AN ABSTRACT OF THE THESIS OF

Richard I. Bowden, Jr. for the degree of Master of Science in Entomology presented on January 28, 2003.

The Influence of Light Intensity on the Phytochemistry of *Chrysolepis chrysophylla* (Fagaceae) and its Relationship to the Herbivory of *Habrodais grunus herri* (Lycaenidae)

Abstract approved

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Jeffrey C. Miller

Defensive chemical and nutritive quality of young leaves were measured for 72 individual trees of *Chrysolepis* [*Castanopsis*] *chrysophylla* in conjunction with light intensities of two different stand types and population numbers of *Habrodais grunus herri* in the Cascade mountains of Oregon. Leaves were collected in the spring and leaf characteristics such as condensed tannins, nitrogen (crude protein), lignin, cellulose, hemicellulose, leaf resistence, and water content were measured. Light intensities were measured for each tree in the two stand types, clear-cut and old-growth stands. Population numbers *H. grunus herri* were measured by timed beating of each individual tree previous to leaf collection.

Population numbers of H. grunus herri were significantly different between stand types. In most cases larva of the butterfly failed to show up in timed beatings of trees in the clear-cut stands compared to equal length timed beatings in old-growth stands.

The two stand types, that were significantly different in light intensities, were found to be have trees that had significantly different levels of nitrogen (crude protein),

leaf resistence, and water content. Old-growth stands had significantly higher levels of nitrogen, and lower levels of leaf resistence and water content. The leaf resistence was found to be explained by a combination of the leaves' lignin, cellulose and hemicellulose content.

Intraspecific patterns of defense mechanisms are discussed in terms of current theories of plant defense.

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Richard I. Bowden, Jr.

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Redacted for privacy

Major Professor, representing Entomology

Redacted for privacy

Chair of the Entomology Department

Redacted for privacy

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of the Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Richard I. Bowden, Jr., Author

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Dr. Jeffrey C. Miller, Dr. Timothy D. Schowalter, Dr. Darrell Ross, and Dr. Barbara Taylor assisted in the editing of the text of the thesis. Penelope Pooler and Dale Usner (Statistics Department, OSU) were involved in the recommendations for analysis of the data.

TABLE OF CONTENTS

TABLE OF CONTENTS

LIST OF FIGURES

The Influence of Light Intensity on the Phytochemistry of *Chrysolepis chrysophylla* (Fagaceae) and the Relationship to the Herbivory of *Habrodais grunus herri* (Lycaenidae)

Introduction

Plant quality has been recognized since ancient times as a factor influencing insect population dynamics, "All trees, it may be said, have worms, but some less, as fig and apple, some more, as pear. Speaking generally, those least liable to be worm-eaten are those which have a bitter acrid juice." (Theophastus, 300 B.C.; from Feeny 1992). But the scientific community did not recognize this aspect of insect herbivore population dynamics until the mid-twentieth century.

The study of insect herbivore population dynamics during the first half of the twentieth century was dominated by the idea that predators, parasitoids, disease, food shortage and climate were the primary causes of herbivore population fluctuations. These ideas, however, did not satisfactorily explain observations that suggested a more complex system of interactions based on plant quality (Blaise, 1952, 1953; Miller, 1957).

In the 1960's researchers began to speculate on other mechanisms influencing insect populations. Plant nutritional quality and secondary metabolites became the focal point of much research (Greenbank, 1963; Morris, 1963), including the possibility that plant nutritional quality might be the primary factor influencing plant-insect co-evolution (Ehrlich and Raven, 1964).

It wasn't until the nutrient recovery hypothesis was proposed (Pitelka, 1964; Schultz, 1964) that changes in plant quality on herbivore population dynamics was emphasized. Also referred to as the lemming cycle model, it suggested a co-

evolutionary relationship, in which, lemming populations influenced plant growth and reproduction, and plant cycles, in turn, influencing lemming population fluctuations. Later, an alternative explanation was introduced, arguing that plant reproductive needs for nutrients, that build up on a four to five year cycle, were the primary factor influencing the relationship, not the lemming populations (Laine and Henttonen, 1983).

Subsequent research on plant quality/herbivore dynamics led to a hypothesis emphasizing plant water stress as a major mechanism influencing herbivore populations, the plant stress hypothesis (White, 1969). Psyllid outbreaks had been observed on Eucalyptus trees in abnormally dry summers that followed abnormally wet winters. It was hypothesized that summer water stress led to increased mobilization of nitrogen. Nitrogen is a primary element in the formation of proteins. Thus, the amount of nitrogen available in a plant is important to insect survival. Even though direct evidence was lacking, the search had begun for mechanisms explaining how plant nutrition influenced insect populations.

At the same time, work was being conducted on the importance of secondary metabolites on insect populations. A moth, *Operophtera brumata*, was found to experience reduced mean larval weights when subjected to an in vitro diet containing condensed tannins (Feeny, 1968). Condensed tannins reduce protein absorption in the insect midgut due to the tannin's property of binding to proteins, making the proteins unavailable. *O. brumata* was also found to avoid high levels of tannin in its food

source, oak leaves, by feeding at a time of year when tannin levels were low (Feeny, 1970).

Later, the introduction of the concept of plant apparency (Feeny, 1975, 1976; Rhoades and Cates, 1976) set the stage for a more comprehensive understanding of insect herbivore population dynamics. Plants were classified as either being ecologically apparent or unapparent . Long-lived plants in homogenous stands were classified as "apparent", and therefore, likely to be found by searching herbivores. Short-lived plants in heterogeneous stands were classified as "unapparent", and therefore, less likely to be found. In turn, the plants' life history stages (apparent or unapparent) selected for the type of secondary metabolites (defensive chemicals). Since apparent plants were more likely to be found by many different species of insect herbivore, it seemed likely that selection would favor a defensive chemical that would deter generalists as well as specialist types of insects. This defensive chemical category, which included terpenes and phenols, was designated as "quantitative". Since unapparent plants were less likely to be found by herbivores, the plant would be best defended with acute toxins that could deter generalists. This defensive chemical category, which included mustard oils and cardiac glycosides, was designated as "qualitative". Reducing attack by generalist herbivores was advantageous even though the plants were more likely to be found by specialist herbivore insects. Specialist herbivore insects are known to use biochemical toxins (qualitative chemicals) as phagostimulants, and even sequester them to function as defensive compounds of their

own (Fraenkel, 1959, 1969; Read et al., 1970).

At the same time as Feeny's work (1976) the concept of plant apparency was expanded to include not just individual plants, but different tissues of plants as well, such as leaf age (Rhoades and Cates, 1976). Later Rhoades (1979) expanded on White's (1969) work to suggest a more complex mechanism. Under stress plants allocate energy to the less expensive qualitative biochemical toxins and reduce production of the more expensive quantitative defensive chemicals, leaving the plant more susceptible to specialist insect outbreak.

However, dealing with physiological stress may be more complex. One strategy of plant apparency that has been described was the strategy to utilize resources quickly to grow, reproduce, and die, before being located by insects (Feeny, 1976; Rhoades and Cates, 1976).

However, resource availability is not always adequate. It has been suggested that resource availability may play a large role in chemical allocation in plants (Bryant et al., 1983). In conditions where light and carbon (CO_2) are adequately available, but nutrient resources in the soil are inadequate, plants may slow their rate of photosynthesis. Specifically, a lack of nitrogen leads to a lack of RuBP carboxylase, which is involved in photosynthesis. Photosynthesis is, thus, slowed. As photosynthesis is slowed, the growth rate of the plant declines. The decline in growth rate is usually greater than the decline in photosynthesis. Thus, excess carbon is now free to be used in the production of large amounts of quantitative defensive chemicals.

We end up with a plant that grows slow and is well defended against specialists and generalist herbivores.

Plants species that have adapted to conditions of adequate or excess nutrient availability and low light and carbon levels, utilize the excess nitrogen to produce qualitative defensive chemicals. Since carbon is the limiting factor, all available carbon is used for tissue growth, leaving excess nitrogen. The excess nitrogen is used for the production of qualitative defensive chemicals, thus, defending the plant against generalists, but not specialists. The carbon-nutrient balance hypothesis (Bryant et al., 1983) helps to account for shifts in plant defense and differing responses by herbivores that were not accounted for in the plant apparency hypothesis.

The plant apparency hypothesis did not account for other aspects of insect-plant coevolution that was accounted for later by Coley (1983). In her plant resource availability hypothesis, forty-six species of tropical trees were examined for insect damage in tree gaps on Barro Colorado Island, Panama. The plant species were categorized as either "pioneer" or "persistent". Pioneer species were defined as those that grew only in light gaps, grew rapidly and probably had short life spans. Persistent species were defined as those that grew throughout the forest understory, usually at a slow rate, and probably had a relatively longer life span. These two definitions are very similar to Feeny's (1975) definitions for unapparent and apparent plants, respectively.

However, contrary to the plant apparency hypothesis, both pioneer and

persistent species experienced non-significant differences in damage to young leaves. This indicated that young leaves are just as "apparent" on both pioneer and persistent species. Mature leaves, however, did have a significant difference in damage to leaves of pioneer and persistent species. The smaller amounts of leaf damage on mature leaves of persistent species correlated with high concentrations of phenols, tannins, fiber, cellulose, and toughness, and lower water content.

Coley (1983) offered an alternative to the plant apparency hypothesis, based on resource availability, not detectability. Plants were just as readily found by herbivores (perhaps specialists) no matter their distribution. However, to avoid excessive herbivory, plants evolved into two groups of strategists. Pioneer species, growing in high-resource habitats, could afford to grow quickly at the expense of reduced defenses, because the high availability of resources made leaves "cheap" to replace. Persistent species, growing in low-resource habitats, could not afford to grow quickly, because of lack of nutrients and light. Therefore, they put more energy into quantitative defenses. From Coley's work, habitat quality became the mechanism for selection of differing defensive strategies among species. The resource availability hypothesis accounts for evolved and persistent differences between species, but does not do so for intraspecific variation.

Concomitantly, Price (1991) proposed that insects-plant co-evolution acts intraspecifically as well. Known as the plant vigor hypothesis, he suggested that insects select the most vigorous plants of a species or population, and the most

vigorous plant parts of an individual. Observations of insects utilizing the most vigorous plants or plant parts have been numerous (Baker, 1972; Furniss and Carolin, 1977; Whitham, 1987; Fritz and Price, 1988; Roininen et al., 1988). Speculatively, the reason may be that rapidly growing tissue has non-limiting nutrients, thus large productions of qualitative defensive chemicals (which will be known as toxins from here on out), low production of quantitative defensive chemicals (which will be know as digestibility reducers), and high nutritive quality. These characteristics are adequate defenses against generalists, but not specialists. Although Price (1991) admits that his work seems to contradict that of White's (1969) plant stress hypothesis, the two ideas are just opposite ends of the same spectrum. An inferred extension of the resource availability hypothesis (which deals with interspecific variation) to intraspecific variation, may create the necessary link between stress and vigor. However, without direct evidence this assumption is very limited.

According to the carbon-nutrient balance and the resource availability hypotheses, plants have evolved chemical defensive strategies that are influenced not only by nutrient availability, but also by light availability. Thus, light and nutrient availability influence leaf quality of a plant. In turn, the leaf quality of the plant community determine the types and numbers of insect herbivores that can be supported.

Leaf quality affects several factors influencing insect population dynamics. Larval growth (Grossmueller and Lederhouse, 1985) and survival (Rausher and Papaj,

1983) are directly affected by leaf quality. Indirectly, larval growth and survival are affected by female ovipositional site selection (Stanton, 1982). A female's response to leaf quality is important if the highest possibility of survival is made available to the majority of her offspring. In many cases, as is the case with H. grunus, the larva does not choose the host plant. The female chooses the host plant. Thus, if a poor choice is made by the female, then the larva's chance of survival is reduced.

In a habitat such as the heavily logged mountains of Oregon, in which the majority of the landscape is being changed, larval survival depends on the female's response to host selection when ovipositing. If the female has evolved very specific cues that do not allow it to adapt to the change in the habitat structure, then eggs may be laid on a host plant of low leaf quality, thus reducing larval survival. On the other hand, very specific cues may be necessary in order that the female does choose a host plant with adequate leaf quality.

After the female has made her ovipositional preference, there are still a large array of factors influencing whether or not the immature insect will reach sexual maturity. Three critical components are the rate of growth, and the behavioral and physiological abilities of the larva to avoid predation (Slansky, 1993). Growth rate of insect larva can be affected by the chemical make-up of the host plant (Feeny, 1968; Bourchier and Nealis, 1993), the environmental temperature (Casey, 1993; Kimberling and Miller, 1988; Miller et al., 1984), or a combination of the two (Stamp and Yang, 1996).

