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The 'slow-growth-high-mortality' hypothesis: how plant species, leaf quality, and the third trophic level contribute to the mortality of two common leaf-tying microlepidopteran herbivores

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THESIS ABSTRACT

I investigated how the survivorship, abundance, and development of two common microlepidoteran leaf-tiers on four species of oak change in response to leaf quality and exposure to the third trophic level, and used those results to validate predictions under the slow-growth-high-mortality hypothesis. In chapter 1, I begin with a review of the literature by examining the components of plant traits that contribute to the success of insect herbivores and how plants can alter both defensive compounds and nutritional quality in order to deter herbivory. I then describe how changes in leaf quality and defense can be overcome by insect herbivores, one means by which is shelter building. Finally, I introduce the slow-growth-high-mortality hypothesis and describe how plant quality, ecosystem engineering, and the third trophic level can be used to validate the predictions of said hypothesis. In chapter 2, I present the results of an experiment that examined the bottom-up and top-down effects on two common leaf-tying microlepidopterans on four species of oaks by manipulating their exposure to the third trophic level. I found that the two leaf-tier species experienced the first trophic level differently but responded similarly to the third trophic level. Plant traits differed among oak species and changed from one generation of leaf-tier to the next. However, plant traits, measured as principal components, were for the most part uncorrelated with measures of survivorship, development, and parasitism, and were, at the very most, inconsistent between the two leaf-tier species. The patterns of mortality for both leaf-tiers did not reflect the effects of tree identity on larval development and, hence, did not follow the predictions of the slow-growth-high-mortality hypothesis.

CHAPTER 1.

Anti-herbivore plant defenses and the third trophic level: combined effects on insect herbivores.

INTRODUCTION

Interactions of plants and herbivores are complex and involve both evolutionary responses in behavior and physiology of plants and the herbivores that attack them (Ehrlich and Raven 1964, Opler 1974). Plants can alter the patterns of attack of phytophagous insects by varying leaf quality, both constitutively and as a response to herbivory, and through apparency to herbivores (Feeny 1976, Rhoades and Cates 1976, Price *et al.* 1980, Coley *et al.* 1985). Because nitrogen is very often a limiting resource in insects and plant nitrogen content is low, phytophagous insects are forced to consume plant material many times their own body weight (Allen *et al.* 1974, Mattson 1980). In addition, water availability can be somewhat unreliable and has been shown to be important in insect growth (Scriber 1984); hence plants have been speculated to vary this resource to increase the mortality of their attackers (Mattson 1980). Both water and nitrogen are vital to plant growth and reproduction, however, their variation may not in all cases be in response to herbivory. Those plant products that are produced directly by all plants are called primary metabolites and are vital for metabolic function. Those compounds that are often restricted to specific plant groups and are not vital to growth and reproduction are called secondary metabolites (Pichersky and Gang 2000). These compounds are both induced and constitutive and have been viewed strictly as an herbivore deterrent (Fraenkel 1959); however, there is some evidence that they might also be allopathic in plant-plant competition (Siemens *et al.* 2002). Anti-herbivore defenses range from qualitative, such as highly toxic glucosinolates, to quantitative, such as tannins and phenolics (Schoonhoven *et al.* 2005). These can vary in their effectiveness and concentration, but, in spite of or as a result of their presence, some herbivores have evolved ways to negate these defenses (Rhoades 1985). In addition to chemical defenses, plants employ a wide variety of physical defenses, such as trichomes and waxy cuticles (Jetter *et al.* 2000, Valverde *et al.* 2001).

When an herbivorous insect consumes a plant, it has to convert that material to energy, which is then used for growth and reproduction (Waldbauer 1968). Some plant compounds have been shown to slow this conversion by reducing digestibility (Rhoades 1979). This has led many researchers to propose that plants use a strategy in which they delay insect growth to increase mortality from abiotic forces and the third trophic level (Champagne *et al.* 1986, Fordyce and Shapiro 2003). This has been termed the ‘slow-growth - high-mortality’ hypothesis, for which there is both supporting and refuting evidence (Williams 1999). Besides detoxification and sequestration, herbivorous insects also have been able to overcome some chemical defenses through behavioral responses. These responses include trenching, shelter-building, and, in the case of tropical herbivores, feeding phenology (Dussourd and Eisner 1987, Cappuccino 1993, Coley and Barone 1996).

Here I will discuss how plants are utilized as food by herbivorous insects and how those plants, in turn, are thought to defend themselves against attack. I will then describe how delayed growth of an herbivore may be a consequence of plant defense and describe the various methods herbivores use to overcome these defenses. Finally, I will discuss the behavior of shelter-building and how it relates to the ‘slow-growth-high-mortality’ hypothesis.

THE CONSEQUENCES OF BEING AN HERBIVORE AND THE FEEDING STRATEGIES TO OVERCOME POOR LEAF QUALITY

Plants as a Food Source for Herbivores

The relationship between plants and their insect herbivores is one of a constant battle. This is because as one tries to prevent the other from attack, the other is selected to evolve new strategies to get around those barriers. The opponents, at first glance, seem unequally matched. Plants are immobile and seemingly cannot actively fight back, for the most part have long generations, and have been shown to possess low recombination rates. Insects, on the other hand, are generally highly mobile, relatively small, and have a high reproduction rate. This allows them to overcome evolutionary obstacles quickly (Schoonhoven *et al.* 2005). The world, however, still remains green in part because plants have evolved developmental, physical, phenological, and chemical attributes that deter feeding by their insect attackers. On top of all these defenses, plants represent extremely heterogeneous hosts in both space and time, and thus in this respect, can be regarded as an unreliable food source. Even within the same individual or leaf, plant tissue quality can vary significantly (Zucker 1982, Bowers and Stamp 1992, Schoonhoven *et al.* 2005). In response to this, herbivores have evolved traits and behaviors to counteract these attempts to prevent feeding, and are thought to have speciated as a result (Thomson 1989, Farrell *et al.* 1992).

Plant Apparency

The first point of the plant-herbivore interface is plant apparency. The plant-apparency hypothesis states that less apparent plants (short-lived, early successional plants) should have more qualitative (toxic) defenses while more apparent plants (trees and late successional plants) should have more quantitative (non-toxic) defenses (Feeny 1976, Rhoades and Cates 1976). Both the apparency and community structure of a host plant can determine the range of defensive strategies utilized by plants against herbivore attackers (Feeny 1976, Agrawal and Fishbein 2006). When both the apparency of a plant is high and the plant community diversity is low, extremely toxic defenses will be less effective because the surrounding plant community is able to provide enough available resource to eventually lead to a counter-adaptation in an insect herbivore. In this case, it is theorized, the plants use digestibility reducers to slow growth and sequestration, resulting in increased vulnerability to the herbivore's own enemies (Feeny 1970).

As a further exploration of the evolutionary associations of plant apparency and insect herbivores, Chew and Courtney (1991) examined an assemblage of pierid butterflies feeding on chapparalian hosts in the arid Moroccan ecosystem. They found that pierid diet breadth is highly correlated with host predictability and density. In addition, palatability and survival were highest on more apparent and predictable plants. While their findings do confirm hypotheses proposed involving plant apparency, their system is somewhat limited in diversity and would need to be explored elsewhere. The researchers do point out, however, that more diverse assemblages of herbivores could confound selection in the herbivore-plant relationship, making it unclear what role plant apparency plays in the interaction.

Nutritional Quality/Defensive Compounds

Insects require the same nutrients to survive and reproduce as most animals; however, they lack the ability to synthesize sterols. This constraint means they must rely solely on their food source for these essential nutrients (Behmer and Nes 2003). Among insect herbivore species, the requirements of nutrients for the best growth and reproduction can vary significantly and mostly are based on protein:carbohydrate ratios (House 1970, 1974). Even within the same plant, herbivores have been known to occupy different 'nutritional niches', an attribute which is hypothesized to contribute to the formation of long-term species coexistence (Behmer and Joern 2008). This process can be the result of differences in activity patterns resulting in the need for specific nutrient ratios (Schoonhoven *et al.* 2005). Researchers have also noted that some insect herbivore species grow much larger than their natural size when feeding on artificial diets, even gaining up to twelve times their normal mass compared to non-laboratory settings, leading researchers to believe that feeding style, which can be affected by herbivore species compositions, is one factor determining ultimate adult size (Reese and Field 1986).

Nitrogen

Of all the components of leaf tissue, nitrogen is one of the most important elements, with respect to insect growth, because it is the least available in usable form in the environment (Mattson 1980). In addition, proteins, which contain nitrogen, are vital for the structure of insect cuticle, whereas, the majority of plant structural elements are carbohydrates. Hence, many plants are a poor source of nitrogen from an animal's perspective (Allen *et al.* 1974). This would explain why plant nitrogen content has been shown in some insect species to be very closely related to insect growth efficiency (Mattson 1980).

As stated before, plants are extremely heterogeneous hosts, even with respect to nitrogen content. An analysis of nitrogen levels in eight plant families revealed that woody species contained the lowest amount of nitrogen and leguminous species contained the highest, due to their ability to fix atmospheric nitrogen (Bernays and Chapman 1994). Additionally, within the same plant species there is a large variety of tissue with an equally large range of nitrogen percentage (Mattson 1980). With this in mind, we can expect that the foraging strategies and species of herbivores should vary drastically among those eight families and host plant use of individual insect species should vary within and between plant species.

