring before canopy closure. *Viola sororia* (common blue violet; Violoacea) is a native herb that is described as being moderately shade tolerant, and drought intolerant. Its distribution covers all of the eastern U.S, growing in various habitats from lawns to forest understories (USDA 2006). *Erythronium americanum* (dogtooth violet/trout lily; Liliaceae) is a common native perennial herb distributed in rich woodlands of the eastern U.S (USDA 2006).

Site Background

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The study was conducted in a woodland in the southeastern corner of Nichols Arboretum. The Nichols Arboretum is a 50 hectare (ha) ~~stretch~~ area of land owned by the University of Michigan, founded on an original 11 ha donation by Walter and Esther Nichols in 1907. It is located along the southern watershed of the Huron River, in the eastern part of Ann Arbor, MI. The glacial history of the land has created one of the more diverse landscapes in this area of Michigan (Tepley 2001).

This study was conducted in a part of Nichols Arboretum known as the Dow Tract (Fig. 2). Acquired in 1943, this is the most recent addition to the Arboretum. The northeastern half of the tract contains a restored prairie ecosystem (Dow Prairie), while the southwestern half includes contiguous forest communities on glacial till slopes. The study plot was contained within what has been classified as "ecosystem 4", near the southern border of Nichol's Arboretum (Fig. 2; Tepley 2001). The site is a dry-mesic, upland site in the Huron River watershed, with clay-loam soil. The soil is moderately well-drained and prone to drought. The site lies on a reworked end moraine, with an average slope of 24% (Tepley 2001).

The area of the site can be best characterized as an oak forest community, with the dominant overstory trees including northern red oak, black oak, white oak and pignut hickory. Dominant understory plants include red maple, black cherry, American elm, common buckthorn, and Norway maple. Other common woody plants include Virginia creeper and poison ivy. Dominant spring herbs include may apple (*Podophyllum peltatum*), trillium (*Trillium grandiflorum*), and wild geranium (*Geranium maculatum*). Dominant summer herbs include jewelweed (*Impatiens capensis*), lily-of-the-valley (*Convallaria majalis*), and jack-in-the-pulpit (*Arisaema triphyllum*).

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Invasive species, such as buckthorn species, honeysuckle species, dame's rocket (*Hesperis matronalis*), and garlic mustard (*Alliaria petiolata*), are quite common in the Arboretum forest communities, despite the fact that they are routinely removed by caretakers and volunteers. In 2001 for example, more than 75% of the understory stems in four different ecosystems consisted of the invasive buckthorn and honeysuckle species (Tepley 2001). However, the chosen site, contains relatively fewer invasives than other parts of the Arboretum (Tepley 2001).

Characteristic of most of the forests in the Arboretum, the dense understory of this site causes low light levels on the forest floor after canopy expansion, and has been cited as the main reason for the lack of oak regeneration (Tepley 2001). The low light levels may also contribute to lower density of invasive species in this area. A four meter square plot was established as a common garden for the study species within this site using flag markers. Vegetation within the plot at the start of the study included large existing clonal populations of *Podophylum* and *Convallaria* (rhizomes), and two *Alliaria* individuals.

Transplantation

From April 21-22, 2006, six specimens of *Podophyllum* , seventeen specimens of *Erythronium americanum* (dogwood violet/trout lily) and nineteen specimens of *Viola* were transplanted into a four square meter study plot in the study area. Transplants were from the central section of Nichols Arboretum about 0.7 km west of the plot location. Only six *Podophyllum* were transplanted because of the substantial native population already located at the study site. Most individuals appeared to have sprouted between

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April 10-14, 2006. Specimens were transplanted directly in the site after excavation, and

only 5-7 plants were taken at a time to minimize stress from water loss. The plants were

also watered liberally after transplantation. Twenty specimens of second-year *Alliaria*

petiolata (garlic mustard) were transplanted on April 22 from a large population

approximately forty meters northwest of the site. Two additional *Alliaria* plants already

established at the plot were included in the study. Individuals of all species were

randomly distributed within the four square meter plot at a density of 20 plants m^{-2}.

Physiological measurements

On each sampling date, photosynthetic measurements were made on a single

healthy leaf of each plant. The largest, uppermost cauline leaf of *Alliaria* was always

used. Before initiating the light response curve program, each leaf was maintained in the

chamber under full irradiance (1700 μmol m^{-2} s^{-1}) until net CO_2 assimilation became

constant. At the end of the light response program, the red LED lamp was turned off to

ensure an accurate measure of dark respiration. Three sets of measurements were made,

on Julian Day 116 (while the forest canopy at the site was still not in leaf), days 136-140

after canopy leaf-out, and days 168-170.

Gas exchange measurements were taken using a Portable Photosynthesis System

(model Li-6400, Li-Cor, Lincoln NE). Photosynthetic light response curves were

generated using an auto-program to modulate red and blue LED light source (Li-Cor,

Lincoln NE). To ensure photosynthetic induction (Naumburg et al. 2000), photosynthetic

light response measurements were made starting at full saturation and progressing step-

wise to lower light levels. The following light levels were used: 1700, 1000, 800, 400,

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200, 100, 80, 50, 20, 10, 0 μmol m^{-2} s^{-1}. Other environmental conditions during these controlled-response curves were ambient atmospheric CO_2 concentration of around 370 μmol mol^{-1}), mass flow rate of 250 μmol s^{-1}, and leaf temperature ranging 18-30°C for all species across all measurement days. On cold days (<~~55 degrees F~~13 ^{o}C), leaf temperature was maintained by setting the chamber block temperature to 22° C. We assume that these environmental conditions are near the optimum for photosynthesis in these plants.

A data logger (Li-Cor, Li-1000) was set up at the plot location to constantly measure the light levels that reached the forest floor and ambient temperatures from April 20-June 3, 2006. Two quantum sensors (Li-Cor, Lincoln NE) were used, placed approximately two meters apart within the plot to obtain an estimate of the spring-summer light variability at the study site. Light data were recorded every ten minutes from 6:00am – 9:10pm local time. A copper-constantan thermocouple was used to measure temperature during the period when light was measured. The data logger was kept in a cooler to prevent weather damage, and the thermocouple was shielded from radiation by a reflective cover.

Additional light data ~~was~~ were taken on May 20 with a Li-Cor, LI-191SA line quantum sensor to get a spatial measurement of light over the plot area.

Data Analysis

Data from photosynthetic light response curves were fitted using a custom program (available from D. Ellsworth: D.Ellsworth@uws.edu.au) provided by D.

Ellsworth, University of Michigan (see Sefcik et al. 2006). Each individual

photosynthetic light response curve is fit using the equation of Hanson et al. (1987)

$$A_{net} = A_{sat} * \left(1 - \left[1 - R_{dark} \middle/ A_{sat} \right] \right)^{1 - Q_i \middle/ Q_{comp}}$$

where A_{net} is the rate of CO_2 assimilation at any given irradiance Q_i, A_{sat} is the light-

saturated asymptote of the photosynthetic light response, R_{dark} is the dark respiration rate

defined as the instantaneous CO_2 efflux at irradiance $Q = 0$ µmol m^{-2} s^{-1} and Q_{comp} is the

light compensation point as the irradiance where CO_2 assimilation equals respiratory CO_2

efflux. Three additional parameters were derived from the fitted data as described in

Niinemets and Tenhunen (1997): Q_{sat}, curvature θ, and V_{cmax} as computed following

Niinemets and Tenhunen (1997) but originally defined in Farquhar et al. (1980). Q_{sat} is

the light saturation point, θ is a dimensionless curvature coefficient, and V_{cmax} is the

maximum velocity of carboxylation in photosynthetic CO_2 fixation. The latter parameter

is estimated in this case from minimal data as compared to the more commonly-measured

photosynthetic CO_2 response curves (Ellsworth et al. 2004), but fits using this technique

have compared favorably with more rigorous fits of the full photosynthetic CO_2 response

curves (Niinemets and Tenhunen 1997; Ellsworth, personal observations).

Statistical Analyses

Environmental data (light levels, oak leaf length, precipitation rates) were

organized and graphed using Microsoft Excel software. Precipitation data were analyzed

using t-tests to identify a possible period of drought in April that may have complicated

results.

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The physiological data ~~was~~ were analyzed using SPSS 10.0 statistical software. A univariate analysis of variance test using Type III sums of squares was performed on seven parameters to find possible differences among species, among time periods, and among species through time. The following parameters were tested: Amax, light compensation point, Rdark, Vcmax, apparent quantum yield, saturation point, and intrinsic water use. For variables in which significant differences ~~between~~ among species and time periods were found, the percent difference between time period 1 and time~~r~~ period 3 was calculated to represent seasonal acclimation to the shaded environment.

Results

Transplantation and Mortality

All transplanted *Erythronium* died within two weeks. *Viola* showed little to no visible signs of stress during transplantation, while *Alliaria* and *Podophyllum* showed moderate wilting. The first spring measurements showed further evidence of drought in the transplants (low stomatal conductance and Amax). Established plants displayed relatively high Amax values, with *Podophyllum* rates slightly higher than *Alliaria*.