Although temperature does have an affect on many lepidopteran larval growth rates (Grossmueller and Lederhouse, 1985), evidence indicates that leaf quality may have a greater impact on growth for some species (Grundel et al., 1998). Many herbivores preferentially feed on leaves with high protein and water content, low toughness and concentration of phenolic compounds (Coley, 1983; Feeny, 1992).

High protein content is dependent on the availability of nitrogen in the soil (Osier and Lindroth, 2001). Nitrogen is an essential component of all living organisms. Only oxygen, carbon and hydrogen are more abundant in higher plant cells. Nitrogen is present in many plant compounds including nucleoside phosphates and amino acids, that are the building blocks of nucleic acids and proteins, respectively (Tiaz and Zeiger, 1991). Nitrogen is a limiting nutrient which can affect other aspects of the plant besides leaf quality, such as defensive chemical production.

Leaf toughness is determined by the amounts of the cell was constituents. Cell wall components may affect insect feeding both nutritionally and physically. Nutritionally, the concentration of nitrogen in plant tissues is inversely proportional to the concentration of the cell wall constituents (Buendgen et al., 1990; Van Soest, 1982). This may occur to such an extent that plants high in cell wall constituents become undesirable (Scriber an Slansky, 1981). One cell wall constituent, lignin, although not considered an ancillary compound due to its more primary function as a structure builder, can act as an herbivore deterrent (Van Soest, 1992, pg. 186; Wainhouse et al., 1990). The more lignin in a leaf, the more leaf matter an insect must

consume in order to get adequate nutrition (Hagerman and Butler, 1991). This increases the time spent having to feed, thus, increasing the amount of time the herbivore is exposed to predators. Cellulose and hemicellulose act in a similar way (Hedin et al., 1996).

Leaf defensive chemicals, also known as secondary metabolites, are found widely in the vast majority of plants, indicating their importance in anti-herbivore defense. One category of quantitative defensive chemicals, tannins, that are associated with the oak family (Fagaceae), have been found to be associated with reductions in herbivory (Feeny, 1968; although see Johnson and Felton, 2001). Some tannins act as feeding deterrents (Behmer, et al., 2002), while other tannins bind with leaf proteins (Feeny, 1970) and digestive enzymes (Rhoades, 1979; Beart et al., 1985), which inhibit protein digestion by herbivores. The primary evidence for this mechanism comes from fecal nitrogen levels which increase significantly when either condensed or hydrolyzable tannins are added to larval diets. Many herbivores grow and survive poorly on diets with high tannin concentrations (Feeny, 1992; Bourchier and Nealis, 1993; Hwang and Lindroth, 1997; for contrary evidence see Bernebaum, 1983, Johnson and Felton, 2001, Close and McArthur, 2002).

All tannins do not have the same function. Instead of being a digestability reducer, one group of tannins, hydrolyzable tannins, may act as phagostimulants and toxins (Bernays, 1981; Mehansho et al., 1987; Clausen and Reichard, 1992), just as many nitrogen compounds act as phagostimulants and toxins simultaneously

(Fraenkel, 1969; Read et al., 1970). Since it is widely accepted that the structure of a chemical determines its function, hydrolyzable tannins differ from condensed tannins in their function due to structural differences. Condensed tannins all have very similar chemical structures, therefore, all act as general purpose defenses (Zucker, 1983). In contrast, hydrolyzable tannins, show diversity in their structure which indicates specificity, possibly to individual proteins (Zucker, 1983; Hagerman and Butler, 1991). Some host specific herbivores, however, have evolved adaptations that reduce the binding potential of tannins to essential proteins (Dussourd, 1993). High gut pH (Feeny, 1970; Berenbaum 1980; Martin and Martin, 1984; Dow, 1992) and surfactants (Feeny, 1969; Martin and Martin, 1984; Martin et al., 1987) in the digestive tract of lepidopteran larvae may reduce or reverse binding activity. However, specialists are still found to succumb to the chemical defenses of their host plants (Berenbaum, 1983; Hwang and Lindroth, 1997). Therefore, tannins have implications in influencing specialist herbivore populations.

The amount of light a plant receives is known to effect the make-up of secondary metabolites (Bryant et al., 1983; Waterman et al., 1984, Crone and Jones, 1999; Loughrin and Kasperbauer, 2001; Burns et al., 2002) and cell wall constituents (Sagers, 1992) in some plants. Light intensity can directly affect insect population dynamics (Gretorix and Davies, 1997). Light intensity is directly associated with stand structure. The more dense the overstory, the less light reaches the understory which, in turn, is a major factor influencing the species make-up of the understory. Stands of

Chinquapin (*Chrysolepis* [*Castanopsis*] *chrysophylla*) with little or no overstory, are exposed to high levels of light. Those stands with a dense overstory are exposed to diffuse levels of light. Differing levels of light intensity are attributed to the production of differing levels of plant chemicals, both structural, nutritional and defensive (Coley, 1983; Shure and Wilson, 1992; Dudt and Shure, 1994, Mendes et al., 2001).

Every photosynthesizing plant must be exposed to some level of light in order to produce the nutritional, structural, and metabolic components required for continued survival. Requirements vary between species based on evolutionary history and the conditions to which they are adapted. Differing environmental conditions may create varying intraspecific nutritional, structural and metabolic compound concentrations. The idea that high light and low light environments affect plant chemical defense production (Bryant et al., 1983) has implications in population dynamics of specialist herbivores. If environmental perturbations (i.e. fire, logging, etc.) change the structure of the habitat of a plant so that higher light intensities are present, the leaf chemistry of the plant may be altered as well. If the altered leaf chemistry is not sufficient for rapid larval growth, then larval survival is compromised.

Study Organism. The importance of the study of *Habrodais grunus herri* (Lycaenidae: Theclinea) is that it is considered a State Candidate Species by the state of Washington (Washington Department of Fish and Wildlife, 2001). Although common in Oregon, *H. grunus herri*, is at the northern edge of its range in southern

Washington. Management of that population is considered a priority. It is therefore essential when human actions may alter the stand structure of the host plant, to determine whether or not those actions will affect the populations survival. If differences in light intensity are associated with differences in leaf quality, then human alteration by clear-cutting will alter the survival of this population.

The butterfly, *H. grunus herri*, a currently accepted sub-species of *H. grunus*, can be found throughout the Cascade mountains and Coast Range of Oregon (Dornfeld, 1980; Hinchliff, 1996). The adult is an orange-brown winged butterfly with brown wing-margins. Individual variation exists in the amount of brown that extends from the distal and proximal wing margins inward to the center of the wing. The adult butterflies are active around the upper parts of their host trees in the evenings and mornings. Adults are seen flying from late August to early November. Female ovipositional activity, however, takes place primarily among *Chrysolepis* [*Castanopsis*] *chrysophylla* (Fagaceae), the host plant of *H. grunus herri*, in the understory. Females lay eggs singly on the underside of leaves.

The egg is the overwintering stage. The egg is a hemispherical shape covered with pentagonal straight-sided depressions, and pointed projections occur at many of the junctures of the depressions.

The larva is light green with the typical lycaenid shape, onisciform (slug-like). Within the study area of the Oregon Cascades, larval emergence occurs between late April to early June, just after bud-break of *C. chrysophylla*. Bud break of *C.*

chrysophylla occurs earlier farther south. The larval stage is an oligophagous herbivore on evergreen oaks (Fagaceae) in Oregon, which in addition to *C. chrysophyll*, includes *Quercus chrysolepis* and *Lithocarpus densiflorus*.

Pupation occurs between early July and mid August. The pupa are light green and are attached to the host plant leaves.

The host plant used in this study was *C. chrysophylla*, the golden chinquapin. In Oregon, C. chrysophylla can be found from 1000 m to 2600 m elevation in the Cascades, and from 600m to 1200m elevation in the Coast Range (Hitchcock and Cronquist, 1973).

The goals of this paper are to determine whether or not increased light intensity is correlated with differing levels of leaf chemistry and physical attributes, and in turn, differing levels of *H. grunus herri* population numbers.

Methods and Materials

Study Time Frame. The research described here was conducted between the summer of 1996 and the spring of 1998. Preliminary work and project design was done during the summer of 1996. All field work took place between the winter of 1996 and the fall of 1997. Lab work was conduced in the winter of 1997-1998.

Study Sites. The Oregon Cascade Mountains run north to south just west of the center of the state of Oregon. They are separated from the Oregon coast by the Oregon Coast Range and Willamette Valley (between 45.4°N and 42.1°N, 123.1°W and 121.5°W). Study sites were chosen in the Cascade Mountains under a predetermined set of criteria outlined below. Study sites were organized in a hierarchy from latitude to the successively smaller units of site, stand type, and tree. The sites were selected to compose a latitudinal gradient of paired sites (which were also used in a life history study). Each site was selected so as to include two adjacent stands, an old-growth stand with *C. chrysophylla* in the understory (referred to as the understory stand) and a clear-cut stand with *C. chrysophylla* plants without an overstory (referred to as the open stand).

The sites were located in the Willamette National Forest and on Bureau of Land Management (BLM) land near the Umpqua National Forest. Four of the sites were located in the Willamette National Forest, two in the Sweet Home Ranger District (Browder Creek site - 44°N 21' 00", 122°W 3' 30"; Heart Lake site - 44°N 23' 00", 122°W 3' 30") and two in the Lowell Ranger District (Tire Creek site - 43°N 49'

30", 122°W 32' 30"; Schwietzer Creek site - 43°N 48' 00", 122°W 37' 00"). The remaining two sites were located on BLM land just east of the Umpqua National Forest (Susan Creek site - 43°N 24' 00", 122°W 53' 40"; Shoup Creek site - 43°N 21' 30", 122°W 57'10"). The sites, from north to south, were located near the head waters of the Santiam River, near the Middle Fork Willamette, and near the South Umpqua River (Fig. 1).

Study sites were chosen based on the following characteristics of the two stand types. The understory stands had old-growth characteristics: heterogeneous age structure of dominant and sub-dominant trees ranging from small *Tsuga heterophylla* to large *Psuedotsuga menziesii*; a diversity of understory trees and shrubs, *Gaultheria shallon*, *Polysticum munitum*, *Rhododendron macrophyllum*, *Berberis nervosa*, *Acer circinatum, Holodiscus discolor*, and *Chrysolepis* [*Castanopsis*] *chrysophylla*); a diversity of herbacious plant species; and an absence of modern human alteration (Franklin and Dyrnress, 1973).

Open stands were clear-cuts. These stands were defined as previously forested areas now lacking large individuals of the dominant tree species once present. The open stands are exposed to large amounts of sunlight. They are dominated by pioneer and invasive species such as, but not limited to, *Rubus discolor*, *Rubus ursinus*, *Rubus lasiococcus*, *Rubus leucodermis*, *Cytisus scoparius*, *Pteridium aquilinum*, *Ceanothus velutinus*, various grasses (Poaceae), and newly planted *Psuedotsuga menziesii.*

The method for tree selection was different for open stands than for understory

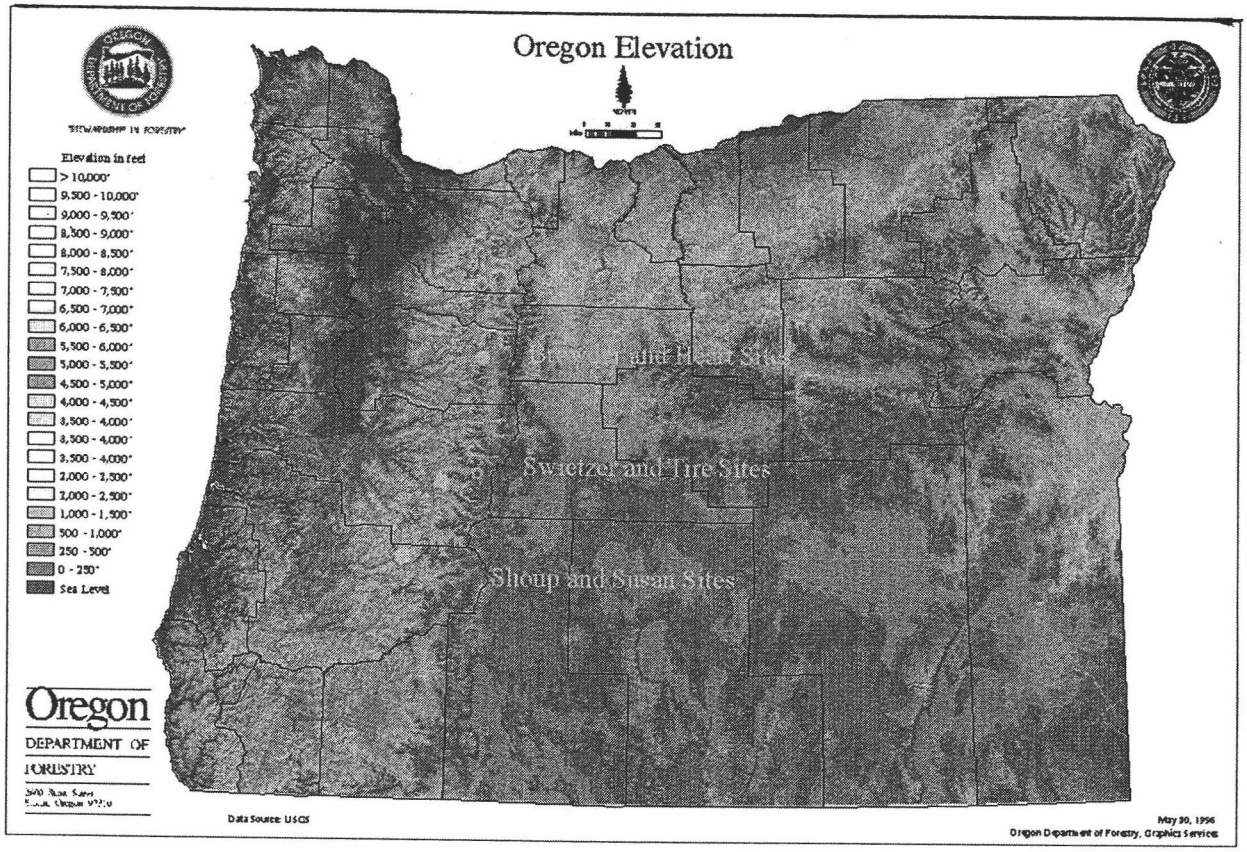

Figure 1. *Habrodais grunus/Chrysolepis* [*Castanopsis*] *chrysophylla* study site locations.

stands. There were many more trees in the adjacent open stands than in the understory stands. Trees in open stands were selected at random. *C. chrysophylla* in the open stands were selected by standing at the roadside near the center edge of the stand, looking at the second hand of my watch at a random moment to get a compass direction (unless the compass direction was outside the stand), walking the compass direction as a transect line, and using the 3rd, 6th, and 9th trees encountered. This process was repeated to choose three more trees. Six tree were selected within each stand.