However, while the nitrogen content of plant material can be somewhat useful when determining plant quality, some nitrogen is bound to be within unusable forms, such as alkaloids. This has resulted in a variety of forms of herbivory that seem to circumvent the apparent deficiency of some plant biomass. Phloem feeders, for example, are at an advantage to chewing herbivores because the majority of phloem nitrogen can be utilized (Douglas 2003). This form of feeding is so superior to that of chewing herbivores that the average absorption efficiency of haustellates (phloem feeders) is around 60% while for mandibulate (chewing) insects it is around 45% (Slansky and Scriber 1985). While nitrogen can be a good indicator of quality, it does not mean high nitrogen content is always good for overall insect growth (Fischer and Fiedler 2000). This can be explained by phenomena, such as, non-optimal nitrogen ratios required for specific herbivores (Duffey *et al.* 1986), and increases in secondary metabolite production (Schoonhoven *et al.* 2005), as well as morphological changes within a plant (*i.e.* leaf thickness and vein toughness) (Forkner and Hunter 2000).

Water

In addition to nitrogen, water content has been shown to be an important component of plant biomass in relation to insect growth and survival, even accounting for a reduction in growth by 40% of herbivorous lepidopterans on artificial diets (Scriber 1984). Notably, tree feeders seem to be more sensitive to water content than forb-feeding insects (Scriber 1979). To add to the complexity, nitrogen and water content seem to co-vary and have been shown to change throughout the season for many plant species (Schoonhoven *et al.* 2005, Slanksy 1993). Unlike nitrogen, however, moisture can be obtained from the environment and caterpillars have been observed drinking from available water droplets on leaves (Dethier and Schoonhoven 1968).

Physical defenses

On top of chemical defenses, plants also possess several other defenses that are physical in nature and have been shown to co-vary with leaf nutritional quality (Agrawal and Fishbein 2006). Every terrestrial plant has a waxy cuticle layer that can vary in thickness. While this is mainly used to prevent desiccation, the thickness, complexity, and chemical composition of this layer is variable and has been speculated, in some species, to also confer defense against insect herbivores (Jetter *et al.* 2000). Crystals can form on some cuticle layers and researchers have shown that the presence of those crystals reduces attachment of insects when compared to 'glossy' mutants of the same species (Gorb *et al.* 2008). This trait, however, can also reduce attachment of predatory insects, thereby releasing waxy-cuticle adapted herbivores from the third trophic level (Eigenbrode 2004, Gorb *et al.* 2008).

Another type of structure arising from the epidermal layer is the trichome, single or groups of hairs that vary in size and shape (Werker 2000). These structures reduce herbivory in some species of plants (Valverde *et al.* 2001) and can reduce the oviposition rate of some lepidopterans (Handley *et al.* 2005). Two types of trichomes exist, with non-glandular providing only a mechanical defense, while glandular, in addition to providing a mechanical barrier, secret toxic allelochemicals (Schoonhoven *et al.* 2005). Non-glandular trichomes prevent some small insects and neonate larvae from contacting the leaf surface, as well as haustellate herbivores from piercing the epidermis (Southwood 1986).

In addition to trichomes, leaf toughness has been shown to be the one of the most important leaf defense characteristic preventing herbivory in lowland tropical forests (Coley 1983). The development of this attribute is the result of the combination and concentrations of cellulose, lignin, and digestibility reducing compounds (Rhoades 1979). The anti-herbivore effect is manifested as a lower consumption rate due to mandibular strain and wear, leading eventually to reduced fecundity (Raupp 1985). Leaf toughness, however, can trade off with leaf hair type and density (Björkman and Anderson 1990) and has been hypothesized, as with other mechanical defenses, to be more costly to produce than chemical defenses because it cannot be recycled and is limited by the same resource as biomass (Skogsmyr and Fagerström 1992). Other possible sources of physical defense include differences between C_3 and C_4 leaf morphology (Scheirs *et al.* 2001), indirect defense due to the presence of domatia (O’Dowd and Pemberton 1998) and extrafloral nectaries (Heil *et al.* 2001), and plant architecture in relation to oviposition and larval movement cost (Alonso and Herrera 1996, Marquis *et al.* 2002).

Secondary Metabolites

Secondary metabolites of plants have been used for centuries by humans for medicinal and religious purposes (Pereda-Miranda 1995). Their main evolutionary reason for being, however, has been hypothesized to be defense against herbivory by a whole suite of attackers (Fraenkel 1959). While some may argue that secondary metabolites are the result of processes that biologists have yet to unravel (Waterman and Mole 1989, Waterman 1992, Jansen *et al.* 1998), there is no doubt that they are pivotal in the ecology of plants and, as a result, have an unfathomable number of variations and effects on animals and plants alike (Schoonhoven *et al.* 2005). Consequently, much research has been conducted on the origin and effects of secondary metabolites.

The major types presently known to affect insect feeding are: glucosinolates, cyanogenic compounds, alkaloids and other nitrogenous compounds, phenolics, and terpenes/sterols. Glucosinolates are compounds common in the plant family Brassicaceae and contain both nitrogen and sulfur atoms. Within the leaf, glucosinolates are held in special vacuoles (Grob and Matile 1979) that, when ruptured due to tissue damage, combine with the enzyme myrosinase to form mustard oils (Bennett and Wallsgrove 1994). These products, for example, significantly reduce the reproduction of the green peach aphid, *Myzus persica*, on both an artificial diet and on *Arabidopsis thaliana* mutants (Kim *et al.* 2008). On the other hand, several specialist herbivores on members of Brassciaceae have been shown to actually be induced to feed in the presence of glucosinolates (Feeny *et al.* 1970).

Cyanogenic compounds are those chemicals that, when hydrolyzed, break down into cyanide. These substances are found in a wide variety of plant species in all vascular plant groups (Seigler 1991). Like glucosinolates, cyanogenic compounds are stored in vacuoles of leaves and are hydrolyzed when released by tissue damage, forming deleterious hydrogen cyanide (HCN) (Gleadow and Woodrow 2002). Hydrogen cyanide disrupts the mitochondrial respiratory pathway by binding to the cytochrome oxidase molecule and "preventing intra-cellular oxygen utilization" (Brattsten *et al.* 1983). Many generalist herbivores are deterred from feeding on plants containing cyanogenic glucosides but, again, some specialist herbivores also have the ability to detoxify and sometimes sequester these compounds for their own defense (Zagrobelny *et al.* 2004).

Alkaloids are a well-known group of anti-herbivore compounds that contain nitrogen and are made up of a select group of amino acids, with nicotine, papavine, and morphine being a few examples (Facchini 2001, Schoonhoven *et al.* 2005). Alkaloids are known to be mutagenic to some dipterans (Frei *et al.* 1992) and have general allelochemical effects on insects including, the inhibition of DNA polymerase I and protein synthesis, as well as the blocking of neuroreceptors, such as acetocholine (Wink *et al.* 1998).

Several compounds that occur widely in all plants are called phenolics (Harborne 1999), with the most diverse and largest group being the flavonoids. These compounds are, again, often stored in the vacuoles of plants and give some plant parts their bright color (Schoonhoven *et al.* 2005). While flavonoids are ubiquitous in plants, their potency still remains high to some herbivores. For example, phaseolin, found in the common bean (*Phaseolus vulgaris* L.), is one of the most potent herbivore feeding deterrents known, having been shown to reduce herbivory by 50% in concentrations as little as 0.03 ppm (Lane *et al.* 1985). Another type of phenolic compound, tannin, occurs in all classes of vascular plants, most often in high concentrations (Schoonhoven *et al.* 2005). Their existence had been known for years before Feeny and other researchers finally hypothesized that their function was to bind to soluble proteins to make them insoluble in the gut of insect herbivores (Feeny 1976, Rhoades and Cates 1976). They also prevent protein breakdown by enzymes and link polysaccharides to nucleic acids and, therefore, are thought to reduce the nutritional content of plant material.

Tannins are of two major kinds, hydrolyzable and condensed. Hydrolyzable tannins can be hydrolyzed with hot, dilute acid while condensed cannot. In addition, hydrolyzable tannins are only found in angiosperms, while condensed tannins can be found in many plant species throughout the plant kingdom (Schoonhoven *et al.* 2005). Some types of tannins have been shown to vary and shift throughout the season, even within the same plant species (Salminen *et al.* 2001).

Lastly, another group of compounds important in deterring herbivory is the group containing terpenes/sterols, which are volatile compounds that comprise the largest group of secondary metabolites, with around 30,000 identified (Pichersky and Gershenzon 2002). Some substances of this group are contained within special glands on leaf surfaces and rupture during herbivory events, while others are only synthesized after damage and are released as aldehydes, alcohols, or esters (Gang *et al.* 2001). These substances provide an indirect defense against attackers by attracting enemies of herbivores (Dicke and van Loon 2000). But recently, evidence has shown that they also provide a direct defense by deterring oviposition in some species of lepidopterans (De Moraes *et al.* 2001, Kessler and Baldwin 2001) and researchers have discovered some links between volatile production and decreased aphid performance (Vancanneyt *et al.* 2001).

Interestingly, one type of sterol, phytoecdysteroid, mimics the insect growth hormone ecdysteroid and is hypothesized to be a feeding deterrent; however recent evidence is lacking (Schmelz *et al.* 1998, Jones and Firn 1978). With all these chemical defenses, however, herbivores still manage to inflict a great amount of damage on plants, leading to, in some cases for example, a reduction of one-third above ground biomass in white oak (Marquis and Whelan 1994) and a 28% of reduction in root biomass in *Erigeron glaucus* by thrips herbivory (Karban and Strauss 1993).

Induced vs. constitutive defenses

As mentioned before, plant hosts are variable throughout space and time, and hence a specific combination of defense traits, both mechanical and chemical, in a species of plant will sometimes not exist at another place or time in a season. One of the reasons for this difference can be attributed to how defenses are allocated within a plant in response to herbivory. As such, researchers have defined four types of plant defense in response to herbivory: direct constitutive, indirect constitutive, direct induced, and indirect induced.