Alliaria had the highest percentage of mortality through 5/17/06 at 58%. 21% of *Viola* and 16% of *Podophyllum* specimens died during this time. Mortality mostly

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appeared to be a direct result of transplantation, although there were also some instances of herbivory and uprooting due to natural disturbances.

Environmental Data

Oak leaf length increased dramatically from late April to late May, while light levels (PFD) generally decreased during this time (Figure 3A).

LI-COR LI-191SA line quantum sensor readings showed an average ~~PAR~~ PFD of 32.5 (μmol photon m^{-2} s^{-1}) over the site area after canopy closure (May 20). This value was higher than the light compensation point (LCP) of all species measured during this time (average LCP of 12).

A t-test indicated that the precipitation in April was not statistically different from the precipitation in May (df=49, t-statistic= –1.5, P=.13; Figure 3B).

ANOVA Results

All physiological measurements taken from the plant species varied significantly over time as the forest canopy closed (Table 1). ~~Significant differences among time periods, without considering species differences, were observed for all parameters (Table 1).~~

Light saturation point (95% of Amax) declined during the course of measurements (Fig 4A, Table 1). The absence of a significant interaction term between species and time period (Table 1) suggests that the saturation point of the three species declined in a similar manner over time.

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Light compensation point (LCP (Fig. 4B) declined from time period 1 to time period 2, but increased from time period 2 to time period 3. No significant difference in LCP was found among species nor was there a significant species*time interaction (Table 1), suggesting that the LCP of the three species decreased and increased similarly over time.

Apparent quantum yield (AQY) decreased over time (Fig. 4C, Table 1). No significant difference was found among species nor was there a significant species*time interaction (Table 1), suggesting that the AQY of the three species declined similarly over time.

The dark respiration rate (Rdark) declined from time period 1 to time period 2, but increased from time period 2 to time period 3 (Fig. 5, Table 1). In addition, Rdark was the only physiological parameter that showed significant differences in the way that plant species changed over time (species*time interaction, Table 1). Specifically, *Alliaria* had the highest relative difference in Rdark between time period 1 and time period 3 (seasonal acclimation) at a 71% decrease. *Podophyllum* showed a 36% decrease in dark respiration, while *Viola* decreased only 3% (Fig. 5).

The maximum net photosynthetic rate (Amax) decreased through time (Fig. 6A, Table 1). Significant differences in Amax were observed among plant species (Table 1). *Alliaria* showed the highest Amax in time period 1, while *Viola* had the highest Amax in the following two periods (Fig. 6A). The relative difference between T1 Amax values and T3 Amax values (seasonal acclimation) was highest for *Alliaria*.

The maximum rate of carboxylation (VCmax) declined over all time periods (Fig 6B, Table 1). Significant differences VCmax were also observed among plant species

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(Table 1). *Viola* had the highest values in each time period (Fig 6B). The relative difference between T1 VCmax values and T3 VCmax values (seasonal acclimation) was nearly identical among species.

Intrinsic water use efficiency (IWUE) decreased between each time period (Fig. 6C Table 1). There were also significant differences in IWUE among plant species (Table 1). IWUE was generally highest in *Viola* followed by *Podophyllum*, with *Alliaria* exhibiting the lowest IWUE (Fig. 6C). ~~Light saturation point (95% of Amax) declined during the course of measurements (Fig 4A, Table 1). The absence of a significant interaction term between species and time period (Table 1) suggests that the saturation point of the three species declined in a similar manner over time.~~

~~Light compensation point (Fig. 4B) declined from time period 1 to time period 2, but increased from time period 2 to time period 3. No significant difference was found among species through time (Table 1), suggesting that the light compensation point of the three species decreased and increased similarly over time.~~

~~Apparent quantum yield decreased over time (Fig. 4C, Table 1). No significant difference was found among species through time (Table 1), suggesting that the apparent quantum yield of the three species declined similarly over time.~~

~~The dark respiration rate (Rdark) declined from time period 1 to time period 2, but increased from time period 2 to time period 3 (Fig. 5, Table 1). Rdark was the only tested parameter that showed significant differences among the way species changed over time. *Alliaria* had the highest relative difference between time period 1 Rdark values and time period 3 Rdark values (seasonal acclimation) at a 71% decrease. *Podophyllum* showed a 36% decrease in dark respiration, while *Viola* decreased 3% (Fig. 5).~~

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The maximum net photosynthetic rate (Amax) decreased through time (Fig. 6A, Table 1). Significant species differences in Amax were observed (Table 1). *Alliaria* showed the highest Amax in time period 1, while *Viola* had the highest Amax in the following two periods (Fig. 6A). The relative difference between T1 Amax values and T3 Amax values (seasonal acclimation) was highest for *Alliaria*.

The maximum carboxylation (VCmax) declined over all time periods (Fig 6B, Table 1). Significant species differences for VCmax were also observed (Table 1). *Viola* had the highest values in each time period (Fig 6B). The relative difference between T1 VCmax values and T3 VCmax values (seasonal acclimation) was highest for *Alliaria* at 74%. The other two species had a seasonal acclimation of 72%.

Intrinsic water use efficiency (IWUE) decreased over each time period (Fig. 6C Table 1). Species differences in IWUE were found to be significant (Table 1). *Viola* consistently had the highest IWUE in each time period (Fig. 6C).

Discussion

Acclimation to changing light conditions is expected in most understory plant species, and I hypothesized that it would be most pronounced in the invasive species *Alliaria*. After canopy closure, the light compensation point of all species was well below the average amount of light reaching the forest floor (PFD), demonstrating that all of the species had adapted to the low levels of light (Figs. 3A & 4B). The declining trend over time of several light response curve variables (Amax, light saturation point, apparent quantum yield, and dark respiration rate) is further evidence of seasonal acclimation in all of the species, as previously predicted (Figs. 4A, 4C, 5, 6).

Alliaria appeared to be the most sun-adapted of the three species studied, having the highest light compensation point (Fig. 4B), dark respiration rate (Fig. 5), and apparent quantum yield (Fig 4C) in the first time period before canopy closure. These results agree with studies demonstrating that invasive plants are more sun-adapted than their native competitors (Pattison et al. 1998).

Alliaria also decreased its dark respiration rate nearly twice as much as the highest native plant (*Podophyllum*), showing a high degree of plasticity in this particular trait (Fig. 5). In other words, *Alliaria* is able to pay very low maintenance costs (respiration) under low light conditions, providing it with a significant advantage after canopy closure. These results are consistent with Daehler's (2003) findings that invasives have significantly greater plasticity in some physiological traits than do many native plants (2003). The traits he looked atconsidered included biomass allocations and germination in response to different environmental conditions, but not light response parameters. Daehler (2003) also found that native plants are more likely to out-compete

invasive plants in low resource environments, including low light environments. The

results with *Alliaria* and dark respiration suggest that it stays competitive with native

plants even in low light environments. No other physiological parameter that I measured

showed a significant interaction between time period and species (Table 1), indicating

that all species changed in an equivalent fashion over time in these variables. This was

expected for apparent quantum efficiency, but not for the other parameters (Vcmax, light

saturation point, light compensation point, and Amax). I had predicted that *Alliaria*

would also be the most flexible physiologically in these traits, but changes over time

were equivalent among species (Table 1). If physiology is a component of the

competitive success of *Alliaria*, it would appear to be based on sun-adaptation before

canopy closure and low levels of Rdark after canopy closure.

There are some weaknesses and limitations to my study. First, ~~the effect of~~

transplantation may have had an impact on spring measurements of physiology. Many

individual plants showed wilting and physiological signs of drought after transplantation,

displaying low stomatal conductance and Amax values. When in drought, a plant usually

closes its stomates in an attempt to regulate evapotranspiration and conserve water

(Lambers et al. 1998). Although the precipitation during April was not statistically

different from the following months, all species showed the highest water use efficiency

during spring. In an effort to adapt to the stress of transplantation, the plants may have

closed their stomates, limiting their CO_2 uptake and lowering their photosynthetic rates.

Lowered spring Amax values would certainly affect attempts to measure seasonal light

acclimation. Since the number of transplants varied among the study species, and no

differentiation was made between transplants and non-transplants, statistical differences

among species could have been affected. In addition, the mortality of *Alliaria* in the

spring was more than twice as high as the highest native plant (*Viola*), and *Alliaria* also

showed the lowest overall water use efficiency. These findings suggest that *Alliaria* is

less tolerant of the effects of transplantation than natives and may have had more of its

physiological variation confounded as a result.

Second, the relatively low sample size in early spring may have also confounded

statistical analysis. The high mortality rate for *Alliaria* and the complete absence of a

third native species for comparison (*Erythronium*) limited thorough analysis of this

community.