C. chrysophylla trees in the understory stands were selected that were at least 20 meters within the stand from the edge. This criteria was chosen to reduce edge effects as a possible interfering factor (Chen et al., 1995). If there were more than six trees within a stand, then each tree was numbered and six trees were chosen randomly. If there were only six trees within the stand, then all were used. Six was the minimum number of trees in any stand. In some cases two or three trees were combined to make "one tree" because of the small size of the tree, and thus the low number of leaves.

The following measurements were taken in each stand: light intensity, temperature, immature stages (egg and larval) numbers, and leaf chemistry (nitrogen

Light Intensity. Light was measured using a LiCore LAI (Leaf Area Index) 2000 (Li-Core, Inc., Lincoln, Nebraska). The LiCore LAI 2000 has been successfully used in coniferous forests by making an adjustment by means of a ratio between shoot area and needle area for the species being measured (Gower and Norman, 1990). This

ratio for *Psuedotsuga menziesii* was used. This instrument measures all visible light reaching the fisheye lens, that is below 490 nm in wavelength (diffuse light). Leaf reflectance and transmittance are minimal below 490 nm, therefore, the instrument "sees" in black and white. The leaves are detected as black areas, thus effectively measuring Leaf Area Index. The instrument also calculates measurements of the white areas, diffuse light. The diffuse light is analogous to relative light intensity when compared to measurements taken at the same time in a nearby open (non-canopied) area.

The open stands were used as base-line measurements, since these stands were in full sun. The amount of light at individual trees in the understory stands were compared to the base-line to calculate a relative percentage of light reaching each tree. Light readings were taken in open stands concomitantly with readings taken understory stands. Two LAI 2000 meters were used to take measurements in each stand at the same time. The LAI meter clocks were synchronized. The first LAI 2000 meter was placed in the middle of the open stand and set to automatically take light measurements at 30 second intervals. The second LAI 2000 meter was taken into the understory stand and held at approximately chest height at the edge of each tree. Six measurements were taken for each tree within 30 second intervals of each other. In order to determine if there was a "best" time of day in which to take light measurements, multiple measurements were taken for each tree throughout the day (9 AM until 5:30 PM) at the Shoup Creek site. It was determined that between 10 AM

and 2 PM were the "best" times in which to take measurements. Measurements at most sites took no more than two and a half hours and were conducted between the aforementioned hours.

Temperature. Temperature was measured using a LiCore Data Logger. The probe was placed at approximately chest height just under the leaves of new growth. The probe was placed here because the larva of *H. grunus* tend to feed on the underside of the new growth.

Immature Stages Sampling of *H. grunus herri*. The sites were sampled for H. grunus herri eggs, larvae and pupae. An egg search preceded the larval and pupal sampling. The egg search was non-destructive in order to account for egg mortality and ovipositional preference, as well as to allow for egg development into the larval stage.

Two thousand leaves in each of the six trees in each of the stands at each of the sites (72 trees total) were scanned for eggs (144,000 leaves total). For trees in the understory stands this was typically most or all of the leaves on a tree. In several cases two or more trees were combined in order to meet this quota. This did not reduce the overall number of leaves scanned in a stand, because there were still a "set" of six trees. All trees, regardless of stand type, were scanned on all sides and from ground level to up to 2 meters. These methods resulted in approximately one hour of scanning, counting and recording per tree (72 hours of scanning and counting total). Direct scanning time was approximately fifteen minutes for each tree.

Individual trees were scanned twice, once in the winter (from October through Novemer moving south as the snows fell) after I was sure the adults had completed egg laying. As leaves with eggs were found with one or more eggs (typically one), a plastic bread bag clip was placed at the node of the leaf stem for each egg on the leaf. The second scanning took place in the last weeks of March before the larvae hatched. This was done not only to determine egg number, but egg survival rate as well. This might have affected the number of larvae found in the spring.

Larval abundance was measured in mid to late June using a timed beating method. The trees that were randomly selected the summer of 1996 and tagged for eggs in the winter of 1996, were the same trees used to determine larval abundance. This was necessary in the understory stands due to the limited number of individual trees in each stand. Thus, the same was done for the open stands.

The timed beating method used in this study was performed with a square piece of muslin (0.56 m^2) supported from each pocketed corner by two wooden dowel rods (1.0 m) which made an "X" across the muslin sheet. A third stick usually chosen from the forest floor was used for the beating. The beating sheet is held in one hand at the intersection of the two wooden dowels, and placed beneath the leaves of the tree to be sampled. The other hand holds the forest floor stick and beats the foliage directly above the beating sheet. The purpose is to knock loose all insects of interest onto the beating sheet.

Each of the stands in the six sites received an equal time sampling (by beating

sheet). Each tree was sampled for 100 seconds for larvae (pupae were recorded seperately, but were considered equivalent to larva; 600 seconds of direct beating per stand). In understory stands alll parts of every tree were sampled. In open stands, trees were sampled on all sides from the ground to about 1.5 meters above the ground.

Counts of other Lepidoptera larva, spiders, and ants were conducted in an attempt to account for competition and predation as a possible factor affecting egg and larval numbers. Due to the ecologically functional role represented by each of these groups it did not seem necessary to classify individuals below this general taxonomic level. Larval Lepidoptera were considered competitors. Spiders and ants were considered potential predators. The counts were conducted using the previous beating method outlined above.

A caging study was also conducted to determine if predation by avian species might account for differences in numbers of *H. grunus herri* between stand types. The study did not generate ample data to be discussed in the results section.

Leaf Chemistry. Leaves were collected in the spring of 1997. Approximately 21 days after bud break (late March), 20 grams of whole leaves from C. [Castanopsis] chrysophylla were collected from each of the six individuals in each stand at each of the sites (72 individuals, 1440 grams). From understory stands every possible young leaf was clipped from each tree. In open stands, leaves were clipped from as many varying areas of the tree as possible, from all sides and heights. The leaves were labeled by pair, site stand and individual. They were then placed in an ice

chest, transported back to the lab the same day, and placed in cold storage (-10°C). Since the sites were located north to south, the southerly sites were anticipated to reach bud break slightly earlier. Therefore, the first sites sampled were the most southerly, Shoup and Susan Creek sites. The last sites sampled were the most northerly, Heart Lake and Browder Creek sites. A generator and electronic balance were used to weigh leaves immediately on site after they were cut.

Leaf water content was determined by weighing leaves at the site of collection, and then again after freeze drying. Using an electronic balance, the mass of the fresh leaves was determined within five to ten minutes after cutting the leaves from the tree (travel time from each tree to the balance in the back of the truck accounted for the elapsed time). The leaves were then stored in a resealable plastic bag, marked and placed on ice in a cooler. On returning to the lab, the samples were placed in the cold room (-10°C). Within seven days the samples were freeze dried. Sets of six bags (each bag representing an individual tree) at a time were wedged and held open with paper clips to prevent their closing during the freeze-drying process. Closing of the bags would prevent complete drying to occur. The bags were then placed in a Lyophilizer.

After drying, the leaves were weighed and ground. Weighing the leaves after drying established the water content of each sample of leaves. The mass was measured using the same electronic balance that was used in the field to measure the fresh weight of the leaves. The leaves were then ground powder-like particles utilizing a 1

mm mesh screen on the vegetation grinder at the Forest Resources Laboratory, Oregon State University. After grinding, each individual sample was separated into three parts to conduct the tannin, nitrogen and fiber assays (~ 3.33 grams in each separated sample). The bags were labeled appropriately.

Nitrogen, cellulose, lignin and hemicellulose of the leaves were extracted and measured using the Kjeldahl method described by Harris (1970). The extraction and analysis were performed by the Forage Analytical Service (Dr. Phil Whanger lab) at Oregon State University. The Kjeldahl procedure measures the total amount of nitrogen per gram of leaf. Since nitrogen, on average, makes up sixteen percent of an amino acid (the components of proteins), multiplying total nitrogen by 6.25 gives a crude estimate of leaf protein concentration, often referred to as crude protein (Robbins, 1983). The neutral detergent fiber analysis (Goering and Van Soest, 1970) determines the percentage of cell wall constituents (CWC) which consists of lignin, cellulose, hemicellulose, suberin, and cutin. Acid detergent lignin (Goergin and Van Soest, 1970) is a measure of the acid indigestible residue (AIR lignin) in leaf tissue, which includes structurally bound tannin and cutin in addition to lignin (Preston et al., 1997). Kjedahl nitrogen, fiber and AIR lignin quantities were expressed as a percentage of dry leaf weight.

Tannin extraction and analysis methods followed those procedures outlined by Hagerman (1995). After the leaves had been freeze-dried, massed for water content, ground down, and separated, a third of each tree sample was used to determine actual

condensed tannin content. The leaves were first subjected to cell wall breakdown with 70% aqueous acetone (Scalbert, 1991). One gram of ground leaves was stirred with 10 ml of the 70% aqueous acetone for 15 minutes, vacuum filtered, and then rinsed with another 20 ml of 70% aqueous acetone. This process was repeated three times, saving consecutive filtrates into one flask. Celite 545 was used as a filtration aid to keep the leaf material from clogging crucible pores. Acetone was evaporated from the filtrate with a rotary evaporator using a 30°C water bath. The resulting aqueous solution was rinsed twice with an equal portion of ethyl ether to remove low molecular weight phenolics. A rotary evaporator was used to remove any ethyl ether remaining in the extract solution after separation. Distilled water was added to the extract in a volumetric flask to raise the volume to 25 ml. Extracts were stored in sealed polypropylene tubes in the freezer at -10°C.

The radial diffusion method was used to assay the amount of tannin extracted from each sample (Hagerman, 1987). Agarose gel was mixed with bovine serum albumin (BSA) and solidified in 10cm petri dishes. Well holes were punched using a #4 cork borer. The well holes were filled with the phenolic extract and placed in incubators at 24°C for four days. The petri dishes were then stored at 4°C for preservation.

Leaf toughness was measured using a "spring punchmeter" designed by Peter McEvoy. The "spring punchmeter" used a blunt needle attached to a spring system to punch through leaves. The leaves were placed on a small platform that has a small

hole that is situated below the blunt needle. The device used a dial that the operator would slowly turn to increase the pressure of the needle on the leaf. As the pressure increased the meter on the dial measured the pressure in J/m^2. When the needle punched through the leaf, the pressure observed on the meter was recorded.

Statistical Analysis. Simple linear regression was used to statistically analyze the data. Simple linear regression was used because of the continuous nature of the independent variable, light intensity. Light intensity was being compared individually with each of the dependent variables (eggs, larvae, water, nitrogen, lignin, cellulose, hemicellulose, tannin, and leaf toughness). The data was processed using Quattro Pro (Corel Corp., Ottawa, Ontario, Canada). The amount of variance explained by the fitted regression is expressed as the coefficient of determination (r2) using ANOVA. The chosen level of significance was 5%.