Firstly, any defense that is labeled as constitutive is one that is always present within a plant, whether under attack or not. These types of defenses tend to be carbon based and are therefore metabolically “cheaper” to produce and store in the long term than nitrogen containing defenses, like alkaloids (Coley *et al.* 1985). A direct constitutive defense is one that has an immediate effect on a target and whose magnitude does not change due to damage caused by herbivory. For example, young willow trees (*Salix dasyclados*) grown under low light conditions (abiotic), which therefore have low carbon content (phenolics), had one-third as much phenolic compound as normal light plants and experienced five times as much herbivory by leaf-chewing beetles than the other treatments (Larsson *et al.* 1986). Indirect constitutive defenses are usually chemicals that are normally released from a host plant, regardless of herbivory, as products of metabolism and are used by the third trophic level as host plant location cues (Price *et al.* 1980). This type of defense includes plant volatiles that are released through gland cell walls, stomata, and cuticles and stimulate predator foraging and oviposition (Schoonhoven *et al.* 2005). For example, intact molasses grass, *Melinis minutiflora*, increases the foraging behavior of the parasitoid of a stem boring lepidopteran species when planted alongside African cereal crops (Khan *et al.* 1997).

Following the resource allocation hypothesis proposed by Coley *et al.* (1985), one would expect then that, as opposed to constitutive defenses, induced defenses are metabolically cheaper to create and store in the short term (Waterman and Mole 1994). The phenomenon of induced plant anti-herbivore defenses is an area of plant-insect interactions that is well studied (Karban and Myers 1989, Agrawal 2000, Karban *et al.* 1999), especially in agricultural systems (Constabel and Ryan 1998), but some studies have focused on natural systems as well (Karban and Baldwin 1997, Wold and Marquis 1997). Within this designation, researchers call those defenses that directly affect an herbivore immediately after producing damage, induced direct defenses. These types of reactions by plants are common and their effects on herbivores are again, widely studied (Karban and Baldwin 1997, Agrawal *et al.* 1999, Karban 2011). These defenses can behave rather specifically within the same plant species in response to different attacking herbivores. For example, when two common insect herbivores (tobacco hornworm and

Colorado potato beetle) fed on tomato plant, two different anti-herbivore responses were induced. These responses are suggested to be caused by chemical differences in herbivore saliva (Chung and Felton 2011).

While direct induced anti-herbivore defenses have been studied in plants, indirect induced anti-herbivore defenses have proven to be just as interesting. These responses are characterized by the release of volatile organic molecules from a plant in response to herbivore damage that then alters the foraging behavior of predators (Karban and Baldwin 1997, Bukovinszky *et al.* 2012). For example, Girling and colleagues (2011) studied the foraging preference of the parasitoid *Cotesia vestalis* on cabbage plants (*Brassica oleracea*) with different levels of damage and numbers of the parasitoid's host herbivores. They found that the parasitoid preferentially foraged on plants with more herbivores and more herbivore damage, corresponding to the headspace profile of volatile organic compounds collected. While chemical defenses are known to be induced by herbivory, direct mechanical defenses, such as trichomes, have also been shown to be induced by herbivory (Young 1987, Agrawal 1999, 2000, Traw and Dawson 2002, Liu *et al.* 2010). Even indirect induced mechanical defenses manifest themselves by way of increased number of domatia and refuges for foraging predators (Palmer *et al.* 2008).

EFFECTS OF PLANT DEFENSES ON INSECT GROWTH AND SURVIVORSHIP

Growth in Insects

Because insects are protected and supported by an exoskeleton, they grow in a different way than organisms with an internal skeleton. Instead of growing progressively, they grow in stages, shedding their old exoskeleton with each growth period or ‘instar’. The nutrient requirements for each instar are different and therefore plant defenses and nutritional quality will have differing effects on each instar (Scriber and Slanksy 1981). Digestion of plant material in leaf chewing herbivores is rather quick, taking as little as a few hours to pass completely through the digestive tract (Barbehenn 1992). However, plant piercing and sucking insects can process plant material even faster, sometimes under an hour (Kingsolver and Daniel 1995). Quick ingestion can be advantageous because of reduced feeding time, but, on the other hand, can also lead to lower absorption of nutrients. Additionally, plants use noxious compounds to slow down herbivore growth and can eventually cause mortality through starvation (Champagne *et al.* 1986). The link between plant defense and insect growth can be characterized as 'utilization' of plant host biomass on the part of the herbivore (Waldbauer 1968). This includes three basic components outlined in Waldbauer's 1968 paper on insect food utilization: approximate digestibility, efficiency of conversion of ingested food to body substance, and efficiency of conversion of digested food to body substance or 'utilization efficiency'.

In the past, utilization of food had been measured gravimetrically, meaning the weighing of food, feces, and body mass before and after feeding (McGinnis and Kasting 1964, Parra and Kogan 1981). This was criticized, though, because it was shown that small errors could build up in data sets and cause inaccurate results (Raubenheimer and Simpson 1992). Also, there was some debate on how the nutritional indices should be interpreted (Schmidt and Reese 1986, Van Loon 1988, 1991, Raubenheimer and Simpson 1992). Recently, researchers have started using bi-coordinate utilization plots, which compare nutrient uptake with the components of a nutrient budget (Raubenheimer and Simpson 1994). Even this method, though, has flaws because researchers do not take into account leaf respiration rates, which can reduce carbon content over time and can be highly variable in field conditions (Axelsson and Ågren 1979, Wightman 1981). One way the performance of a herbivore can be measured is by calculating its relative growth rate, which is expressed as growth attained per unit body weight per unit time (Koricheva *et al.* 1998), and can be determined by the product of consumption rates and nutritional indices (Schoonhoven *et al.* 2005). This means that the relative growth rate of an herbivore can be increased either by an increase in the utilization of plant biomass or an increase in its consumption.

Plant Nutritional Quality

Herbivorous insect growth rates are assumed to be nutrient-limited (Schroeder 1986, Slansky and Feeny 1977) and, as a consequence, without the presence of secondary compounds growth rates should be determined exclusively by limiting nutrient amounts in biomass, such as nitrogen or water content. But it has also been suggested that the ratios of nutrients could be more important than base nutrient percentage (Karowe and Martin 1989). To complicate matters, the utilization efficiency of insects is known to vary between guilds and even between instars of the same herbivore (Slansky and Scriber 1985, Scriber and Slansky 1981). Altogether, when limiting nutrients are not at optimal levels, growth rate is reduced. One way this can be counteracted, however, is by compensatory feeding: increasing the consumption of an item to obtain optimal nutrient levels (Simpson and Simpson 1990). There are, however, limits to compensation through increased consumption that are related to constraints on rate and efficiency. This is because an increase in ingestion rate will, at some point, lead to reduced retention time in the gut, thus fewer nutrients will be absorbed per gram of plant material (Simpson and Simpson 1990). Compounding this problem, an increase in feeding rate could lead to the ingestion of more allelochemicals, further decreasing nutrient absorption and survival (Slansky and Wheeler 1992). Lastly, when feeding rate is increased, one nutrient could be ingested in excess of the needed amount, leading to decreased utilization efficiencies because of “incidental restriction” through feeding cessation. For example, when excess carbohydrates were consumed by fifth instar *Locusta migratoria,* they stopped feeding even though their required amount of optimal nitrogen was not reached (Raubenheimer 1992).

Distinct from leaf-chewing insects, some insect herbivores have evolved to form galls, which direct extra nutrients toward a feeding larva (Inbar *et al.* 1995). Feeding behaviors, such as gregarious feeding, selection of undamaged plants, and initiation of foliage search after a reduction in plant nutrients, are also considered to be advantageous strategies to circumvent reductions in plant quality in response to herbivory (Dixon and Wratten 1971, Brown and Weis 1995, Kause *et al.* 1999).

Allelochemicals

Complimentary to decreased nutrient content, allelochemicals also can impact insect herbivore growth. For non-adapted herbivores, plant defensive compounds have been known to reduce feeding behavior, food utilization efficiency, and poison feeders by inhibiting metabolic processes. First, compounds common in plants, such as alkaloids and terpenoids, can have several neurological effects and can be extremely bitter, leading to altered feeding behavior and lower herbivory (Wink 2003). Second, carbon-based defenses, such as tannins, were first proposed by Feeny *et al.* (1970) to reduce the digestibility of proteins in the gut. Subsequently, many studies have shown tannin concentrations within plants to be correlated with reduced insect growth as a result of tannin molecules complexing with salivary and gut proteins thereby making them insoluble (Meisner *et al.* 1978). On the other hand, for some herbivores this relationship does not seem to be the case (Martin *et al.* 1987, Karowe 1989). Furthermore, some researchers have suggested that tannins have more of an oxidative effect, destroying gut tissue rather than acting as digestibility reducers (Appel 1993). Lastly, molecules such as glucosinolates and cyanogenic glucosides reduce and prevent metabolic processes and lead to reduced growth and survival (Chew 1988, Agerbirk *et al.* 2009, Li *et al.* 2000). Besides compensatory feeding, herbivores have also found several other strategies around allelochemicals. For example, herbivores can modify the activity of these chemicals by producing proteins and enzymes that inhibit their function (Wadleigh and Yu 1988). Additionally, behaviors such as trenching and gland avoidance can circumvent plant allelochemical strategies by preventing their flow through plant tissue (Dussourd and Eisner 1987). Finally, herbivores that have adapted to feeding on extremely toxic plants utilize sequestration strategies to deter their enemies (Gardner and Stermitz 1988).