Overall, the invasibility of *Alliaria* may be partially explained by its flexible dark

respiration rate, which gives it a competitive edge over native species in a changing light

environment. This finding is consistent with theory of invasibility, which states that

invasives are able to out-compete natives by taking advantage of fluctuating resources

(Davis et al. 2000). Further studies may correct the flaws in this methodology and

possibly discover flexibility in other light response parameters.

There are other theories about invasive species that may explain how garlic

mustard out-competes natives, most notably the evolution of increase competitive ability

(EICA) hypothesis (Blossey and Notzold 1995). This theory maintains that invasives are

able to sustain a competitive ability over native plants due to increased resource

allocation to growth and reproduction instead of herbivore defense. A study by Rebek

and O'Neil (2005) that simulated herbivory on *Alliaria* monocultures showed the

potential for a successful biological control method, suggesting that *Alliaria*'s

invasiveness can be partly explained by the lack of natural herbivores (2005). However,

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recent chemical analyses of *Alliaria* do not show reduced chemical defenses in invasive populations as would be expected under the EICA hypothesis (Cipollini et al. 2005). These conflicting findings, paired with my own ~~indefinite~~ equivocal results, illustrate the complexity involved in explaining *Alliaria*'s invasive ecology.

The successful invasion of forest understories by exotic plants has been well documented, and ~~has been observed~~continues ~~in North America by several different species~~ (Blossey et al. 2001, Rosen et al. 2006, Woods 1993). Invasive species that invade understories are likely successful because they are shade-tolerant or respond positively to disturbance regimes that increase light availability (Leicht and Silander 2006). Light is the most important limiting resource in an understory ecosystem, and it is crucial in invasive plant management to identify how non-native plants are able to deal with this low light availability. ~~A~~ The study by Leicht and Silander (2006) demonstrated how two closely related species (one native and one invasive) had two very different strategies for persisting in a shaded forest understory ~~(2006)~~. More experiments addressing the ability of non-native plants to obtain light resources are needed to fully understand understory invasions.

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Tables and Figures

Table 1: Analysis of Variance in physiological measurements among plant species and sampling dates Significant *P*-values are highlighted. Significant differences among time periods were observed for all parameters. Amax, Vcmax, and Intrinsic Water Use Efficiency differed among plant species, while Rdark showed a significant species by time interaction. ~~Table 1: Analysis of Variance Between Study Species and Within Time Periods. Significant P-values are highlighted in yellow. Significant differences among time periods were observed for all parameters. Amax, Vcmax, and Instrinsic Water Use all showed significant differences among species, while Rdark showed significance among species through time.~~

Parameter	d.f.	Source of Variation	F-Statistic	P-Value	R-Squared
Amax	3	Species	4.105	0.015	0.796
	2	Time Period	46.113	0	--
	5	Species*Time Period	0.973	0.449	--
Light CP	3	Species	1.235	0.314	0.367
	2	Time Period	5.374	0.01	--
	5	Species*Time Period	0.651	0.663	--
Rdark	3	Species	0.855	0.475	0.53
	2	Time Period	9.143	0.001	--
	5	Species*Time Period	2.896	0.029	--
Vcmax	3	Species	11.338	0	0.857
	2	Time Period	68.641	0	--
	5	Species*Time Period	1.831	0.136	--
Quantum efficiency	3	Species	2.564	0.073	0.779
	2	Time Period	44.546	0	--
	5	Species*Time Period	0.817	0.139	--
Saturation Point	3	Species	1.361	0.273	0.55
	2	Time Period	11.909	0	--
	5	Species*Time Period	0.956	0.46	--
Intrinsic Water Use Efficiency	3	Species	8.14	0	0.575
	2	Time Period	9.736	0.001	--
	5	Species*Time Period	0.668	0.65	--

Figure 1A: The five components of a typical light response curve.
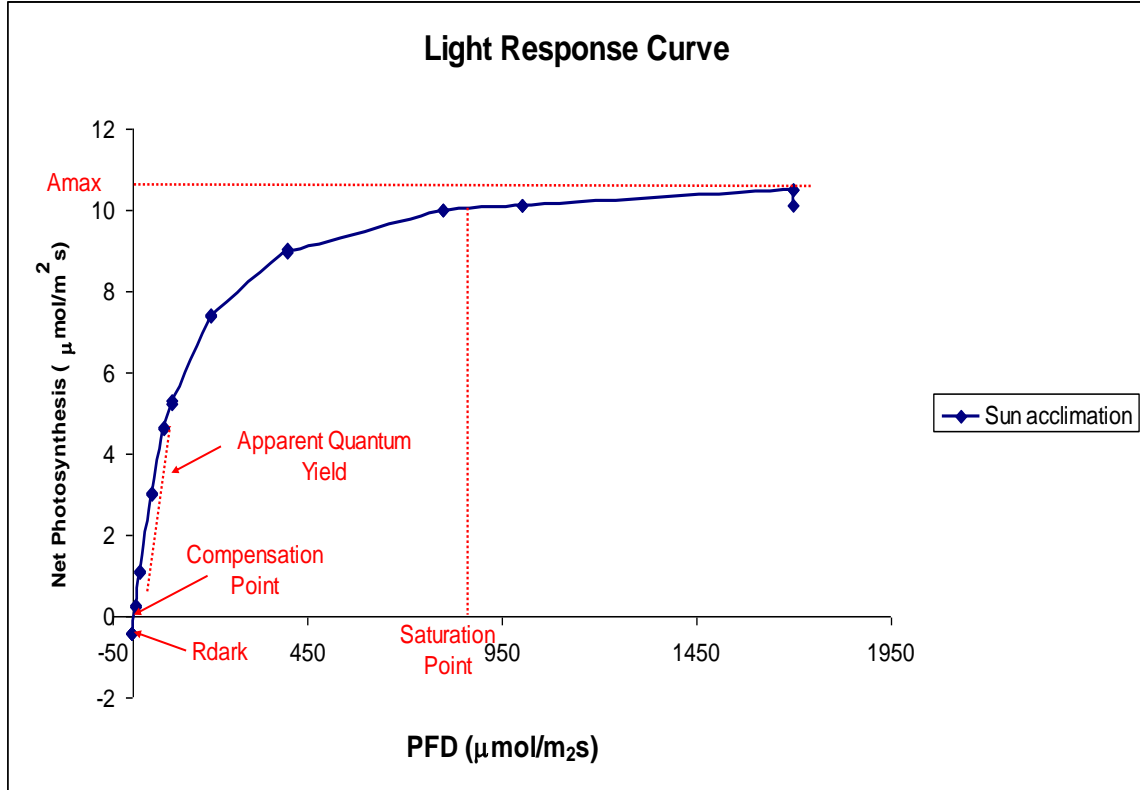
Figure 1B: Example of photosynthetic acclimation to changing light environments. The light response curve shifts down in response to a shaded environment.
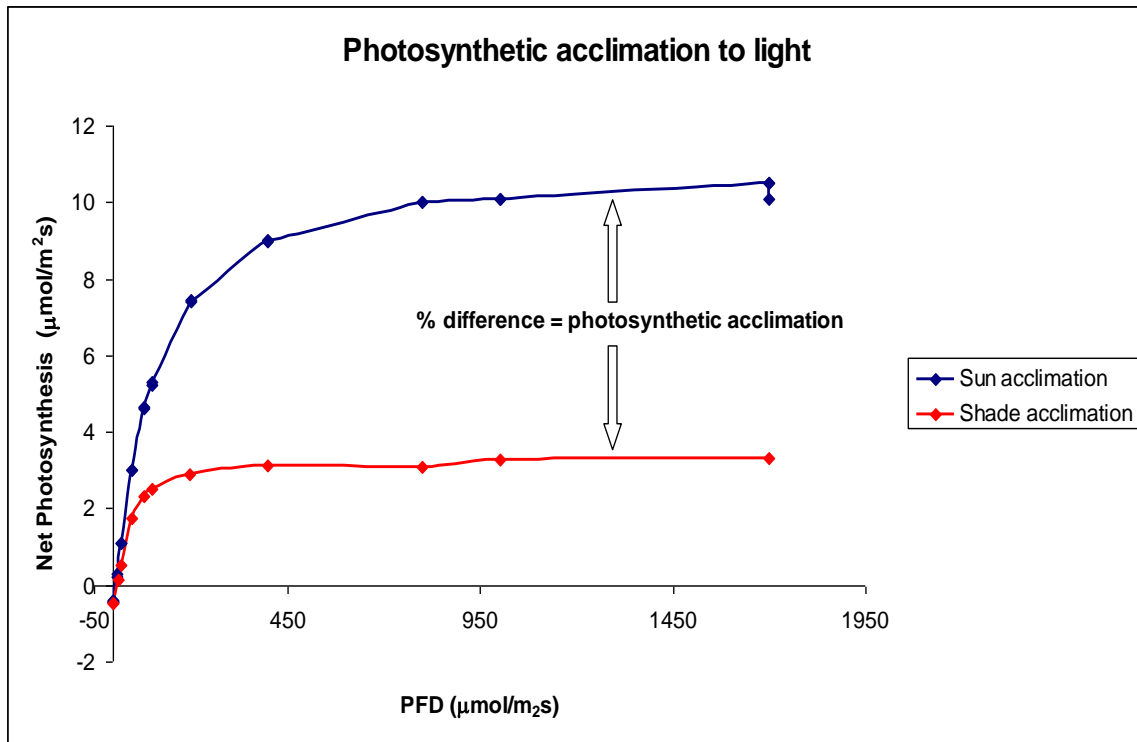