Results

The goals of this paper were to determine whether or not increased light intensity was correlated with differing levels of *C. chrysophylla* leaf chemistry and physical attributes, and in turn, differing levels of *H. grunus herri* population numbers. I had predicted that plants exposed to lower light intensities would have higher numbers of *H. grunus* eggs and larva, higher concentrations of water and nitrogen, lower concentrations of lignin, cellulose, hemicellulose and condensed tannins, and less toughness. Concomitantly, the reverse would be true for plants exposed to higher light intensities. The results, in general, did support my prediction.

Light Intensity. There were two stand types, open and understory. The open canopy stands were always situated in clear-cuts. Therefore, the open canopy light intensities were all at 100 percent of available light. The understory stands were always situated in old-growth stands. The understory stands had a wider range of light intensities (2.3 to 47.3 percent) and thus a continuum. The mean light intensity for the understory stands was 14.76 percent (Fig. 2). There was a large disjunction in light intensity levels between the understory and open stands creating a break in the continuum between 47.4% and 99.9%.

Temperature. The temperatures in the understory stands were 5.5°C lower on average. Open stand ambient air temperatures averaged 25.75°C. Understory ambient air temperature averaged 20.25°C.

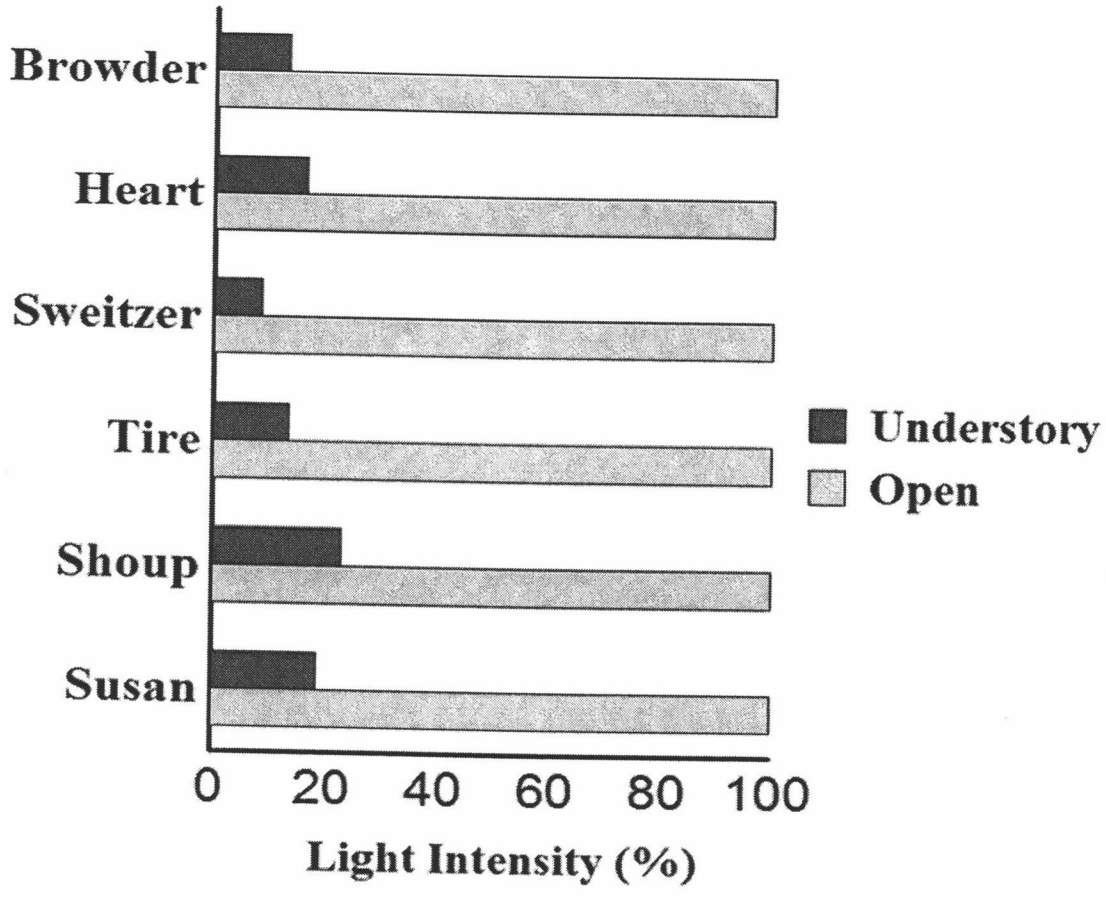

Figure 2. Light intensity for understory stands and open stands for each of the six sites.

Egg Population Numbers. The number of eggs found on leaves was inversely related to light intensity (Fig. 3). The data indicated a significant relationship between egg numbers and light intensity. The light intensity explains slightly more than 40% of the variation in the egg numbers (r^2=0.404, n=68, p<<0.001, SE of Y=7.06).

Larva Population Numbers. While a relationship exists between the stand type and the presence of larva, the larval numbers were not related to light intensities. There was a statistically significant inverse relationship between the two variables (r^2=0.139, n=68, p<0.001). However, the variance of the data from the regression line was high (SE of Y=0.997), indicating no relationship between these two variables (Fig. 4).

Other Arthropod Densities. All of the three groups of arthropods that were measured had fewer number in the open stands than in the understory stands. This indicates that competition and predation are greater in the understory stands than in the open stands. Therefore, competition and predation are not factors influencing the low H. grunus population numbers in the open stands.

Water Content. Leaf water content was predicted to be lower in open than in understory stands due to the assumption that higher transpiration rates occur in warmer environments (+6°C on average) than in cooler environments. The water content of leaves was inversely related to the amount of light they received (Fig. 5). This

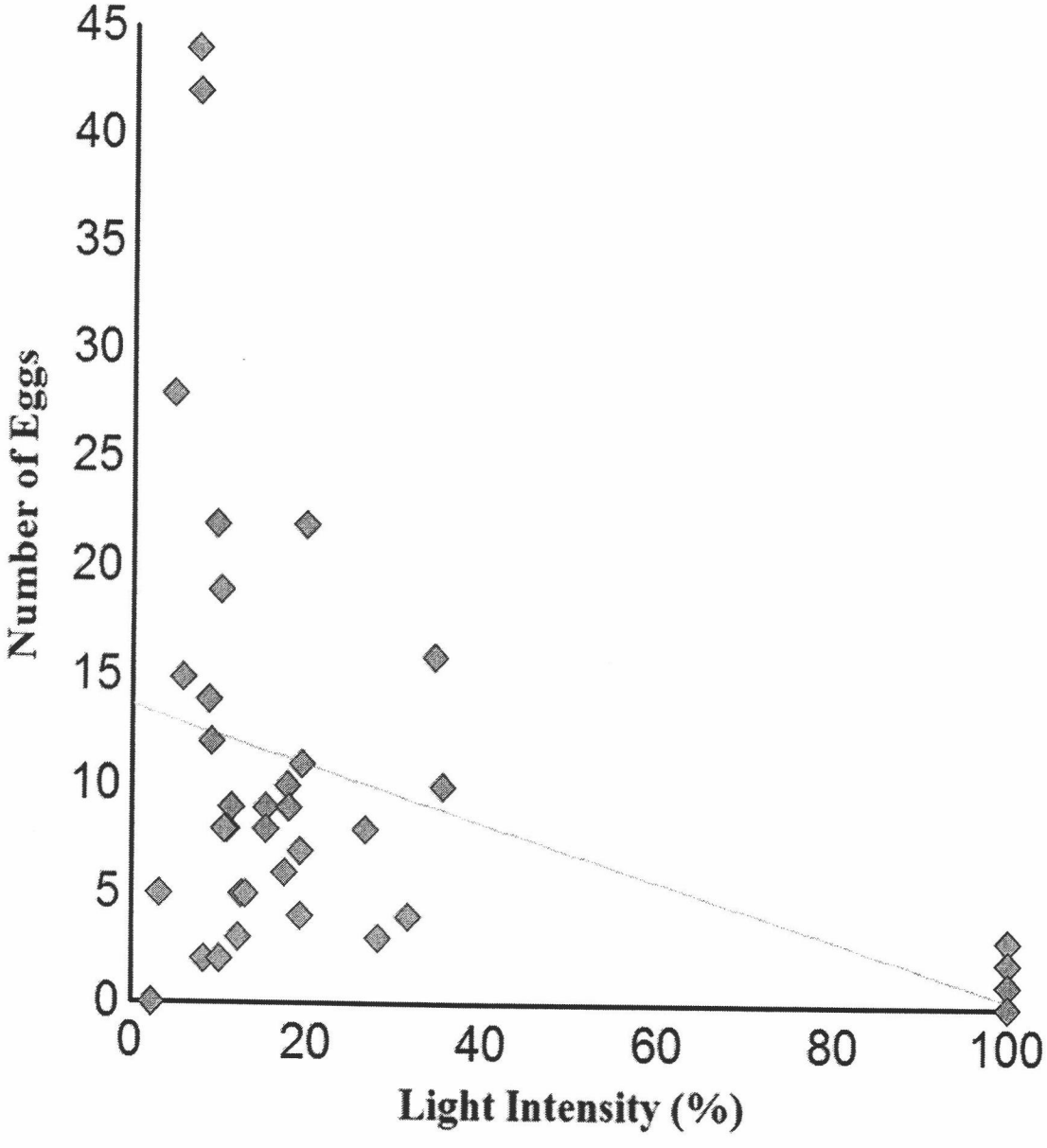

Figure 3. The relationship between the number of eggs per tree and the amount of light to which that tree is exposed (r^2=0.404, n=68, p<<0.001, SE of Est.=7.06).

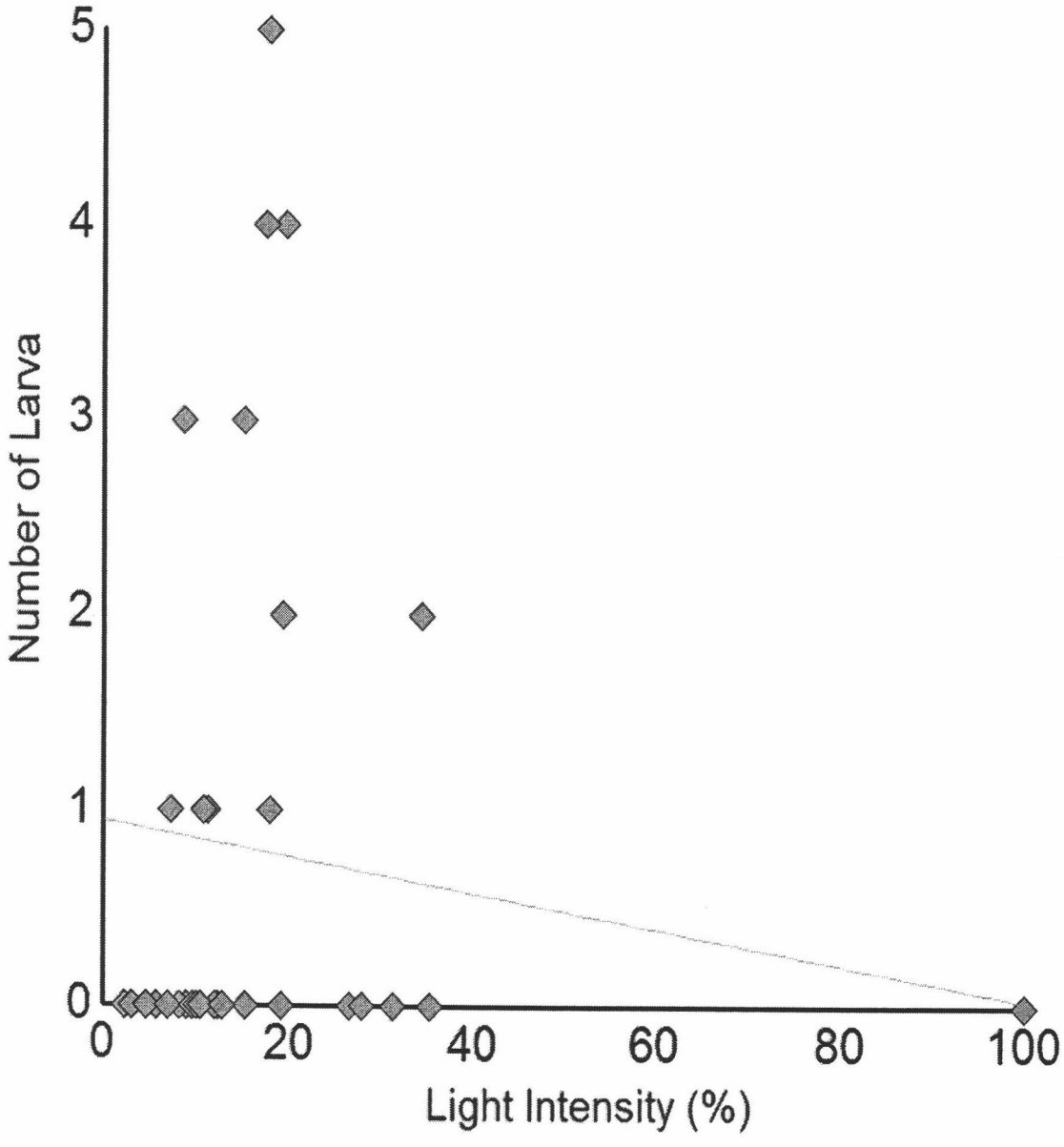

Figure 4. The relationship between the number of larva on a tree and the amount of light to which the tree is exposed (r^2=0.139, n=68, p<0.001).