Physical Defenses

Physical defenses as well as chemical defenses have been shown to reduce the performance of herbivorous insects. For example, when both of types of trichomes were removed from the leaves of tomato plants, caterpillars spent significantly more time probing for leaf material and significantly less time cleaning mouth parts. When just exuding hairs were removed, an immediate reduction in the amount of time spent cleaning mouthparts was recorded (Wilkens *et al.* 1996). Movement speed, as well, is reduced in caterpillars on tomato and soybean leaves (Cribb *et al.* 2010) and herbivores have been observed being trapped in the curved leaf hairs of *Mentzelia pumila* (Eisner *et* *al.* 1998). Glandular hairs not only exude noxious compounds that are bitter and have detrimental effects on herbivore physiologically, they can also produce sticky substances that, when glands are ruptured, glue herbivores to leaves and prevent movement. In fact, up to 98% of aphids feeding on lettuce inflorescences, *Lactuca sativa*, were found glued to the surface of the leaves, unable to move (Dussourd 1995).

In addition to reduced movement on tomato and soybean, Cribb and colleagues (2010) noted reduced movement on pea leaves with wax crystals when compared to leaves that had wax removed. Cuticular wax can also reduce attachment efficiency and cause more falling events, leading to an increase in feeding times (White and Eigenbrode 2000). For example, juvenile wax on leaves of *Eucalyptus globulus* reduced attachment of all three psyllid species studied (Brennan and Weinbaum 2001). Latex, a well studied plant product, is a major defense component not only because of its toxic property, but it has also been shown to drastically reduce walking and feeding (Dussourd and Eisner 1987). In fact, Dussourd and Eisner (1987) found that 1µl of latex from a fresh plant placed next to the mandible of a feeding caterpillar stopped feeding immediately and caused the herbivore to engage in cleaning. The researchers even observed the mandibles of beetles ceasing to function because of dried latex from *Asclepias syriaca*. Lastly, there have been reports of the siliques of *Cardamine scutata* entangling or even expelling caterpillars dozens of centimeters away (Yano 1997). While the mechanism is most likely for the dispersal of seeds, it still deters feeding and could make herbivores more apparent to predators.

BEHAVIOR OF SHELTERBUILDING – ADAPTIVE VALUE

What is ecosystem engineering?

With plants containing all of these defenses, that are both suspected and proven to prevent or reduce feeding, herbivores have in turn developed methods to improve their survival in the face of these obstacles. One way for insect herbivores to overcome the natural heterogeneity in resource quality represented by plants is to construct a mini-ecosystem within a host plant, effectively altering its state. This is one example of abiotic modification by organisms that has been coined ‘shelter building’. This habitat alteration manifests as either changes in the structure of the environment (allogenic) or changes in the structure of the engineer itself (autogenic). The abiotic changes resulting from shelter building may affect both the engineer and by-standers and can often lead to drastic changes in an ecosystem, a process called ecosystem engineering (Jones *et al.* 1994). More specifically, engineering herbivores can affect plant communities through a combination of effect types (intrinsic effects of herbivory, associated and unassociated effects of ecosystem engineering) and interaction types (trophic, physical, and transport engineering interaction) (Wilby *et al.* 2001).

Firstly, effect types can be classified either as intrinsic effects (direct effects on the plant through herbivory) or effects from the process of engineering itself. From a plant’s perspective, intrinsic effects are trophic in nature, and can be either direct or indirect. Directly, the removal of plant tissue by an herbivore causes reduced fitness for the plant being attacked. This is because removal can lead to decreased seed set and growth or even increased plant mortality (Facelli 1994, Hanley *et al.* 1996). Indirectly, the removal of plant tissue can lead to reduced competitive ability and increased susceptibility to disease of the plant that is being manipulated (Nowak *et al.* 1990, Clay and Brown 1997).

In addition to intrinsic effects, ecosystem engineers also have ‘engineering effects’, which are those effects that are immediately connected to, but that are not a part of, the process of herbivory and do not result in the consumption of plant biomass. A well known example of associated ecosystem engineering is called transport ecosystem engineering (Crawley 1983, Levinton 1995). For example, nest building carpenter ants in South Africa have been shown to alter the area around their nests by depositing both seeds and organic material, whose deposition is the result of herbivory, within their nest. The nutrients in the refuse then leach into the surrounding area. Several species of plants are specifically associated with this structure and significantly more nutrient-rich plant species with higher seed production occur in these areas (Dean and Yeaton 1993).

Finally, unassociated ecosystem engineering effects are those that are not directly linked to either consumption or the engineering process. This could include nest construction, wallowing or trampling, tunnel construction in soil as a result of movement, and the incidental transportation of plant material or propagules. For example, Wright and colleagues found that nest construction of the dam-building beaver, *Castor canadensis*, increased the species richness of herbaceous plants by 33 percent in the riparian habitats of the Adirondacks (Wright *et al.* 2002).

How are ecosystem engineering and shelter-building related?

Besides eating plant tissue, herbivorous arthropods can modify their food to provide shelter. This act can be classified as ecosystem engineering because the environment is modified and resource use can change when the shelters are present (Cappuccino 1993). In these cases, to both the plant and the arthropods that utilize the newly formed refuge, this can be both advantageous and disadvantageous (Crutsinger and Sanders 2005).

Herbivores are constantly faced with mortality through abiotic, bottom-up, and top-down forces (Gaston *et al.* 1991). However, the construction of these shelters is thought to mitigate these threats to the actual constructor while, at the same time, provide other individuals that inhabit these shelters with refuge (Fukui 2001, Eubanks *et al.* 1997) without incurring the cost of making it (but see Lill *et al.* 2007, Nakamura and Ohgushi 2003, Gentry and Dyer 2002). These costs include vulnerability to predators (Loader and Damman 1991), resources lost from reduced foraging during construction (Despland and Le Huu 2007), energy lost due to construction (Cappuccino 1993, but see Loeffler 1996b) and a metabolic cost from silk production (Berenbaum *et al.* 1993). The type of builder, however, can alter the benefits afforded by refuge through good 'housekeeping' habits. Poor housekeeping can lead to increased disease risk, crowding, and predator attraction through frass accumulation (Weiss 2003). For secondary inhabitants of leaf shelters, the effects of shelter building can lead to three types of species interactions: shelter-mediated interactions (provision of shelter) (Lill and Marquis 2003), food-resource mediated interactions (alteration of plant quality from one species to another) (Fukui *et al.* 2002), and enemy-mediated interactions (changes in population and foraging of shared enemies) (Fukui 2001).

WHY ACTIVELY BUILD A SHELTER?

Amelioration of harsh abiotic conditions/Microclimate control

There are many differences in environmental variables inside a shelter compared to outside. These differences can be condensed into four main environmental properties: temperature, wind, humidity, and solar radiation (Willmer 1980, Joos *et al.* 1988, Hunter and Willmer 1989). Because desiccation is a major concern for arthropods during dry periods, constant respiration of leaves inside the shelter increases humidity and also can prevent desiccation due to wind (Willmer 1982, Zalucki *et al.* 2002). In addition, thermoregulation by arthropods is very important to survival and is related to humidity control (Block *et al.* 1990, Neven 2000). However, the many types of shelters that arthropods are known to build vary in the degree to which they mitigate this environmental attribute (Henson 1958). The complex nature of some shelters allows different thermal gradients (Costa 1997), which can be utilized depending on conditions, and can vary in position and orientation to suit needs (Alonso 1997). Because habitat would change the relative humidity, it is expected that these structures would be more beneficial in drier environments. In fact, the non-shelter building beetle larva *Galerucella lineola* has been shown to be more attracted to and have better survival in shelters as humidity is lowered (Larsson *et al.* 1997). However, there is evidence from tropical habitats show that there are some phytophagous insects that feed within shelters even when relative humidity is high (Greeney *et al.* 2010). Overall, there are some general microhabitat characteristics that have been identified to be important to the inhabitants of shelters: orientation, ventilation, exposed surface area to volume of shelter, exposure to incidental radiation, and absorptive properties of foliage (Henson 1958, Willmer 1982, Fukui 2001).

Alteration of plant tissue quality

It has been shown that arthropods within shelters experience better quality plant tissue than they would encounter feeding freely. This phenomenon stems from reduced exposure to light, which can alter tissue quality (Oki and Varanda 2000, Fukui *et al.* 2002) and reduce deleterious effects caused by feeding in light (Berenbaum 1978).

Additionally, structural defenses on leaves and defensive compounds within leaves can be modified through the activity of shelter building (Coley *et al.* 1985, Sagers 1992, but see Costa and Varanda 2002). For example, trenching, a behavior known to reduce the effectiveness of chemical defensives in leaves through the severing of vessels, by the Indian Red Admiral Butterfly (*Vanessa indica*) is both important in shelter construction and in feeding (Ide 2004). While the effects of galling on plant quality are still not clear, some research points to the behavior improving the nutrient quality of tissue and the reduction of defensive compounds. For example, two species of gall midges on four different species of Japanese trees in the genus *Ilex* provide both refuge and an improved quality leaf tissue source to two species of moths and seven species of parasitoids (Sugiura *et al.* 2006). Some herbivores have been known to preferentially select lower quality leaf tissue, leading to the speculation that leaf quality is secondary to other factors in these systems. For example, lepidopteran larvae feeding on their individual host plants were found to select leaves of low quality to use in their shelter construction. This led to lower survival and pupal mass, but in some cases faster development, because lower quality (older) leaves were more rigid and thus provided a better barrier to predation (Damman 1987, Reavey 1991). Additionally, oecophorid moths have been shown to build shelters on previously damaged oak leaves, which contained induced defenses and lead to reduced survival (Hunter 1987). The reasons behind these choices remain unclear but it has been suggested that the building material of the shelter takes precedence over the quality of the leaf tissue (Ruehlmann *et al.* 1988, Loeffler 1996b). We can look again to *Vanessa indica* for an example of this phenomenon. A recent study found that small and middle apical leaves that young larvae used as construction material showed no difference in quality. However, older and larger larvae obtained the ability to trench, and hence modified parts of their shelter to improve quality (Ide 2009).