Photosynthetic acclimation to light

% difference = photosynthetic acclimation

Sun acclimation
Shade acclimation

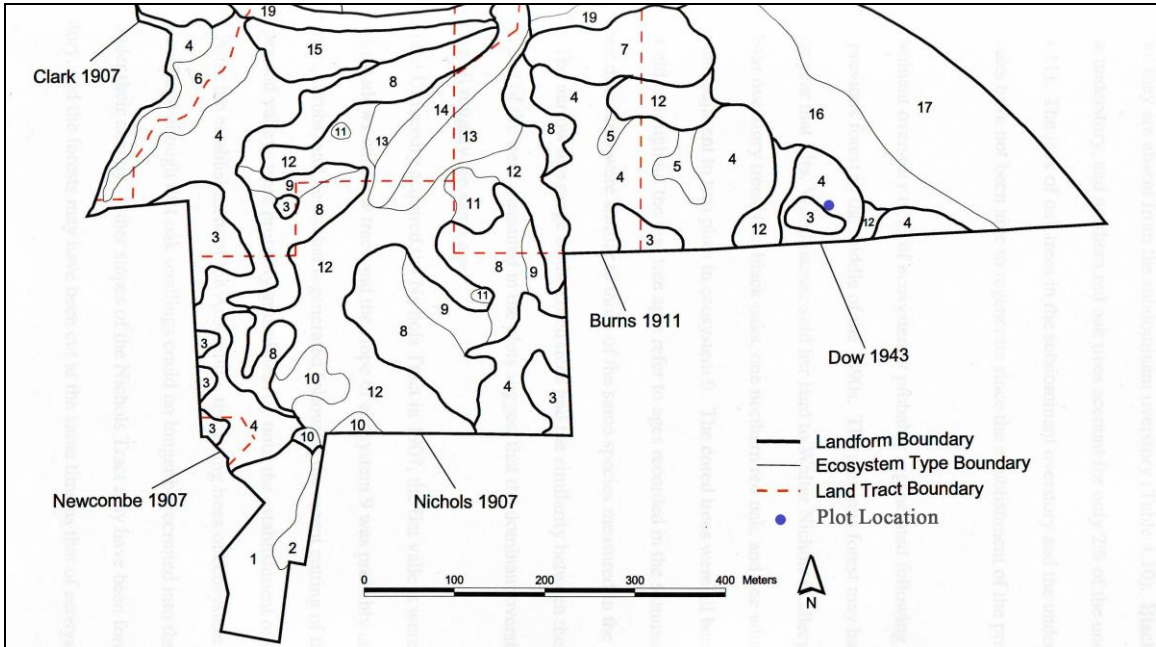Figure 2: Ecosystem Mmap of Nichols Arboretum in Ann Arbor, MI, USA (Tepley 2001). The plot was located near the southern boundary of Dow Tract.

Figure 3A: Depiction of canopy closure using daily measurements of photon flux density (PFD) and oak leaf length. The three time periods of gas exchange measurements are indicated with arrows~~Figure 3A: Depiction of Canopy Closure using Daily PFD and Oak Leaf Length. The three time periods of gas exchange measurements are indicated with red arrows.~~

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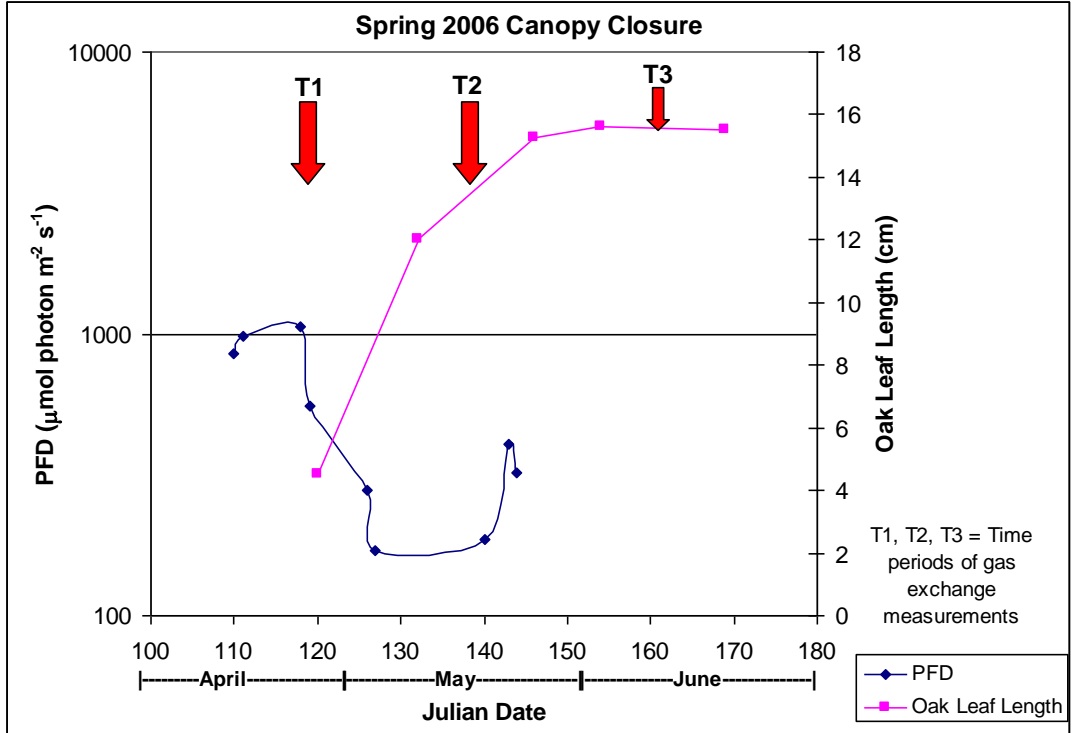
Figure 3B: Daily Pprecipitation from April – June 2006. The mean precipitation of April and May were not statistically different from one another (df=49, t-statistic= −1.5, P=.13).

2006 Ann Arbor Precipitation
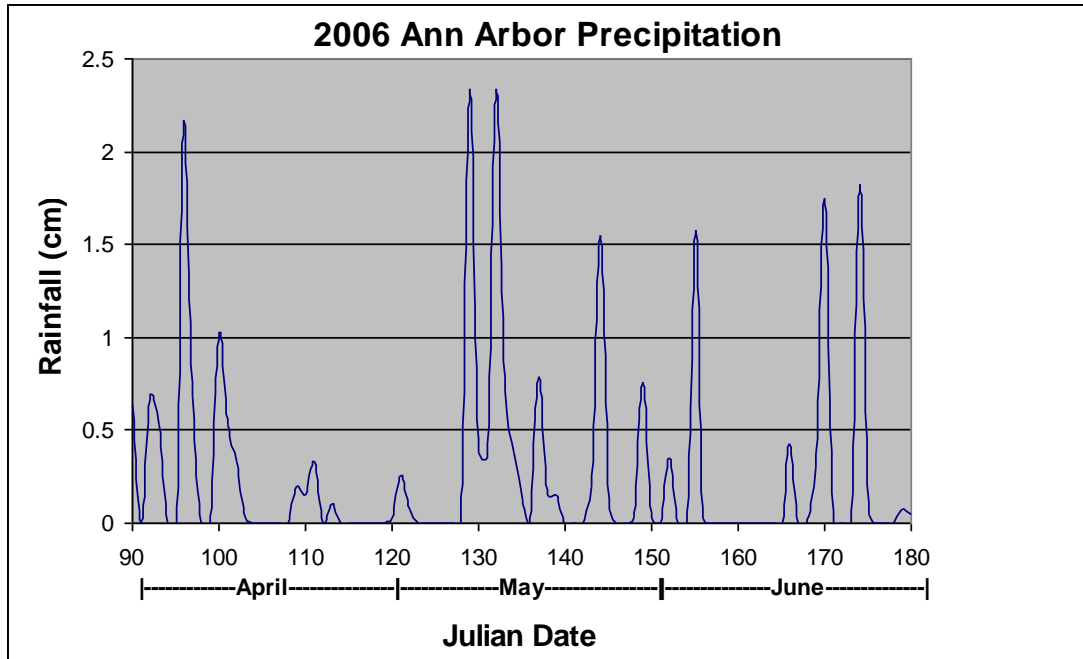
Fig 4A: The average light saturation point for each species at three time periods. Values ~~were significant~~differed significantly among time periods, but not among species.