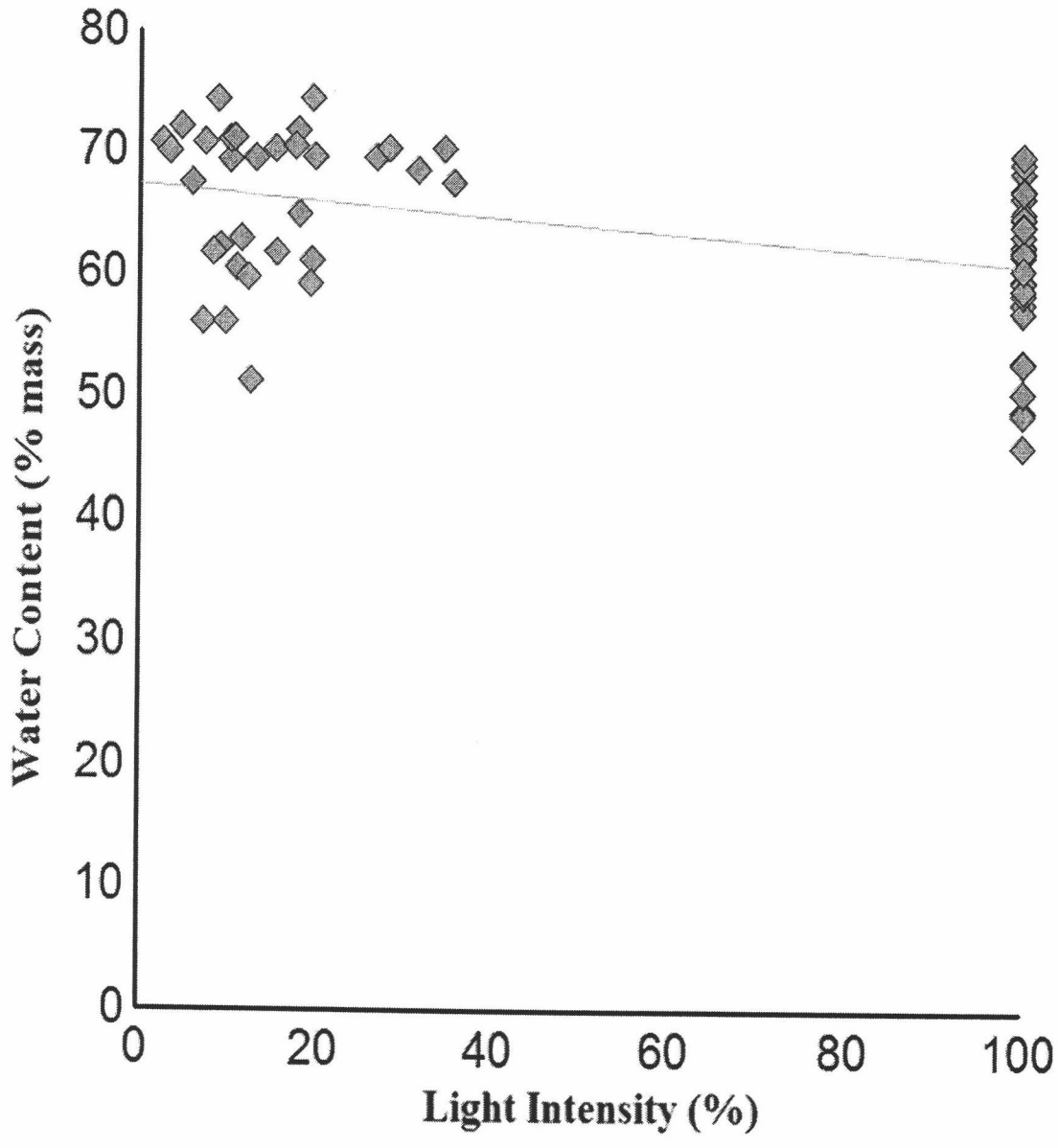

Figure 5. The relationship between water content of leaves and exposure to light (r^2=0.17, n=68, p<0.001, SE of Y=6.06).

relationship was significant, and 17% of the variance in the water content was explained by the light intensity (r^2 =0.17, n=68, p<0.0005).

Nitrogen Content. As predicted, the nitrogen content of leaves was found to be inversely related to light intensity. As light intensity increased, the nitrogen content of the leaves decreased (Fig. 6). According to the data, a significant relationship exists between the light intensity and the percentage of nitrogen per leaf. Twenty-eight percent of the variation in the nitrogen levels is explained by the light intensity levels (r^2=0.28, n=67, p<<0.0001).

Lignin. The lignin content of the leaves was directly related to light intensity (Fig. 7). The relationship was found to be significant. Slightly more than thirteen percent of the variance in the lignin content of the leaves was explained by the association with light intensity (r^2=0.135, n=66, p=0.0024).

Cellulose. Cellulose content of *C. chrysophylla* leaves was not related to light intensity (Fig. 8). The relationship was found to be insignificant. Only 0.4% of the variance in the cellulose content was explained by light intensity (r^2=0.004, n=65, p=0.62). However, cellulose was inversely and significantly related to nitrogen content (Fig. 9; r^2=0.300, n=65, p<<0.001).

Hemicellulose. The hemicellulose content of leaves was not related to light intensity (Fig. 10). The relationship was insignificant. Only 0.8% of the variance in the hemicellulose content was explained by light intensity (r^2=0.008, n=60, p=0.50).

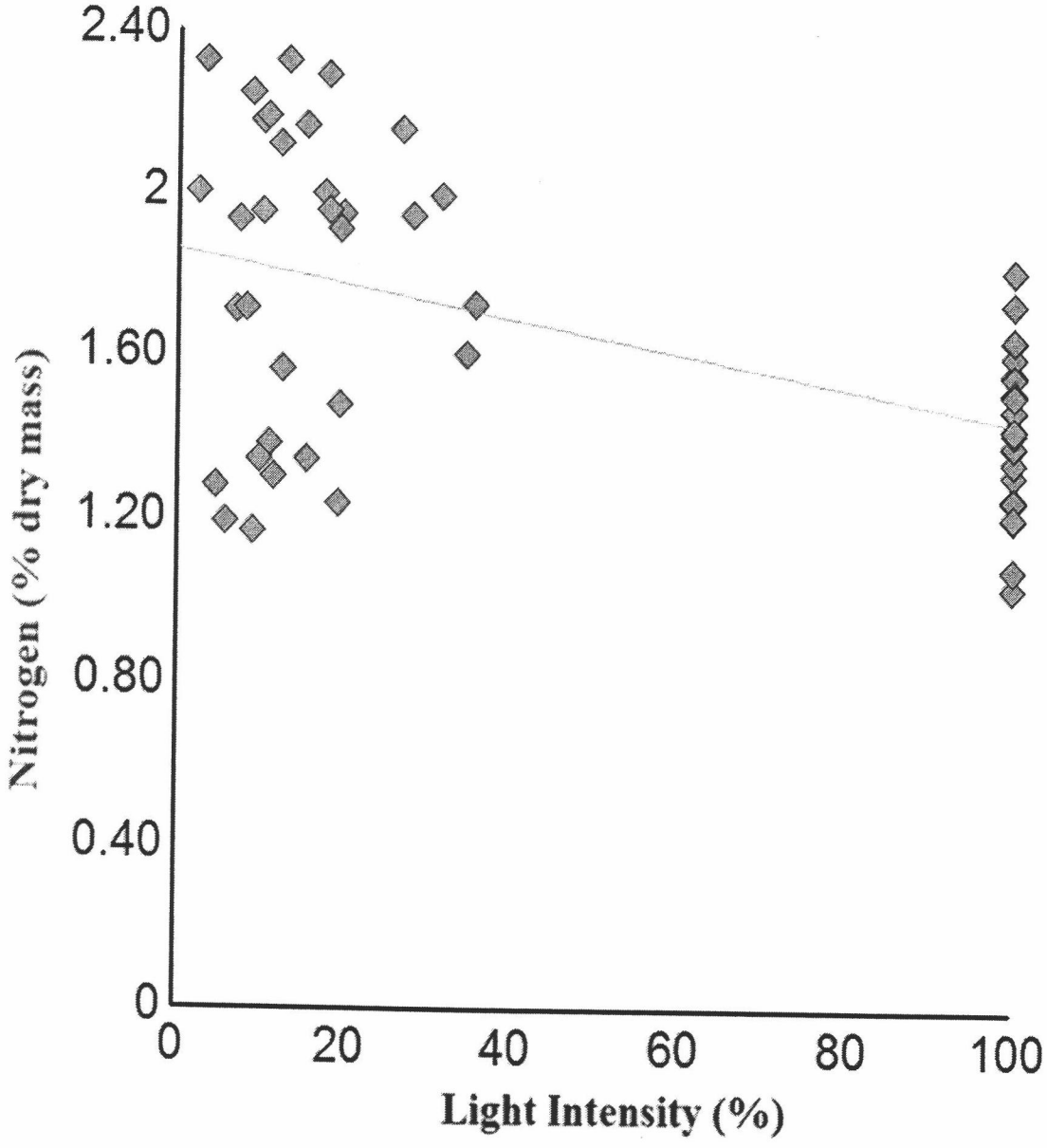

Figure 6. The relationship of nitrogen content of leaves to the amount of light to which the leaves are exposed (r^2=0.28, n=67, p<0.001, SE of Y=0.296).

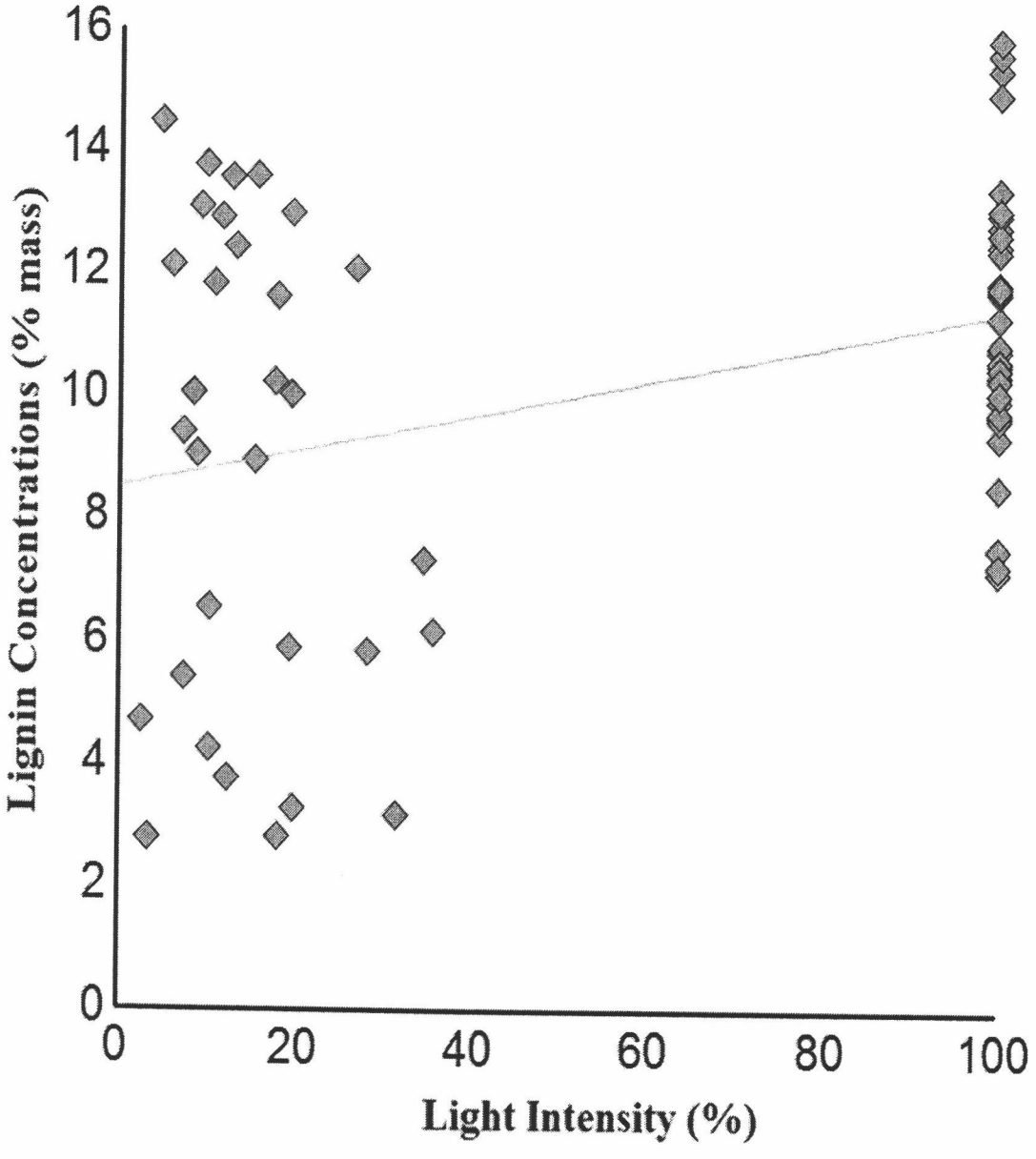

Figure 7. The relationship between lignin concentration in leaves and the amount of light to which the leaves were exposed (r^2=0.135, n=66, $p < 0.005$).