While a different study by Abarca and Boege (2011) does not explicitly state that selection of material for new shelter construction would be secondary to quality, in fact they say that "fresh shelters should provide the highest food quality because they combine trenching benefits with high water content". They suggest that new shelter construction would be more risky than adding new leaves to an existing shelter because more time spent outside a refuge increases predation risk. Finally, some insects use shelter-building to ameliorate abiotic effects in conjunction with plant quality, such as phototoxic effects. For example, tortricid moths have been found building shelters on *Hypericum perforatum* and feeding on the leaves within those shelters. Researchers altered the artificial diet levels of hypericin, the phototoxic chemical in *H. perforatum*. They found that when larvae of *Platynota flavedana* were fed in natural light (simulated outside shelter) compared to filtered light (simulated inside shelter), individuals in filtered light survived significantly more than those in natural light (Sandberg and Berenbaum 1989).

Predator Avoidance

Like the many shelters constructed by most prey species, the shelters built by herbivores have mainly been hypothesized to be a refuge from predators. This idea has been explored for many systems involving predators such as ants (Fowler and McGarvin 1985, Heads and Lawton 1985), spiders (Damman 1987, Loeffler 1996a), wasps (Damman 1987, Jones *et al.* 2002), birds (Atlegrim 1989, Sipura 1999), and Coleoptera/Neuroptera (Lucas *et al.* 2000, Messina *et al.* 1997). The construction of these shelters has been experimentally proven to provide refuge from predation to both the constructor and any secondary users (Cappuccino 1993).

One hypothesized advantage of constructing a shelter as refuge is the ability to feed while concealed from most predators, thereby reducing predation (Larsson *et al.* 1997). This is because most enemies that rely on visual cues have been found to be good at detecting movement (Bernays 1997). This can also confer benefit to other insects that naturally occur outside of a tie by providing temporary refuge while not feeding (Lill and Marquis 2004). Because increased feeding time leads to more rapid development, some shelter-building larvae feed exclusively within a leaf or shelter (Fitzgerald and Clark 1994, Lill and Marquis 2001). This pattern of predator protection, however, is not a widespread phenomenon and shelter-building individuals have been shown to still suffer from high predation and parasitism even while inside a shelter (Remsen and Parker 1984, Le Corff *et al.* 2000, Gentry and Dyer 2002, Jones *et al.* 2002, Connahs *et al.* 2011). This is mainly due to the fact that some visual predators use signs of shelter-building and activities related to shelter-building as foraging cues (Raveret Richter 1988, Weiss 2003). For example, birds have been shown to focus attack on leaf rolls and can be trained to do so through experience (Heinrich and Collins 1983).

Predatory wasps, as well, have been shown to use shelter-builder clues to forage more efficiently (Weiss *et al.* 2004). These cues include the visual presence of a shelter, damage patterns in leaves, and volatiles from leaves and frass released as a result of herbivore attack (Mattiacci and Dicke 1995). In order to prevent predators from utilizing such clues, herbivores have developed shelter habitation techniques that minimize the apparency of these clues. These techniques range from defecation outside of shelters and forceful ejection of frass from within the shelter itself (Weiss 2003) to head flicking in response to the sound of predators to confuse them (Myers and Smith 1978). While there are numerous types of shelters herbivores can build, three main types are leaf-mines, leaf-rolls, and leaf-ties.

Leafmining

One method of concealed feeding is leaf mining (Lepidoptera, Coleoptera, Diptera, Hymenoptera) (Price *et al.* 2011). This involves a larva living within a leaf and feeding on the plant cells between the upper and lower epidermis all or most of its larval stage. All species, however, do not feed in the same manner and some prefer to feed on different cells of a leaf, at different locations within a leaf, or on different aged leaves (Opler 1974). For example, although there is a high diversity of leaf-mining insects on northern Florida oaks, at least four known species only attack newly formed leaves, with two attacking at early season bud-break and two attacking at late season bud break. The remaining species feed on fully mature foliage until leaf-fall. Miners that feed exclusively on new leaves have been hypothesized to do so because their ovipositors cannot penetrate tough mature leaves (Faeth *et al.* 1981). Additionally, some mining larvae have been found to prefer certain tissues over others within a leaf (Kimmerer and Potter 1987). When the tissue preference for a grass-mining dipteran species was assessed, researchers found that the larvae preferred to feed on the mesophyll layer because it is the most nutritious and least tough tissue of grasses (Scheirs *et al.* 2001). Lastly, phytophagous larvae have been shown to preferentially feed at different locations within a leaf, a behavior which is species specific (Gall 1987). Within leaf-miners, research has shown that larvae from both Lepidoptera and Hymenoptera show preferences for both the size of a leaf and location within a leaf to mine (Sato 1991). This behavior is widespread in many herbivorous orders of insects and has led to the study of the evolutionary relationships between host plants and the species specific miners that attack them (Opler 1974, Mopper *et al.* 1995, Connor and Taverner 1997).

Leafrolling

While leaf-miner eggs are confined because they are deposited directly into leaf tissue, leaf-rolling behavior by phytophagous insects is an active and ongoing process from the first instar to pupation and provides a somewhat lesser mode of concealed feeding while allowing for greater freedom of movement. Leaf-rolling is thought to confer benefits to the constructor such as concealment from predators and favorable alteration of leaf quality (Hunter 1987, Sagers 1992); however there are many instances where leaf-rolls may actually be detrimental to the constructor (Murakami 1999, Jones *et al.* 2002, Denno and Kaplan 2006). Leaf-rolling behavior in phytophagous insects has barely been explored, however, except for those leaf-rollers found on black cherry, *Prunus serotina* (Fitzgerald and Clark 1994). Researchers found that the larvae of *Caloptilia serotinella* used the tension in silk, produced by stretching strands between the spinneret and the leaf, to slowly roll up the shelter leaf. This action multiplied over a hundred silk strands combined with the property of shelter-builder’s silk to shrink when exposed to moisture makes what must seem like an impossible task much more achievable (Fitzgerald 1995). The larvae will continue to feed within the leaf-roll until pupation, theoretically concealed from predators and sheltered from abiotic forces. As the larva consumes its house, it slices through the main veins of the leaf, further reducing the resistance of the leaf to remain rolled. Researchers studying *Omphalocera munroei* larvae on pawpaw (*Asimina* spp.) found that gregarious leaf-rolling/shelter-building behavior began shortly after egg hatch and progressed until the fifth instar, the point at which single individuals could roll leaves themselves. When sixth and seventh instar larvae were secured within leaf-rolls they suffered essentially no mortality compared to larvae tethered to either the top or bottom of a leaf (Damman 1987).

Leaf Tying

Lastly, several species of phytophagous insects have been observed constructing what is referred to as a "leaf-tie" or "leaf-tent". These constructions can be anything from simply a leaf section cut and folded over, two leaves sandwiched together, to an entire nest made up of leaves and branches commonly constructed by gregarious caterpillars (Fitzgerald and Peterson 1988). Similar to leaf-rolls, these shelters are thought to reduce or eliminate causes for mortality such as abiotic, top-down, and bottom-up effects (Fukui 2001). These shelter-builders are considered "physical ecosystem engineers" and have been shown to benefit arthropods that secondarily inhabit them (Martinsen *et al.*2000, Lill and Marquis 2003, Crutsinger and Sanders 2005), though they could also attract predators, especially those with the ability to learn to forage efficiently (Jones *et al.* 2002, Weiss *et al.* 2004). Some leaf-chewing herbivores form shelters by tying two touching leaves together and exclusively feed on the interior surfaces of the leaves, essentially constructing a leaf sandwich (Lill and Marquis 2001).

SLOW-GROWTH-HIGH-MORTALITY

Origins/Background

Plants can change the utilization efficiency of herbivores with either qualitative or quantitative defensive strategies. The main effect of quantitative defenses is that they reduce the nutritional quality of plant material by reducing their digestion, thus requiring an herbivore to ingest more plant material to achieve optimal growth. However, the view that these plant traits have evolved to deter herbivory has been met with some skepticism (Bernays 1978, 1981, Moran and Hamilton 1980, Bernays and Woodhead 1982, Berenbaum 1983, Augner 1995). The critics of this viewpoint believe that plants with these defenses will cause more herbivory and, hence, the trait will end up being a detrimental and would be selected against (Clancy and Price 1987). This scenario can only exist if the hypothesis that Feeny (1976) proposed holds true; herbivores that feed on plants with low nutritional quality should be subjected to higher rates of enemy attack than rapidly growing organisms. This idea has been coined as the 'slow-growth-high-mortality hypothesis' and states that slower growing herbivores spend more time in a vulnerable life stage and experience higher levels of attack by natural enemies (Feeny *et al.* 1970, Feeny 1976, Clancy and Price 1987).