Light Saturation Point at Three Time Periods

Light Saturation Point at Three Time Periods
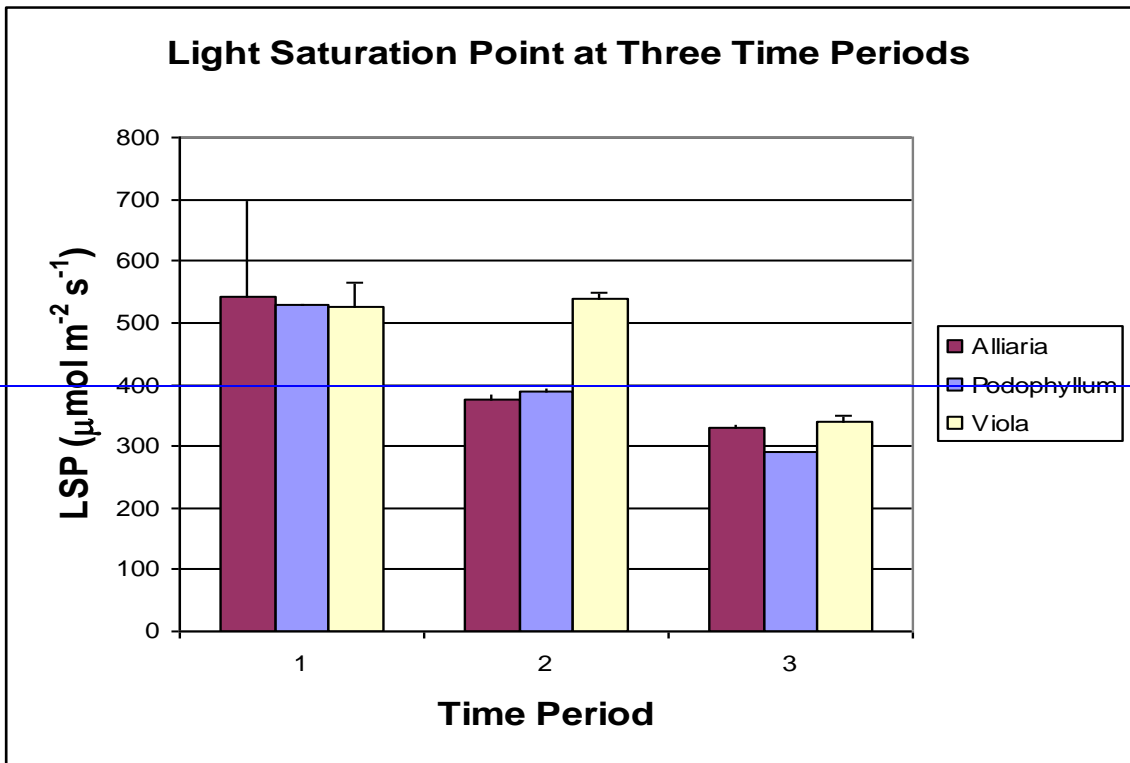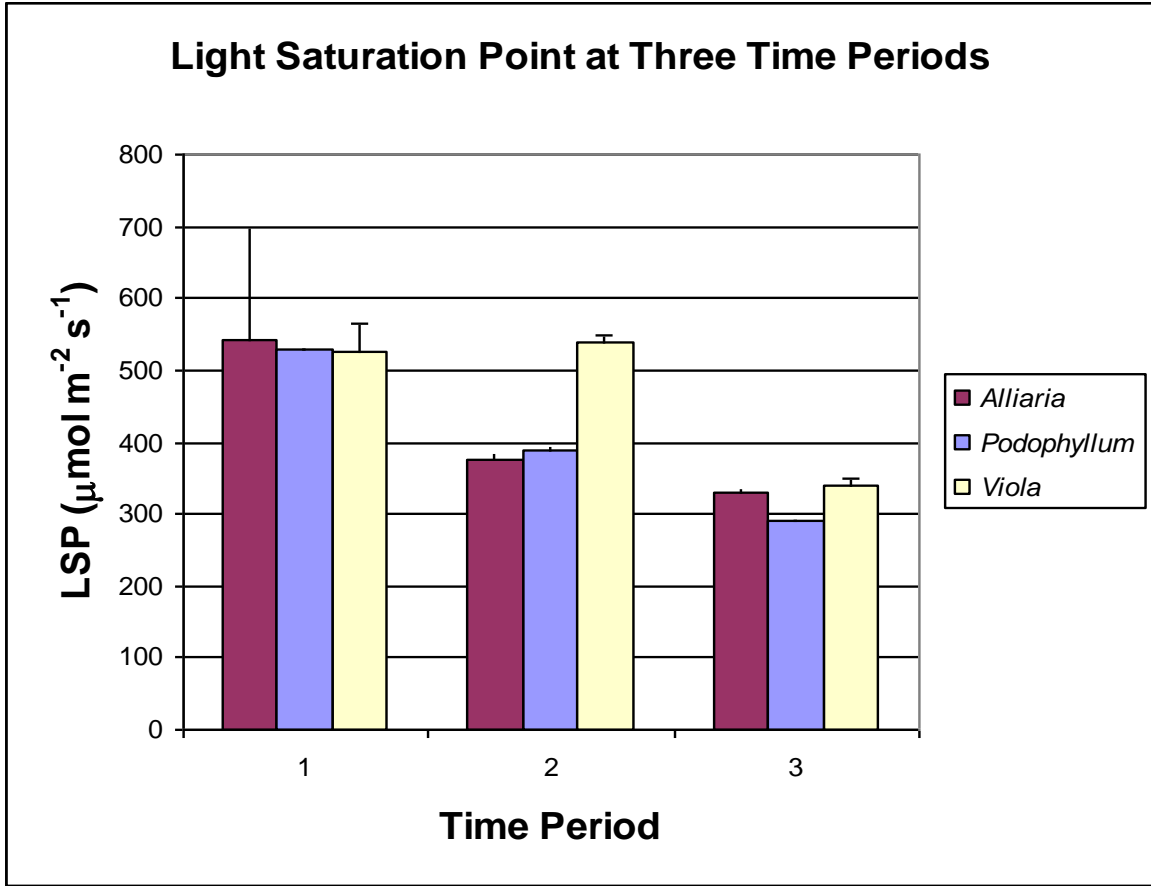
Fig 4B: The average light compensation point for each species at three time periods.
Values differed significantly ~~were significant~~ among time periods, but not among species.