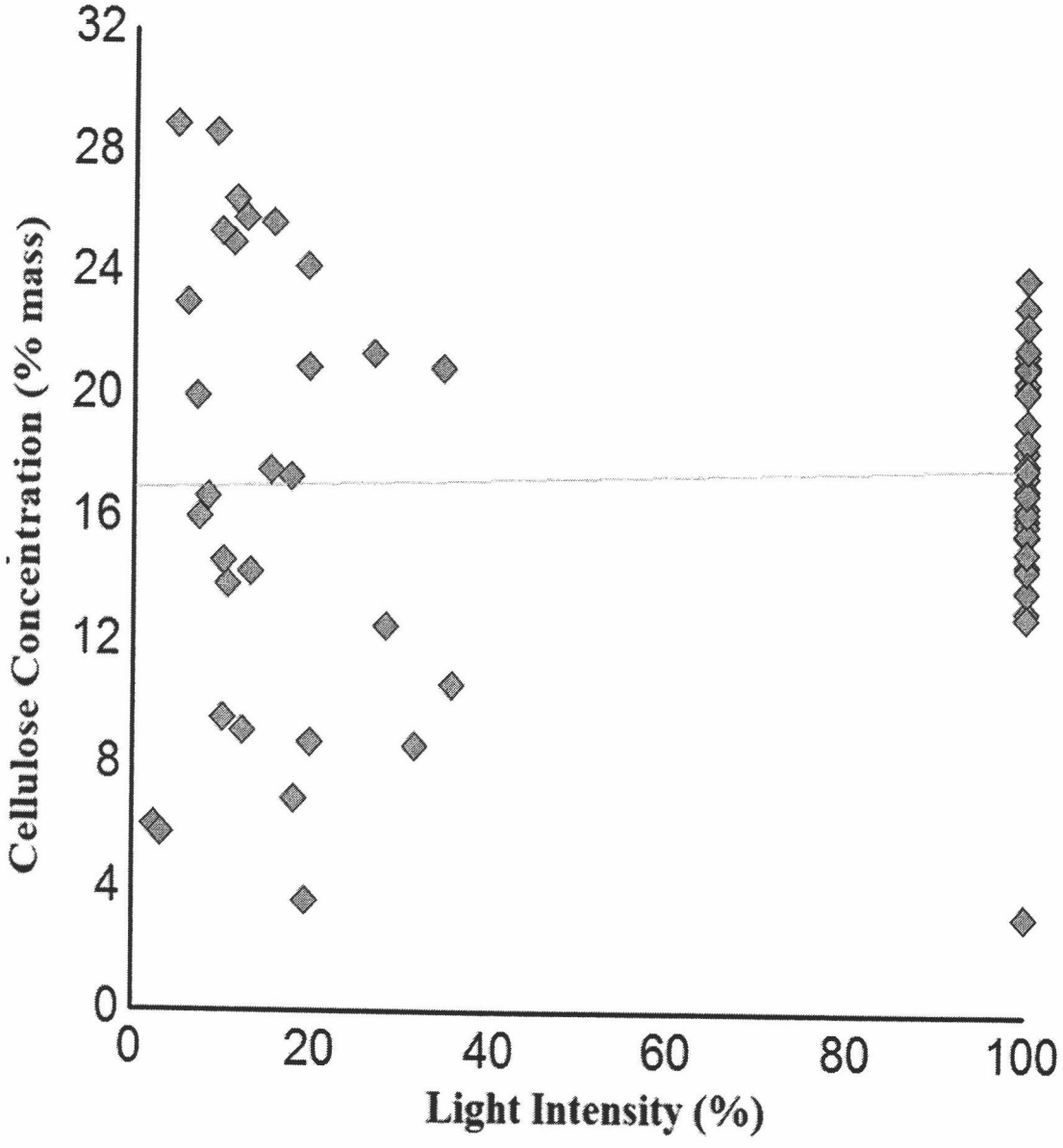

Figure 8. The relationship between the cellulose content of leaves and the amount of light to which the leaves were usually exposed (r^2=0.004, n=65, p>0.5).

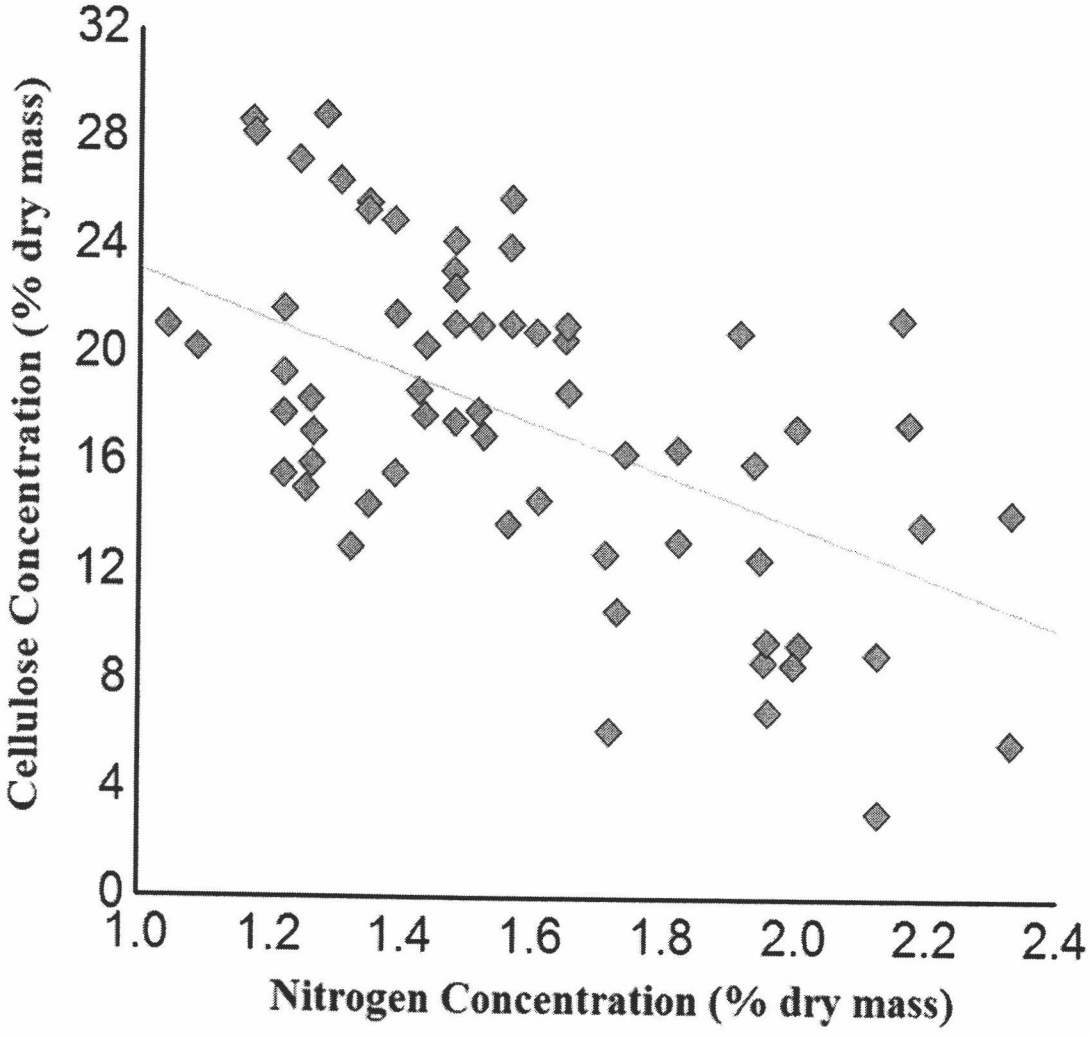

Figure 9. The relationship between the cellulose content of leaves and the nitrogen content of the same leaves (r^2=0.300, n=65, p<<0.001).

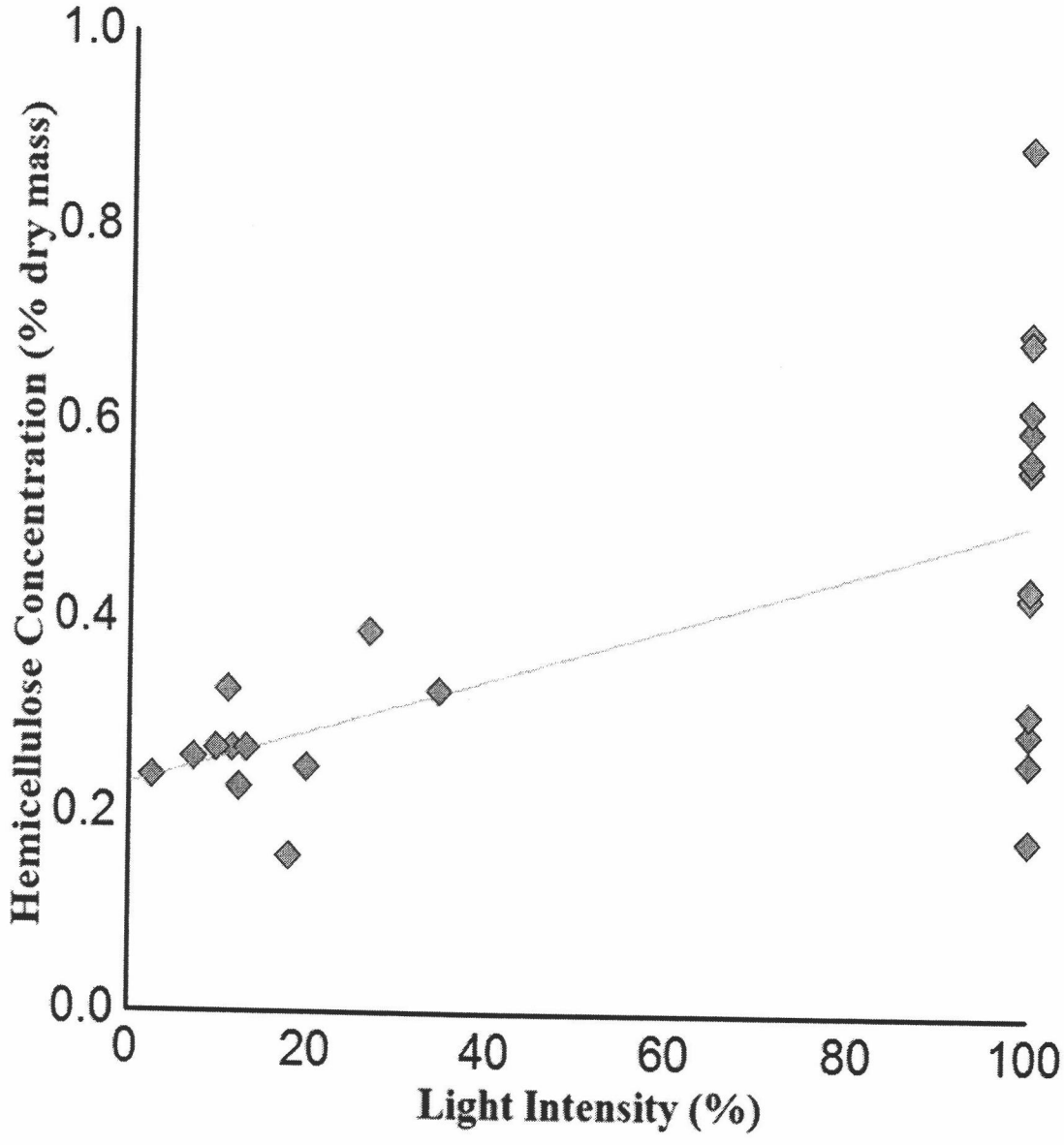

Figure 10. The relationship between hemicellulose concentration in leaves and the amount of light to which they are exposed (r^2=0.008, n=60, p<0.5).