Early Examples

The ability of plant defenses to slow phytophagous insect growth had been noted before Feeny proposed the idea that this might be an evolutionary adaptation in plants. For example, while examining thousands of varieties of rice, researchers at the International Rice Research Institute found that crambid moths that feed on resistant varieties displayed slower growth and higher mortality, leading to a lower overall body-size of those individuals that survived (Pathak 1969). Shortly thereafter, both Feeny (1976) and Price *et al.* (1980) described how poor quality plant tissue could lead to higher mortality in insect herbivores. This discussion initiated an increase of research in the area of tritrophic interactions. For example, Clancy and Price (1987) examined the relationship between enemy attack and herbivore growth in a leaf-galling sawfly (*Ponania* sp.) that feeds on arroyo willow (*Salix lasiolepis*). They predicted that sawflies that were bigger and developed faster would be less vulnerable to attack by ectoparasitoids. Their data, however, showed the opposite trend: bigger and faster developing sawflies were attacked more than slower-growing individuals. The researchers believe that the parasitoids were targeting larger larvae (ones that had developed fastest) because they represented the best host for offspring. Alternatively, there could be an interaction between gall tissue density and growth rate which could influence parasitism rates because parasitoid drilling levels might be affected.

In another study, Benrey and Denno (1997) looked at the growth and attack of *Pieris rapae* on four different host plants that presumably had different levels of anti-herbivore defense. Additionally they raised first instar *P. rapae* in both cool and warm environments and varied the amount of protein in a synthetic diet, thus altering development time. Those larvae that had warm temperatures and better quality diet grew significantly faster than the larvae subjected to the protein deficient warm treatments and the cool treatments. This translated into significantly less parasitism in faster developing larvae, a trend that only strengthened with each instar. Researchers explained this phenomenon by pointing out that faster developing larva encapsulated parasitoid larvae and eggs significantly more than the other treatments. They also found a significant effect of plant host species on development time, with the most favorable host plant allowing the larvae to reach pupation in 17 days and the least favorable in 25 days. Combined with a separate experiment that showed exposure time had a significant effect on parasitism, this result strongly hinted that the slow-growth-high-mortality hypothesis might prove to be correct in this system. This pattern, however, was not true when parasitism was compared across all four plant species studied. Parasitoids targeting galling/shelter-building larvae mostly rely on host plant volatiles to locate host larvae (Cortesero *et al.*1997) and this could have confounded the results by causing parasitoids to forage less efficiently on some host plants than others.

Recent Examples

More recently, researchers have been examining this hypothesis in greater detail, taking more factors into account to test the hypothesis' reliability. For example, Medina *et al.* (2005) measured both the development time and parasitism levels on *Orgyia leucostigma* on two different host plant species, willow and box elder. For this study, researchers took both the gender of the herbivore and the species of parasitoid into account. They found a significant interaction between gender and host plant with female larvae developing faster and gaining more mass on willow compared to box elder. Male larvae showed no response to plant host species identity. However, overall parasitism was higher on female larvae reared on willow than box elder, refuting the slow-growth-high-mortality hypothesis. Researchers point out that parasitoid species respond differently to different host plants, so in some situations the hypothesis can be proven to be true, while in others it may not be. In a unique examination of the slow-growth-high-mortality hypothesis, Lill and Marquis (2001) studied the development time and mortality of the leaf-tying herbivore (*Psilocorsis quercicella*) on white oak (*Quercus alba*). *P. quercicella* is a bivoltine leaf-tying phytophagous insect that feeds exclusively within a shelter through its entire development from egg to pupa. Their study specifically examined the effects of family and generation on development time and parasitism, in conjunction with leaf quality of a single host plant. While leaf quality had no effect on development time, it did increase mortality for the first generation larvae but not the second. The third trophic level remained a constant source of mortality for both generations. Herbivore family was a good predictor of development time and no association between it and parasitism was found, therefore refuting the slow-growth-high-mortality hypothesis. Lastly, leaf quality was shown to be a good predictor of pupal mass, with higher quality leaves producing heavier pupa.

Taken together, these studies offer a glance at the many facets of the slow-growth-high-mortality hypothesis; however, many other factors still remain to be examined. Simplified experiments may be the clearest way to test this hypothesis, but these are not based in reality. Unfortunately the more factors a researcher takes into account, the more of a chance there is for those factors to confound each other. In the end, evidence supporting this hypothesis is not strong. For example, a review of the slow-growth-high-mortality hypothesis showed that out of the 67 studies that they examined, 28 supported the hypothesis while 27 rejected it (Williams 1999). The hypothesis remains to be tested in all scenarios and needs to be further examined to better understand and predict under which scenarios it might prove to be true.

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CHAPTER 2. The ‘slow-growth-high-mortality’ hypothesis: how plant species, leaf quality, and the third trophic level contribute to mortality of two common leaf-tying microlepidopteran herbivores

ABSTRACT

In this study, I tested the slow-growth-high-mortality hypothesis, which states that plants, as a defense, slow the growth of herbivores to increase their exposure to the third trophic level. In the few systems tested for this effect the evidence is unclear and begs to be further examined. To test the hypothesis, I manipulated exposure of two common leaf-tying microlepidopterans (*Psilocorsis quercicella* and *Pseudotelphusa quercinigracella*) to the third trophic level on four species of oaks (*Quercus alba*, *Q. velutina*, *Q. rubra*, and *Q. stellata*). I found that plant traits differed among oak species and changed across the two generations of leaf-tiers. The two leaf-tier species experienced the first trophic level differently but were similarly affected by the third trophic level. Overall, mortality differed between generations, and leaf-tiers experienced much stronger bottom-up effects than top-down effects. Tree species identity resulted in differences in development time and pupal mass, however measured plant traits were not correlated with mortality, development time, or mass in *P. quercinigracella* and were inconsistent in *P. quercicella*. Additionally, the abundance of both leaf-tiers and predators, and pupal mass were highest on *Q. alba,* however this tree species had neither the highest or lowest leaf quality in terms of nitrogen availability. Overall the results from this study are not consistent with the predictions of the slow-growth-high-mortality hypothesis.

INTRODUCTION

Plants have evolved strategies that both directly and indirectly influence the ability of herbivores to use plant tissue as a source of energy and nutrition. One direct strategy utilized by plants is to make tissue unavailable for consumption. Traits that have direct impacts include secondary compounds such as tannins (Feeny 1970), enzyme inhibitors (Ryan 1973), phenolics (Feeny 1975, Rhoades and Cates 1976), resins (Langenheim *et al.* 1980), certain minerals (Massey *et al*. 2006), and structural defenses, such as trichomes (Levin 1973). As a result of these plant traits, herbivores may completely ignore the plants, or if they do choose to feed, they may die as a result of being poisoned or starved to death because of low tissue availability.

Plants can also have indirect effects on herbivores, two of which cause them to be vulnerable to top-down forces (natural enemies) and abiotic factors. Tannins, for example, can both slow digestion and reduce nutrient availability (Mattson 1980, Moran and Hamilton 1980, Coley *et al*. 1985, Haukioja *et al.* 1991). Plant traits that have these kinds of effects on herbivores are known as quantitative defenses (Marutani and Muniappan 1991, Benrey and Denno 1997, Steppuhn and Baldwin 2007). These traits can increase the time required by herbivores to reach their optimal nutrient intake (Coley *et al.* 2006), thus exposing them to the third trophic level and abiotic factors for a longer time period when they are vulnerable. The idea that these traits have evolved as a plant defense strategy against herbivores has been termed the slow-growth-high-mortality hypothesis (Clancy and Price 1987). Evidence supporting this hypothesis has been found in some (Haggstrom and Larsson 1995, Fordyce and Shapiro 2003) but not all systems (Williams 1999, Lill and Marquis 2001, Medina *et al*. 2005, Cornelissen and Stiling 2006).

The chemical defenses of *Quercus* species have been classified as quantitative (Feeny 1970, Faeth 1985). Plant traits, including chemical defenses, water and nitrogen content, and leaf hairs, vary among oak species and can have consequences for their associated insect communities, such as indirect interactions among herbivores (Ohgushi 2005), oviposition preferences (Taper and Case 1987, Thompson 1988), and impacts of shelter-building herbivores on associated arthropods (Lill and Marquis 2003, Forkner *et al*. 2004). Tannins can have both direct (Benrey and Denno 1997) and indirect (Havil and Raffa 2000) effects and therefore their interactions with herbivores should be relevant to the slow-growth-high-mortality hypothesis.

A major component of the insect herbivore fauna associated with *Quercus* in Missouri and the eastern United States consists of various species of microlepidopteran leaf-shelter builders (Carroll and Kearby 1978, Lill and Marquis 2003). These larvae form leaf “sandwiches” by tying two leaves together with silk. They then feed on the inside leaf surfaces until pupation (Carroll and Kearby 1978). In creating ties, these caterpillars can act as ecosystem engineers (Jones *et al.* 1994), as ties are often utilized by a number of arthropod species during and after occupation by the shelter-builder (Lill and Marquis 2004).

The abundance of these leaf-tying caterpillars on individual plants is determined in part by plant traits, both chemical (Forkner *et al.* 2004, Marquis and Lill 2010) and architectural (Marquis *et al.* 2002). These traits are likely to have direct effects on plant colonization by leaf-tying caterpillars, but also indirect effects, as two hypothesized advantages of building shelters are that they (1) protect against natural enemies, and (2) ameliorate the effects of stressful abiotic environment (Fukui 2001, Lill and Marquis

2007). Together, the available evidence demonstrating the role of leaf traits, these hypotheses, and the impact of leaf-tying caterpillars as ecosystem engineers all provide impetus for determining the direct and interactive effects of leaf quality through the third trophic level on survivorship and growth of leaf-tying larvae. Leaf-tying caterpillars are amendable for testing the slow-growth-high-mortality hypothesis because they will remain in place once placed in artificial leafties, but the ties themselves are sufficiently open in construction that arthropod predators can enter them (Wang et al. 2012), and the tie-makers can be parasitized (Le Corff and Marquis 1999; Lill and Marquis 2001).