Light Compensation Point at Three Time Periods

Light Compensation Point at Three Time Periods
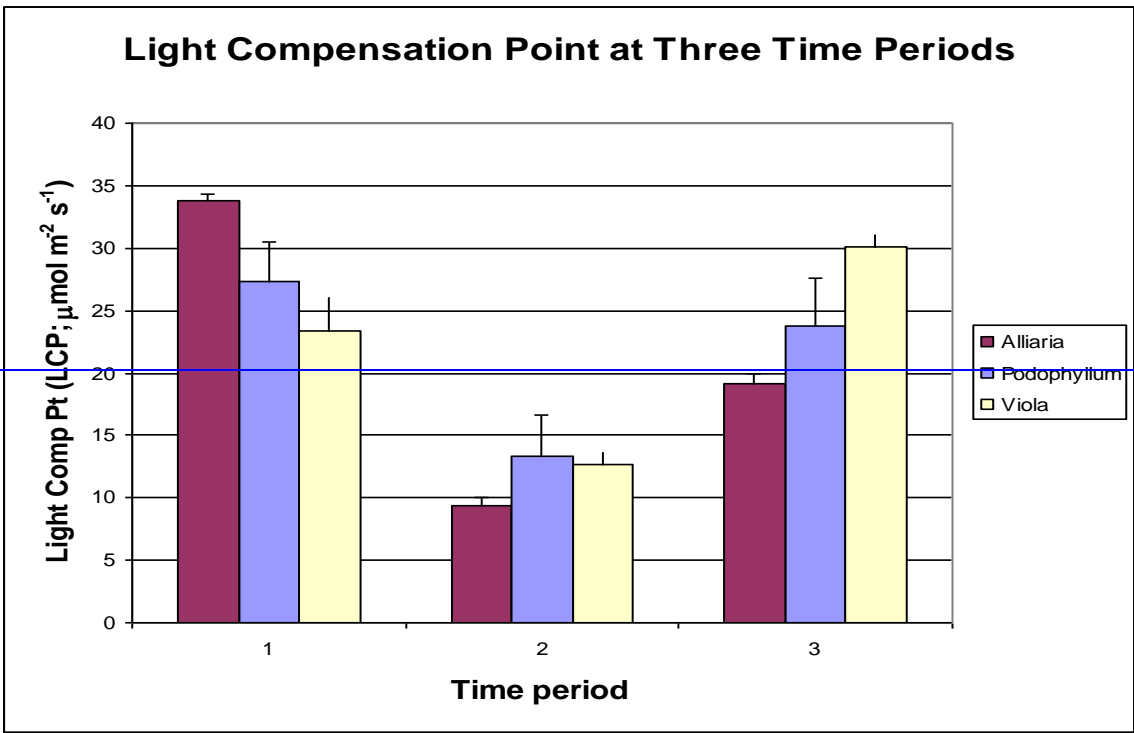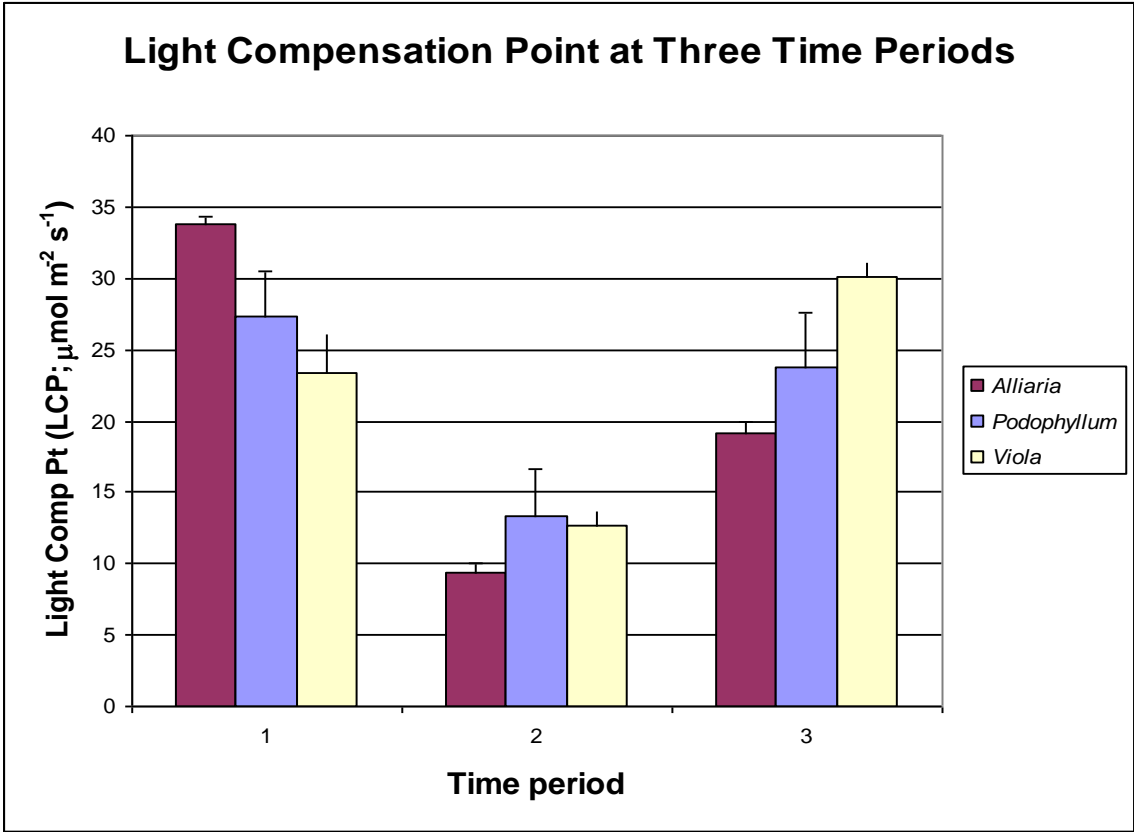
Fig 4C: The average apparent quantum yield for each species at three time periods. Values differed significantly were significant between among time periods, but not among species.

Apparent Quantum Yield at Three Time Periods

Apparent Quantum Yield at Three Time Periods
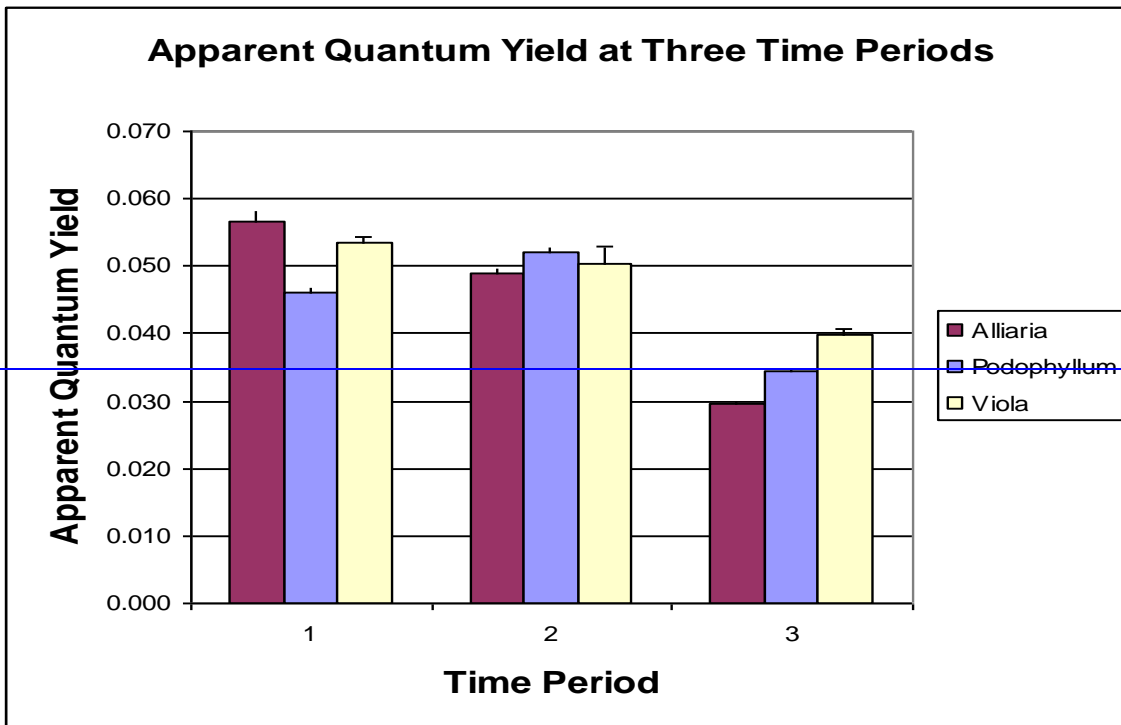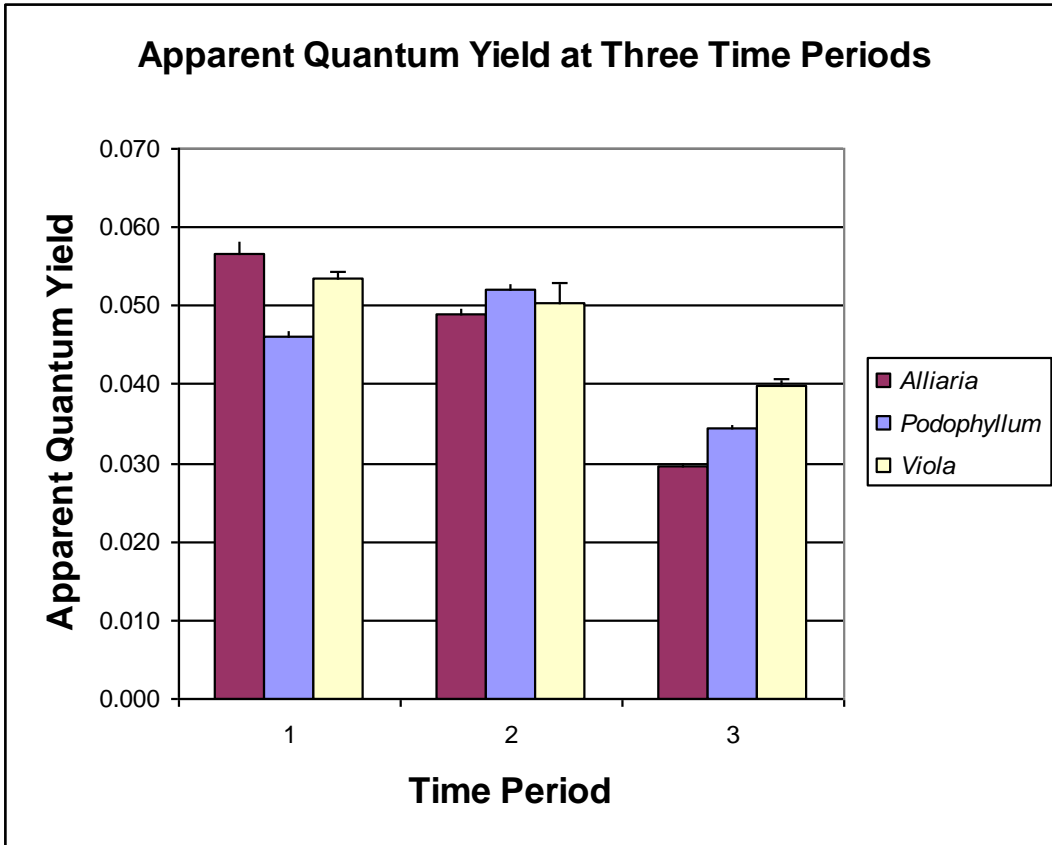
Fig. 5: The average dark respiration rate for each species at three time periods. Rates of change in Rdark over time varied among plant species. The relative difference between T1 Rdark values and T3 Rdark values (seasonal acclimation) w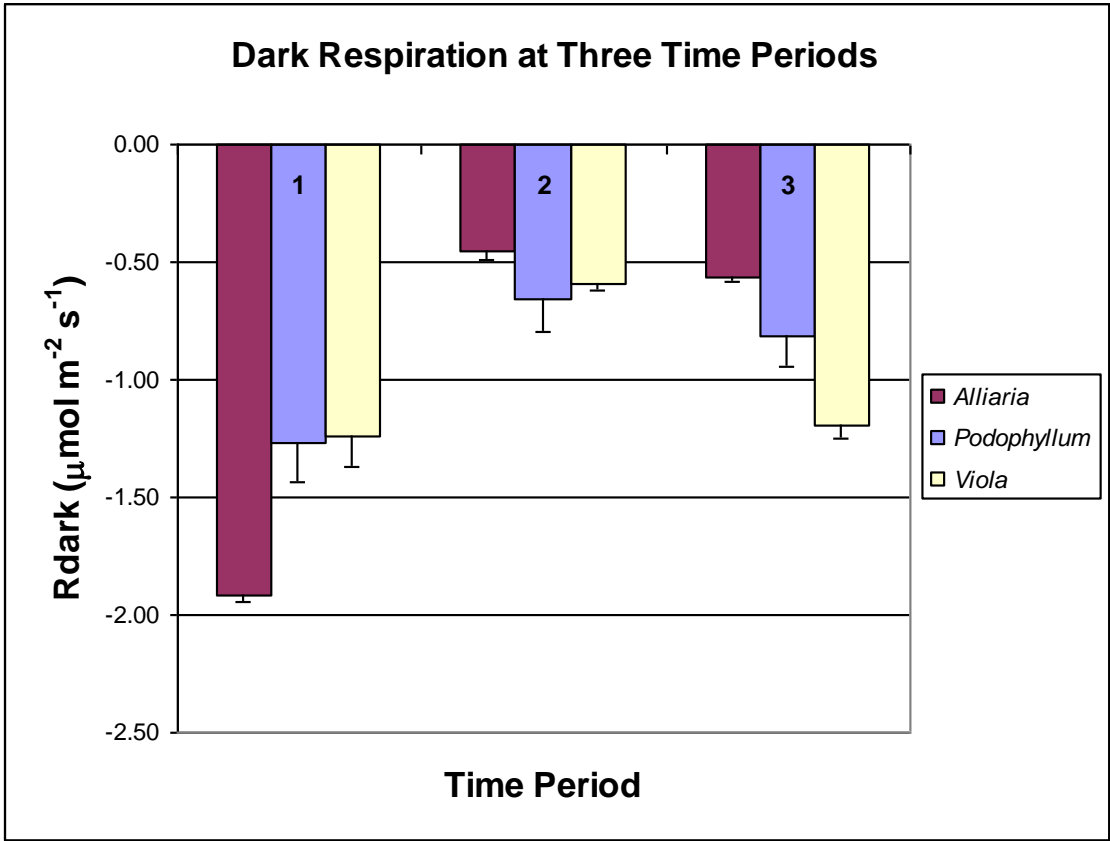as as follows: *Alliaria*=71%, *Podophyllum*=36%, *Viola*=3%.Fig. 5: The average dark respiration rate for each species at three time periods. Values were significant among species over time. The relative difference between T1 Rdark values and T3 Rdark values (seasonal acclimation) was as follows: *Alliaria*=71%, *Podophyllum*=36%, *Viola*=3%