Condensed Tannins. The tannin content of leaves was found to be directly related to light intensity. As light intensity increased, the condensed tannin content of leaves increased (Fig. 11). The data indicate a significant relationship between the two variables. However, only ten percent of the variation in the condensed tannin content was explained by light intensity (r^2=0.101; n=65; p=0.01).

Leaf Toughness. Leaf toughness was directly related to light intensity. As light intensity increased, leaf toughness increased (Fig. 12). The relationship was significant. Nearly thirty-eight percent of the variation in the leaf toughness was explained by light intensity (r^2=0.375; n=24; p=0.0015). However, as can be seen in Figure 11, the leaf toughness varied considerably in the leaves from the open stands. The standard error of the Y estimate for the entire sample population was 0.157, compared to the same statistic for just the understory stands was 0.04. Comparison of these statistics indicates the disparity in the data from the open stands.

The chemical composition of leaf toughness was explained by two chemicals, lignin and cellulose. Leaf toughness was positively related to the amount of lignin in the leaf (Fig. 13). As the amount of lignin increased, the leaf toughness increased. Lignin accounted for 26% of the variation in leaf toughness (r^2=0.258, n=22, p<0.01). Leaf toughness was also positively related to cellulose content (Fig. 14), which accounted for thirty-six percent of leaf toughness variation (r^2=0.361, n=18, p<0.007).

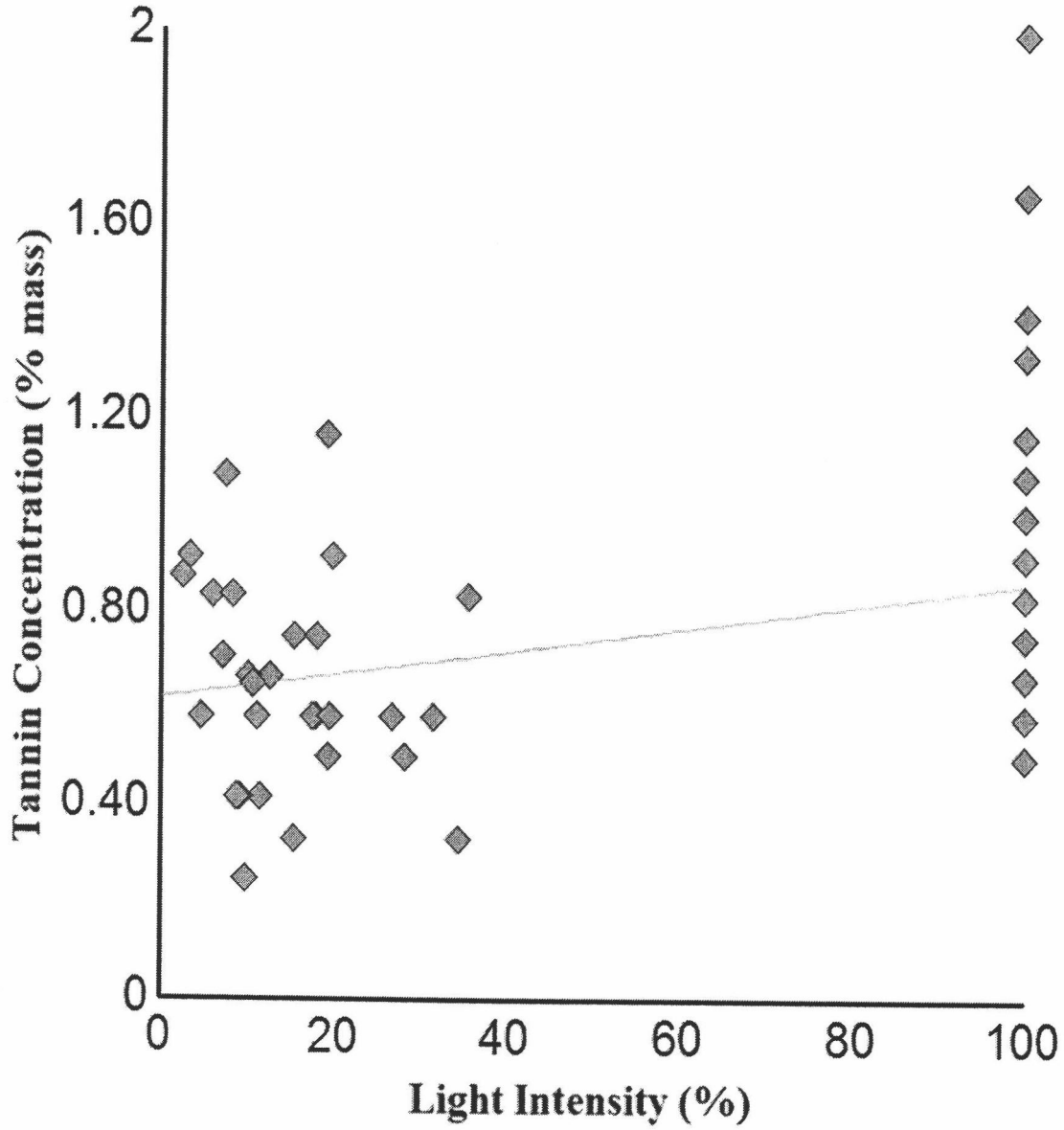

Figure 11. The relationship between the amount of condensed tannin in leaves and the amount of light to which they are exposed (r^2=0.101; n=65; p<0.02).

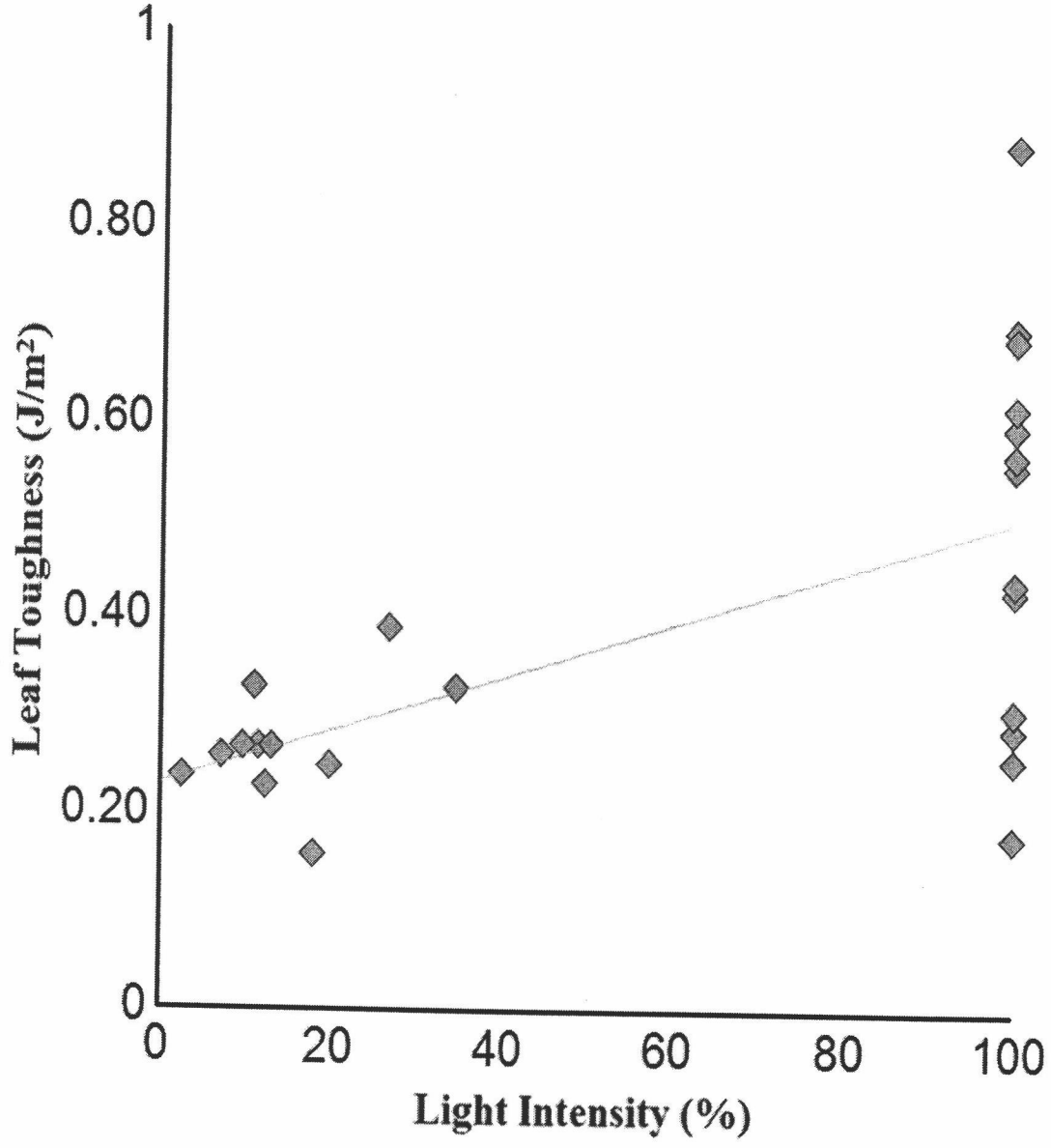

Figure 12. The relationship between a leaf's toughness and the amount of light to which it is exposed (r^2=0.375; n=24; p<0.002).

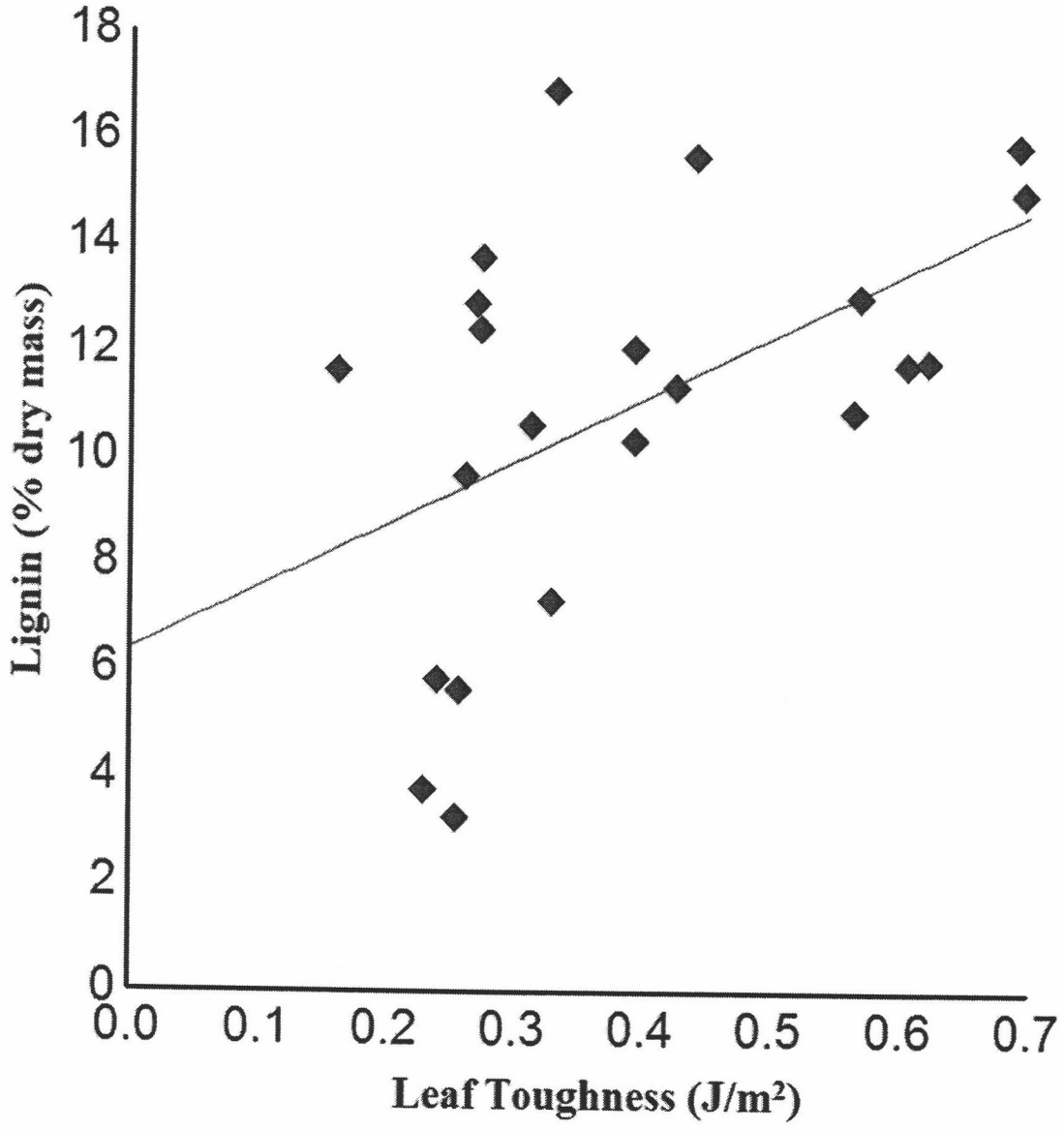

Figure 13. The relationship between the amount of lignin in a leaf and the leaf's toughness (r^2=0.258, n=22, $p<0.01$).