In a previous study, Lill and Marquis (2001) tested the slow-growth-high-mortality hypothesis using one species of leaf-tying caterpillar on different plant individuals, all of the same plant species. In a manipulative experiment, I quantified the impact of the host plant and natural enemies, and their interactive effects, on survivorship, larval development rate, and pupal mass in two species of leaf-tying caterpillars across four species of oak. Different species of leaf-tiers respond differently to interspecific leaf quality (Marquis and Lill 2010), and have differential effects on associated arthropod species (Wang *et al.*2012). In comparing two species of caterpillars and multiple species of oaks, my goal was to determine the generality of previous results (Lill and Marquis 2001). Specifically I asked: 1) How does plant quality differ between the host plants studied? 2) Does host plant influence the abundance of leaf-tying caterpillars and arthropod predators? 3) How does the presence of the third trophic level influence the impact of host quality on survivorship and growth? And finally, 4) Are the interactions in this system consistent with the predictions of the slow-growth-high-mortality hypothesis? Mortality attributed to either the first or third trophic level, larval development rate (measured as days from second instar to pupation), and measured plant traits were used to evaluate the evidence for the slow-growth-high-mortality hypothesis.

I predicted that larvae feeding on host plant species with lower quality foliage would grow more slowly and, as a result, would incur higher mortality due to the third trophic level. These are the main predictions of the slow-growth-high-mortality hypothesis. Ancillary predictions are that both insect herbivore species should be more abundant on higher quality foliage, and that predators should be more prevalent on lower quality foliage, and parasitism and predation levels higher on that foliage, because prey encounter rate will be higher on low quality foliage due to increased feeding time by herbivores. Previous studies have attempted to evaluate this hypothesis but few examined concealed feeders, measured development and attack rates over the most of the larva lifespan, or used multiple host and herbivore species within the same ecosystem (Lill and Marquis 2001, Williams 1999).

METHODS

Study Area and Study Species

This study was conducted at Cuivre River State Park (CRSP) located 52 miles northwest of St. Louis Troy, Missouri. The park is an extension of the Missouri Ozark plateau and contains a second growth mixed oak-hickory forest with a variety of oak species. The four oak species studied (*Quercus rubra* L., *Q. stellata* Wangenh., *Q. alba* L., and *Q. velutina* Lam.) co-occur at several locations in the North Woods section of the Park, an unmanaged natural area and the specific location of the study. The two study caterpillar species, *Psilocorsis quercicella* Clemens (Oecophoridae) and *Pseudotelphusa quercinigracella* Chambers (Gelechiidae) are common leaf-tiers within the park. Both are bivoltine (Carroll 1977, Lill and Marquis 2004). They are most commonly found on oak and appear to show preferences for certain species of oaks (Marquis and Lill 2010, R. Marquis, pers. ob.). Because leaf quality decreases and parasitism/predation declines as the season progresses (Lill and Marquis 2001), I predicted that the relative importance of these two factors to shift across the two generations, with survivorship, as affected by leaf quality, and parasitism both lower in the second generation than the first.

Ten plants of each of four tree species were marked, two species of the red oak subgenus (*Q. rubra* and *Q. velutina*) and two species of the white oak subgenus (*Q. alba* and *Q. stellata*). Trees were similar in height and leaf number (minimum 150), with all leaves accessible from the ground. These plants and their associated arthropods served as the basis for both estimating the impacts of leaf quality on natural arthropod abundance, and a manipulative experiment to test the relative importance of third versus first trophic level effects on survival and growth of the two species of caterpillars.

Interspecific variation in leaf quality

For plant quality analysis, five leaves per tree were sampled at the time of *P. quercinigracella* larval collection at each generation of the experiment (see below). Trees were scattered throughout the understory of North Woods section of the Park. Chemical analysis of leaves was conducted in the same manner as Forkner *et al*. (2004). Leaf toughness, water content (water per dry mass), percent dry weight carbon and nitrogen, and concentration of condensed tannins, hydrolysable tannins, and total phenolics were measured. Leaves collected at the end of each field experiment were kept on ice, returned to the laboratory and freeze-dried, ground into powder, and stored at -80ºC. Leaf toughness was measured at the time of leaf collection using a leaf penetrometer (Force Dial FDK 32, Wagner Instruments, Greenwich, CT). The water content of leaves was obtained by subtracting the dry weight from the weight at collection. For missing water content (*Q. velutina* = 2, *Q. rubra* = 3, *Q. stellata* = 3, *Q. alba* = 4), a species average was used for the PCA. Percent dry weight carbon and nitrogen were measured using a CHNS/O analyzer, using microcombustion to break down and estimate the elemental composition of organic samples (Perkin-Elmer Series II CHNS/O Analyzer 2400). For condensed tannin concentrations, an acid-butanol technique was used (Rossiter *et al.* 1988), with hydrolysable tannin concentrations estimated using the potassium-iodate assay (Schultz *et al.* 1982), and total phenolic concentrations estimated using the Folin-Denis assay (Waterman and Mole 1994). Nitrogen availability was calculated by dividing nitrogen content by total phenolics. For the phenolic assays, a single bulk standard containing leaf tissue for each tree was prepared and purified by washing the leaf powder multiple times with 95% ethanol, followed by extraction using 70% acetone with Sephadex LH-20 in a Büchner funnel. Acetone was removed through rotary evaporation, resulting in pure oak tannin in aqueous solution. This was then freeze-dried, leaving only purified oak tannin powder. Individual aqueous extracted samples were obtained by purifying with multiple 95% ethanol washes followed by extraction with 70% acetone. Individual samples were compared with the bulk standard for each assay and species, and colorimetrically quantified using a microplate reader (Versamax Microplate Reader, Molecular Devices Corporation, Sunnyvale, CA).

Natural abundance of arthropods

At the beginning of the experiment (June 2010), and at each collection of experimental larvae (see below), I recorded the abundance of all arthropods, including *P. quercinigracella* and *P. quercicella*, encountered on each of the marked trees. I did so by physically examining the top and bottom of all leaves on each tree. All Lepidoptera were identified to species, while all others were identified to morphospecies.

Leaf-tier mortality experimental design and methods

At the beginning of the first generation of leaf-tying caterpillars in 2010 (early June), I conducted a three factor, fully-crossed experiment, with tree species, caterpillar species, and exposure of caterpillars to the third trophic level as the three factors. The two species of caterpillars were placed on each of the four oak species, and were either exposed to the third trophic level or not (i.e., covered in a mesh bag). The experiment was conducted once for each of the two caterpillar generations. To start the experiment, each experimental branch was inspected and all arthropods were removed. Caterpillars were then collected from non-experimental trees of various oak species and placed on the experimental trees, four individuals per tree per caterpillar species, two within net bags and two outside of net bags. Bags were constructed of nylon bridal tulle that had 1 mm^2 squares holes, affixed around an artificial leaf tie (Marquis and Lill 2010) created by clipping two adjacent leaves together with a metal hairclip (Sally's Beauty Supply). The artificial tie was created to increase the likelihood of establishment of the caterpillars. It has been observed previously that larvae remain within the tie once established (Lill and Marquis 2001). Bags were then closed around the branch with plastic gardening ties to prevent entry of other animals. Mortality from the third trophic level was calculated as mortality in the unbagged treatment minus the bagged treatment and was assumed to be the result of attack by arthropod predators.

Surviving larvae were collected 13 days later from the tie in which they were placed, and then brought to the laboratory for rearing. Mortality was noted as remaining larvae within the leaf-tie from placement to collection. At the time of collection the contents of experimental ties were examined for the presence of predators. For the first generation, *P. quercinigracella* and *P. quercicella* were placed out from June 30 - July 24 in two sets, half placed out on June 30, and the other half placed out on July 12. For the second generation, *P. quercinigracella* was placed out from August 25 to September 6 and *P. quercicella* from October 3 to October 15.

All surviving caterpillars were reared in the lab on leaves from trees on which they were originally placed. Rearing occurred under ambient light in individual plastic containers supplemented with wetted filter paper to maintain leaf freshness. Upon collection, head capsule width of all caterpillars was measured to determine instar, using Dyar's Law (Dyar 1890) as modified by Carroll (1977). Larvae were placed on a dissecting microscope stage with a digital camera attached (Cannon Rebel T1i) and a photo taken, calibrated with a stage micrometer. Images were then measured using the image manipulation program ImageJ (NIH). Caterpillar individuals were reared until pupation or parasitism and date was noted. Parasitism was counted separately from mortality in the field experiment. In addition, mass was recorded of all surviving pupae and because only the mass of *P. quercicella* varies by gender (Lill *et al.* 2007), gender was recorded only for this species using the gender determination method in Villard (1975; Lill and Marquis 2001), based on pupal characteristics.

Statistical analysis

Principal components analysis in JMP 9.0.2 (SAS Institute 2010) was used to determine the impact of plant quality traits on caterpillar survival between generations. All data were normalized by subtraction from the mean of each trait and dividing by the standard deviation. If the first two principal components explained over 50% of the variation they were correlated with larval abundance, survival, parasitism, and pupal mass. A multivariate repeated measures ANOVA using SAS (version 9.2) was used to examine how plant traits changed among tree species across generation. Some plant traits showed unequal variances, however Pallai's Criterion is robust enough to overcome this.