Dark Respiration at Three Time Periods

Dark Respiration at Three Time Periods
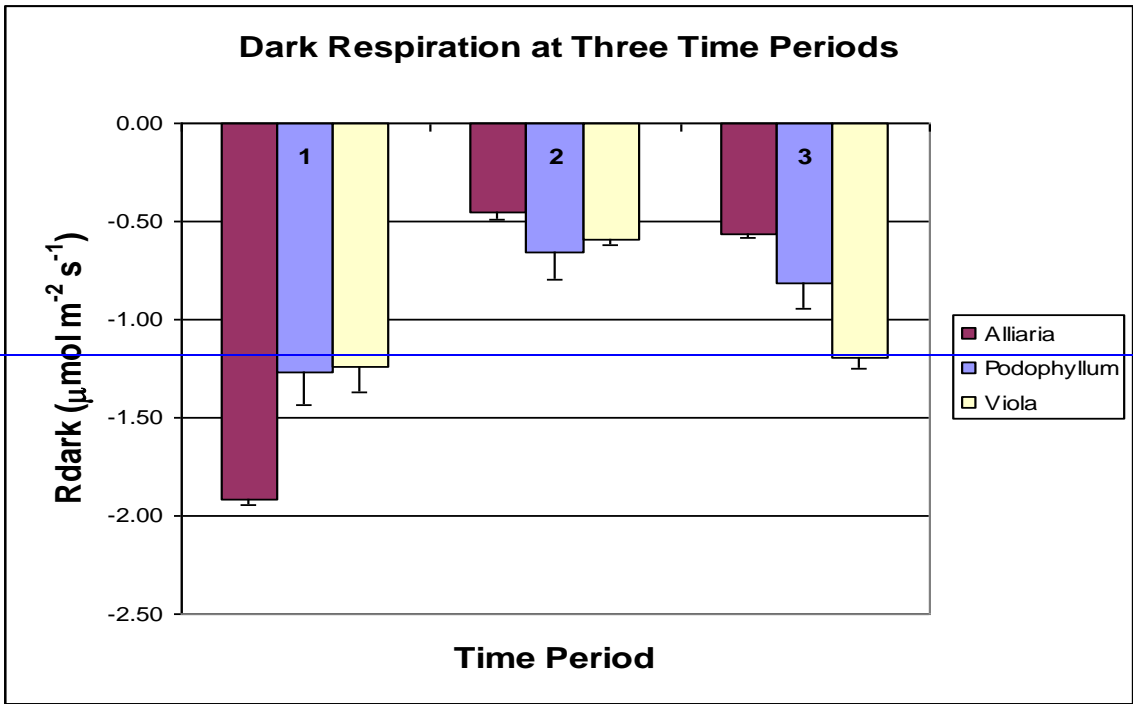
Fig. 6A: The average net photosynthetic rate for each species at three time periods. Values differed among species (regardless of time period), and among time periods (regardless of species). The relative difference between T1 Amax values and T3 Amax values (seasonal acclimation) was as fo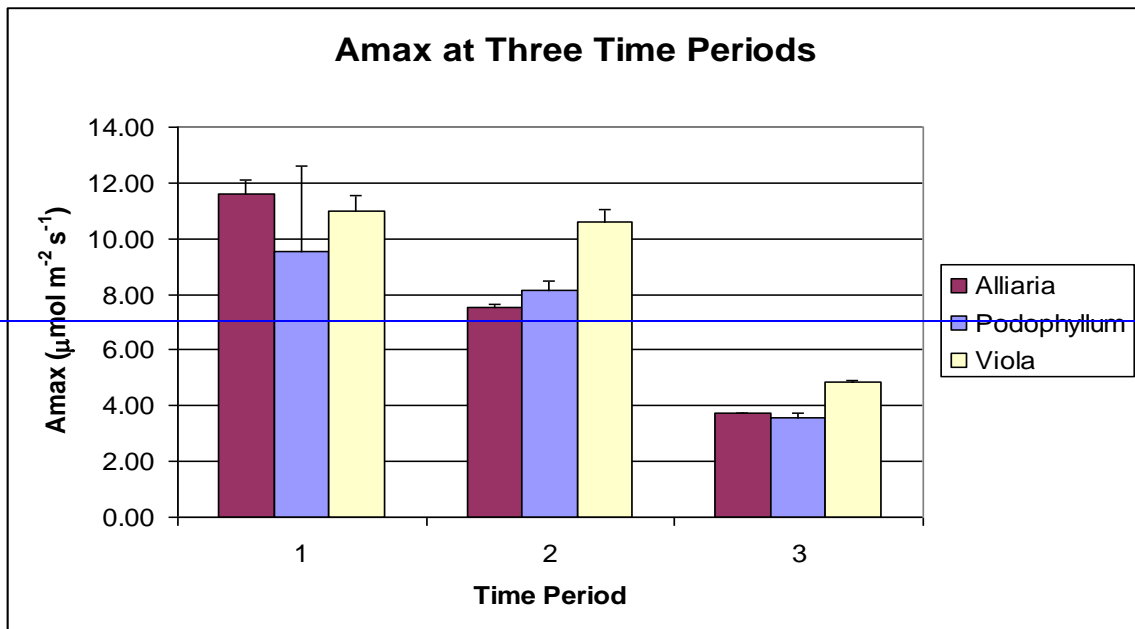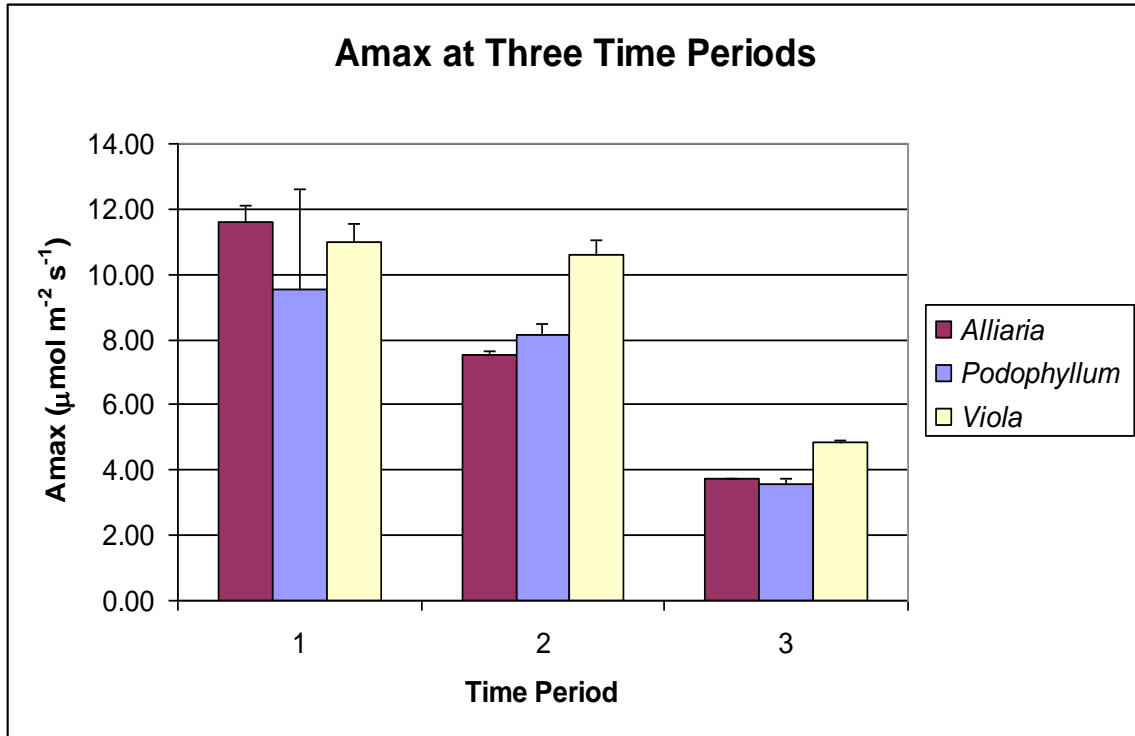llows: *Alliaria*=68%, *Podophyllum*=62%, *Viola*=56%.~~Fig. 6A: The average net photosynthetic rate for each species at three time periods. Values were significant between species (regardless of time period), and among time periods (regardless of species). The relative difference between T1 Amax values and T3 Amax values (seasonal acclimation) was as follows: *Alliaria*=68%, *Podophyllum*=62%, *Viola*=56%~~