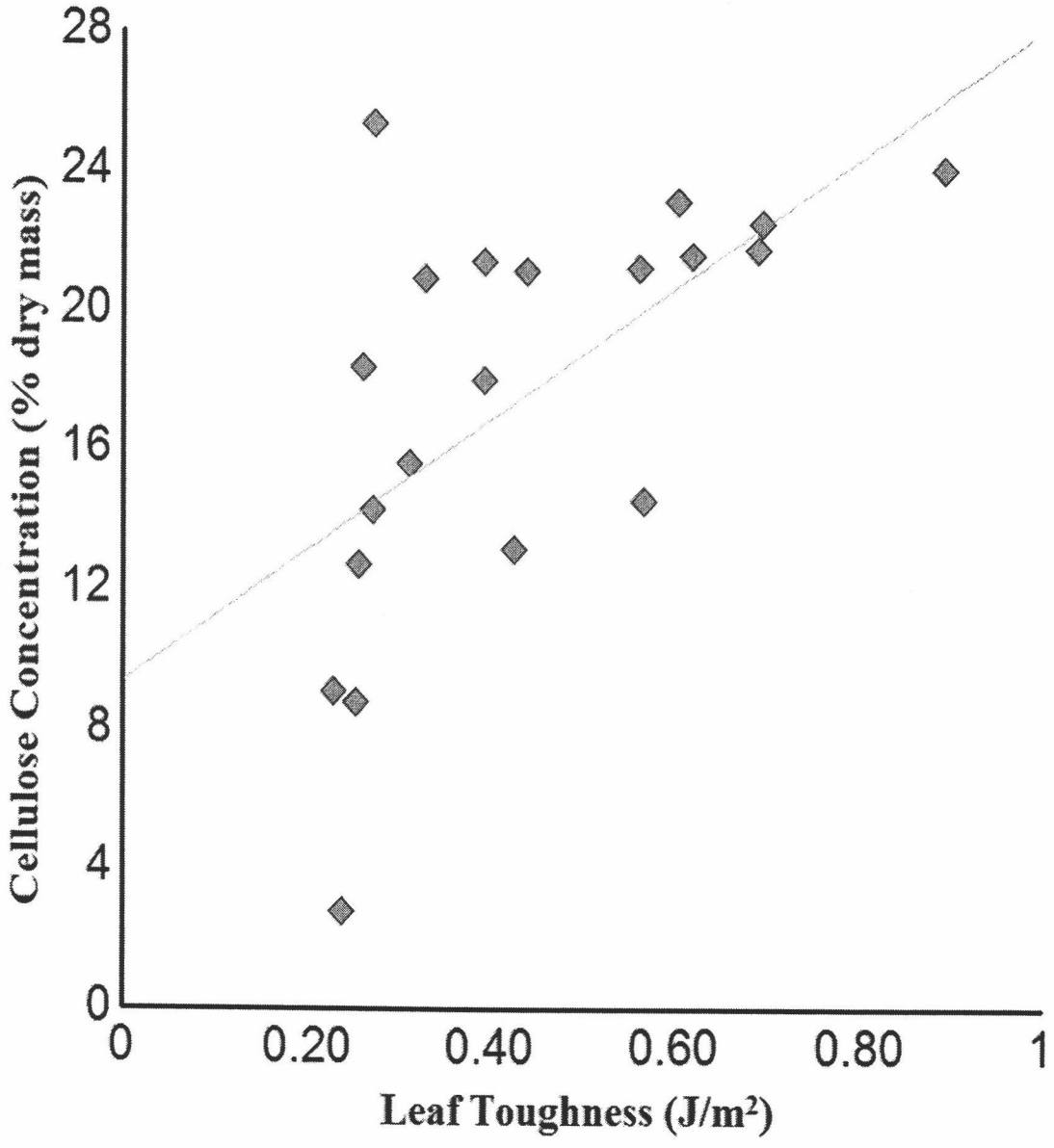

Figure 14. The relationship between the amount of cellulose in a leaf and the leaf's toughness (r^2=0.361, n=18, p<0.007).

Discussion

The primary objective of this study was to examine the possible role light intensity plays in shaping the nutritional quality and chemical defense of plants in relation to insect herbivores. The results indicate that as *C. chrysophylla* plants are exposed to higher light intensities, the nutritional quality of the plant for *H. grunus herri* decreases and the chemical and structural defenses of the plant increase. Consequently, the number of eggs oviposited on plants exposed to higher light intensities decreases.

Fewer eggs on open stand trees indicates that female *H. grunus* have a preference (Singer 1986) for the *C. chrysophylla* trees in understory stands on which to oviposit. It has been suggested that female adult insects will typically oviposit on plants of higher nutritional quality that maximize larval performance (Wiklund, 1974, 1981, 1984; Whitham, 1980; Rausher, 1982; Price and Clancy, 1986), and more specifically, on plants of higher water content (Preszler and Price, 1988). However, other research indicates that the female insect does not discriminate (Thompson, 1988; Courtney and Kibota, 1990). Whichever the predominant case, based on the evidence of this study, *H. grunus* does seem to have a preference for plants of higher nutritional quality. However, the mechanism for that preference remains to be seen.

Water content of leaves is espoused to be one of the more important factors in larval growth rates of Lepidoptera (Feeny, 1992). Higher water content in *C. chrysophylla* does seem to be an important factor influencing *H. grunus* larval

numbers.

Nitrogen was also found to be higher in understory stand plants. Nitrogen is an important building block of living organism, making up sixteen percent of protein composition. Therefore, the acquisition of nitrogen from the soil is very important to plants. Most plants acquire nitrogen from the soil through their roots in the form of ammonium and nitrates. Consequently, acquisition of nitrogen from plants is very important to insect herbivores. The need for nitrogen rich plant material may be so great that insect herbivores will accept higher levels of defensive chemicals in exchange for higher levels of nitrogen (Nichols-Orians, 1991).

The results of the relationship between light intensity and nitrogen suggest that there is either more nitrogen available in the soils of the understory stands (which was not tested) or that the plants in the open stands are carbon limited, which in turn would lead to nitrogen becoming limited (Chapin et al., 1987). Assuming *C. chrysophylla* is a shade adapted plant, these results contradict what has been "generally found in numerous studies"; that low nitrogen levels exist in the leaves of shade adapted plants (see Chapin et al., 1987, pg. 53). On the other hand, evidence exits indicating that increasing age and increasing light exposure reduce the amount of available nitrogen in slow-growing woody shrubs that produce carbon-based defensive chemicals such as tannins (Perry, 1984).

In either case, the fact that there is more nitrogen available in the leaves of plants in the understory stands is an indication of why more *H. grunus* eggs and larvae

were found in understory stands. Because nitrogen is a limiting factor in many situations having a host with more available nitrogen can be advantagous (however, see Di Giulio and Edwards, 2003).

Nitrogen was negatively associated with both cellulose and lignin. This indicates that as cellulose production increases in *C. chrysophylla* nitrogen assimilation decreases. In addition, as the lignin (which has been shown to be a primary agent of leaf toughness in *C. chrysophylla*) increased, nitrogen decreased, making the leaves of the open stand trees even less palatable and nutritionally adequate to *H. grunus*.

Even though cellulose is the most abundant organic molecule in plants, it does not seem to play a role in deterring insect herbivory on *C. chrysophylla*. This may be due to its chemical inactivity towards proteins. In contrast, lignin, although structurally important, is chemically active with proteins. Sorting through large amounts of leaf matter and discarding large amounts of cellulose may be a common task for the insect herbivore gut. Cellulose, equally abundant and sparse in both stand type plants, does not seem to be affected by light intensity. Furthermore, hemicellulose has been known to act as a deterrent to herbivory in some plants (Hedin et al., 1996). However, in the case of *C. chrysophylla* this does not seem to be the case.

Another group of carbon-based chemicals that are know to deter herbivory are the tannins. Higher tannin levels in plants can affect insect herbivore assimilation of

proteins. The results of my study support work indicating that intraspecific levels of tannins are significantly higher at higher light intensities. Higher tannin levels have been found at higher light intensities in oaks (Fagaceae) (Reed and McCarthy, 1996), in other families of woody plants (Dudt and Shure, 1994; Shure and Wilson, 1993), and in other plant families (Waterman et al., 1984; Nichols-Orians, 1991). In the same vain that Reed and McCarthy (1996) found support for the carbon-nutrient balance hypothesis, my research indicates that plants in conditions of higher light intensity have higher levels of tannins, and that cellulose and nitrogen have an inverse relationship, which also supports the carbon-nutrient balance hypothesis (Bryant et al., 1983). The significantly higher levels of tannins at higher light intensities are another factor possibly contributing to the absence of eggs and larva from *C. chrysophylla* trees in open stands.

After tannins, lignin plays a primary role in plant defense for plants that use carbon-based defensive chemicals. Plant cell wall rigidity is due primarily to lignin. Lignin is the second most abundant organic molecule in plants after cellulose. The chemical structure of lignin (a phenol-like compound bonding with cellulose and proteins) makes cell wall carbohydrates virtually indigestible to herbivores (Taiz and Zeiger, 1991). The stability of the carbon-carbon and ether bonds in lignin contributes to the stability of lignin against chemical or enzymatic attack (Hagerman and Butler, 1991).

Lignin has been shown to be the primary structural agent in the lower

epidermis of leaves (Casher, 1996). Leaf toughness has been shown to reside primarily in the lower epidermis of several oak species (Choong, 1996, Casher, 1996). Thus it may be extended that lignin is the principal molecule responsible for leaf toughness. The data from my study indicate a positive relationship between leaf toughness and lignin, with lignin accounting for over 25% of the variation in leaf toughness, which also supports the assumption that lignin is the chief agent of leaf toughness.

Leaf toughness may be such an important plant defense that it may affect a wide range of insect characteristics (in an evolutionary sense) including morphology, feeding behavior, and spatial and temporal patterns (Raupp, 1985). As suggested by Feeny (1970) toughness in leaves may be the single most important deterrent to leaf feeding by Lepidoptera larva. A closely related tree species, *Castanopsis fissa*, was examined by Choong (1996) for toughness. Toughness was found to be most prominent in the midrib of each leaf which was also the least consumed by the caterpillars feeding on the plant. The next toughest part of the leaf were the secondary veins which were also the second least consumed part of the leaf. Avoidance of these areas by caterpillars lends support to the idea that leaf toughness deters herbivory. Therefore, it is understandable that higher concentrations of lignin, alone, could deter larval feeding by *H. grunus* on plants in open stands.

Conclusions

The idea that low-light conditions affect the nutrient availability and the amount of carbon-based defenses produced by a plant (Bryant et al., 1983) was supported by the evidence of this study. Trees in understory plots had higher levels of nitrogen and lower levels of condensed tannins compared to trees in open stands (nitrogen content was inversely proportional to light intensity, and condensed tannin concentration was proportional to light intensity).

The resource availability hypothesis (Coley, 1983) suggests that an evolutionary survival strategy is selected for in plants due to resource availability. Plant species with high resource availability (light gaps) compensate for tissue loss to herbivores by rapid growth (and regrowth) at the expense of reduced defenses. Plant species adapted to low resource availability take longer to grow, and cannot compensate for tissue loss by the strategy of rapid growth. Therefore, these species attempt to deter herbivore attack by producing greater quantities of defensive chemicals. The results from my study indicate that understory individuals produce fewer defensive chemicals (condensed tannins) and more nitrogen. "Light gap" (open stand) individuals produced greater quantities of defensive chemicals and assimilated less nitrogen, contrary to Coley's work (1983).

The evidence from my research would indicate that the carbon-nutrient balance hypothesis and resource availability hypothesis are contradictory of each other. However, Coley and Bryant et al.'s work (1983) advocated for evolutionary mechanisms between species, and did not encompass intraspecific variation of plants

that my work does.

According to Price (1991) herbivores select the most vigorous individuals within a population. My evidence supports the idea that this specialist herbivore, *Habrodais grunus herri*, has evolved an adaptation to utilize individuals of *Chrysolepis chrysophylla* with higher nutritional quality and lower defensive compounds based possibly on light intensities. However, these were not the most vigorous plants as hypothesized by Price (1991). The fastest growing individuals, those in the open stands, had few, if any eggs, and no larva. Egg numbers in the two plot types indicate that females are predominantly choosing to lay eggs on understory plants that have higher nitrogen content, lower toughness, and lower condensed tannin content of the leaves. Larval numbers indicate that larvae are surviving better on these plants as well. There is a "critical importance of plant biochemistry" that plays a role "in governing the relationships between" (Ehrlich and Raven, 1964) *Chrysolepis chrysophylla* and *Habrodais grunus herri*.

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