Amax at Three Time Periods

Amax at Three Time Periods

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Fig. 6B: The average maximum carboxlyzation rate for each species at three time periods. Values differed among species (regardless of time period), and among time periods (regardless of species). The relative difference between T1 Amax values and T3 VCmax values (seasonal acclimation) was as follows: *Alliaria*=74%, *Podophyllum*=72%, *Viola*=72%.

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Vcmax at Three Time Periods
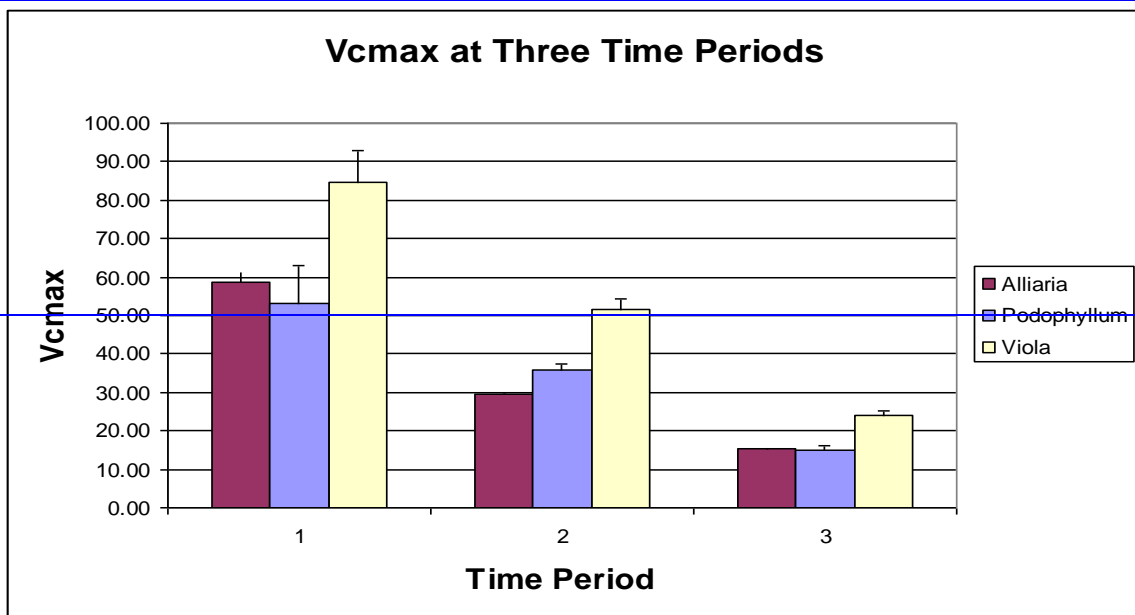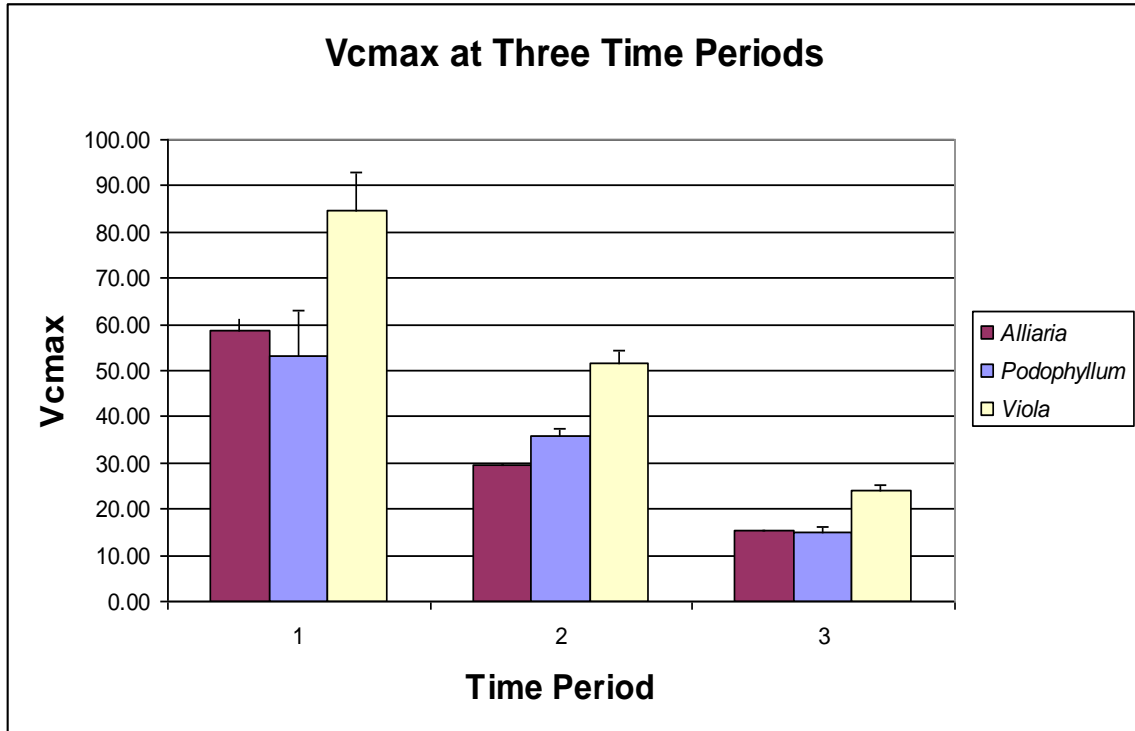

Vcmax at Three Time Periods

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Fig. 6C: The average intrinsic water use efficiency for each species at three time periods. Values differed among species (regardless of time period), and among time periods (regardless of species).Fig. 6C: The average intrinsic water use efficiency for each species at three time periods. Values were significant between species (regardless of time period), and between time periods (regardless of species).

Water Use Efficiency at Three Time Periods

Water Use Efficiency at Three Time Periods