Natural first generation larval abundance (number of larvae per km^2 of leaf area) was analyzed using a generalized linear model in R stats (version 2.14.2) and a post hoc fixed effect procedure (Newman *et al.* 2012) with tree identity as a random effect nested within oak tree species to control for genetic effects. Because natural abundance data were zero-inflated and continuous, a generalized linear model utilizing a Tweedie compound Poisson distribution (package 'tweedie' in R) was used to test for the effect of principal components on the abundance of each caterpillar species (Zhang 2012). The number of predators per km^2 leaf area during leaf-tier abundance measurements was tested with generalized linear mixed model using a Poisson distribution and correlated with principal components and plant traits separately with Pearson’s product-moment in R.

Mortality in the field (those individuals recovered from the field experiment) was analyzed using a generalized mixed model approach with tree identity as a random effect nested within *Quercus* species. The bivariate response mortality was evaluated with a

Laplace approximation maximum likelihood estimation using the 'lme4' package in R stats (version 2.14.2) (Bates *et al.* 2011). Model comparison using the AIC approach was used to determine which variables were most important to the model, which included generation, caterpillar species, tree species, treatment (bagged or unbagged), random effect of tree identity, presence of predator in the collected tie, the interaction between generation and tree species, generation and caterpillar species, treatment and tree species, treatment and generation, treatment and caterpillar species, and finally, treatment by caterpillar species by tree species. The model with the lowest AIC value was selected as the most accurate and the variable therein deemed important to the response. All models were checked for overdispersion using Pearson's chi-squared test (Bolker *et al.* 2008). If tree species was significant in the model, a *post hoc* analysis was performed for all tree species and interactions and upper and lower p values were evaluated as in Newman *et al.* (2012). Effect size of the third trophic level (Cohen's *d*) was calculated as the difference between average mortality of the unbagged treatments and average mortality in bagged treatments, divided by the pooled deviance (Fern and Monroe 1996). This value describes the magnitude of effect of a given treatment, with any value over 0.8 indicating a very strong effect. The first two principal components of plant traits were compared to field mortality using a linear model and Pearson's product–moment correlation with mortality as the response variable in R stats (version 2.14.2), specifically examining each principal component and the interaction of principal components and caterpillar species.

Pupal mass data for *P. quercinigracella* were not normal distributed so they were square-root transformed. Pupal mass data for *P. quercicella* were normal and did not contain any outliers as a whole. All tested variables had equal variances according to the

O'Brien test (O'Brien 1981). For *P. quercinigracella*, only the second generation had sufficient survivors to analyze pupa mass, although the linear mixed model did not have sufficient degrees of freedom to calculate lower p values in the *post hoc* test. The mass data of *P. quercicella* also did not have sufficient degrees of freedom to calculate lower p values in a *post hoc* analysis. Mass was analyzed by linear mixed model fit by REML comparisons with generation, *Quercus* species, caterpillar species, treatment, gender (for *P. quercicella* only), and interactions between generation and *Quercus* species and gender (for *P. quercicella* only) and *Quercus* species with tree identity nested within tree species as a random effect in R (version 2.14.2). The first two principal components of plant traits were fitted to pupa mass for both species between generations using a linear model approach in R (version 2.14.2) with gender of individual included in the model with *P. quercicella*. In cases where outliers had a major influence on the regression, a robust linear regression with a Huber M-estimate was used in conjunction with an f test in order to determine significance. Parasitism across generations, caterpillar species, and treatment (bagged or unbagged) were analyzed using a generalized linear model with model comparisons and selection for the lowest AIC value in R (version 2.14.2) (Bates *et al.* 2011). A generalized linear model was used to analyze the first two principal components against the binomial response of parasitism between generations for each caterpillar species in R (version 2.14.2) and Pearson’s product-moment correlations calculated. Lab survival was defined as those larva that survived from collection to pupation and was analyzed using a generalized mixed model approach with generation, caterpillar species, tree species, an interaction between generation and caterpillar species, an interaction between generation and tree species, and tree identity as a random effect nested within *Quercus* species in the model. Model comparisons were used to generate *P* values and models with the lowest AIC values were selected using R. Principal components were compared to lab survival using a generalized linear model in R. Finally, days to pupation for both species of caterpillar was analyzed with a generalized mixed model approach with tree species, caterpillar species, and treatment as factors in R. If tree species was important, a *post hoc* analysis was conducted. Development time (measured as days to pupation) was also correlated with the principal components in both generations separately, leaf-tier mass, average parasitism, and the probability of predation (average third trophic level mortality for each tree in each generation separately) using both Pearson's product-moment, using R.

RESULTS

Did the studied host plant species vary in quality?

A repeated measures MANOVA revealed that plant traits differed significantly by generation ($F_{6,20} = 0.6893$, $P = 0.003$) and tree species ($F_{18,66} = 1.2450$, $P = 0.0025$), however there was no tree species by generation interaction ($F_{18,66} = 0.6564$, $P = 0.4434$) (Table 1, Figure 1). Plants declined in quality (increased phenolic concentration and decreased nitrogen availability) from the time of generation 1 to generation 2, except for water content, which increased (Figure 1). These same traits varied significantly by tree species. For example, nitrogen availability was highest in *Q. stellata* and lowest in *Q. rubra*, with the other two species intermediate (Table 1, Fig. 1). Multivariate differences in plant species were mostly due to differences in phenolic and tannin concentration, on the one hand, and nitrogen availability on the other (Figure 1). In the PCA of leaf quality factors measured during the first generation of leaf-tiers, total phenolics (-0.957) and nitrogen availability (0.903) loaded on principal component 1, and percent nitrogen (0.801) and water content (0.565) loaded on principal component 2. In the second generation, nitrogen availability (0.942) and total phenolics (-0.861) loaded on principal component 1, and percent nitrogen (-0.610) and condensed tannins (0.638) loaded on principal component 2 (Fig. 2, Table 2).

Did host plant and plant quality influence the abundance of leaf-tying caterpillars and arthropod predators?

The two caterpillar species and predators varied significantly in abundance across tree species, but in general abundances were not correlated with differences in plant quality. The abundance of *P. quercinigracella* did not vary by tree species (P = 0.2121), while that of *P. quercicella* did (P = 0.0073), with the biggest differences between *Q. alba* and *Q. velutina* (P = 0.0009), *Q. alba* and *Q. stellata* (P = 0.0183), and *Q. rubra* and *Q. velutina* (P = 0.0464) (post hoc analysis of the generalized linear model; Fig. 3). There was also a difference in predator density among *Quercus* species (P = 0.0066), with *Q. alba* having the highest density of predators and *Q. velutina* the lowest. The abundance of neither leaf-tier species, however, was not correlated with any combined measure of plant traits (the principal components) (*P. quercinigracella*: PC1: P = 0.5478, PC2 – P = 0.1781, *P. quercicella*: PC1: P = 0.4473, PC2: P = 0.1413). In addition, neither principal component correlated with predator density (PC1: P = 0.3390; PC2: P = 0.1283) and only percent nitrogen correlated positively with predator density (r = 0.3850, n = 40, P = 0.0154). Thus, abundance patterns for the herbivores and their predators were generally not consistent with the slow-growth-high-mortality hypothesis.

Did the presence of the third trophic level influence the impact of host quality on survivorship and growth?

Mortality in the field experiment was relatively high, ranging from 43% to 72%. For the field experiment, the best model (*i.e.*, with the lowest AIC value) explaining field mortality contained treatment (P = 0.0086) (unbagged higher than bagged), caterpillar species (P < 0.0001) (*P. quercinigracella* higher than *P. quercicella*), tree species (P = 0.0143) (*Q. alba* significantly higher than *Q. rubra*, with the other two species intermediate), the interaction between caterpillar species and generation (P < 0.0001), and the interaction between tree species and generation (P = 0.0056) (Table 3-4, Fig. 4).

I assumed that mortality in the bagged treatment was due to the first trophic level alone. I further assumed that the difference in mortality between the unbagged and bagged treatment was due to the third trophic level (see appendix). The slow-growth-high-mortality hypothesis predicts a difference in third trophic level mortality (unbagged treatment versus bagged treatment) among tree species. The lack of a significant interaction between treatment and oak species (P = 0.1966) in the above model is contradictory to the slow-growth-high-mortality hypothesis.

Bagging reduced overall mortality by an average 9.5 percent and mortality was higher in the first generation for *P. quercinigracella* but not for *P. quercicella* (Table 4, Fig. 5). In both generations, mortality was mainly due to the first trophic level: mortality was six times higher in the bagged treatment than the difference between the unbagged and bagged treatments (Fig. 6, 9,Table 5-6). First generation average bagged mortality in the field for *P. quercicella* was marginally positively correlated with principal component 1 (r = 0.2624, n = 40, P = 0.0994), positively correlated with nitrogen availability (r =

0.3212, n = 40, P = 0.0433), and marginally negatively correlated with total phenolics (r = -0.2886, n = 40, P = 0.0709). *P. quercinigracella* average bagged mortality was positively correlated with principal component 2 (r = 0.283, n = 40, P = 0.0768) and percent nitrogen (r = 0.3751, n = 40, P = 0.0171). These results are contradictory to the slow-growth-high-mortality hypothesis, which predicts higher mortality due to the third trophic level on plant species of lower quality. In the second generation, only bagged mortality for *P. quercinigracella* was correlated with plant traits, and these included negative correlations with principal component 1 (r = -0.3136, n = 40, P = 0.0488) and nitrogen availability (r = -0.2935, n = 40, P = 0.0660), and a marginal positive correlation with total phenolics (r = 0.2845, n = 40, P = 0.0752). These results are consistent with the slow-growth-high-mortality hypothesis.

Parasitism levels, measured in the laboratory on caterpillars collected from the field experiment, were relatively low, ranging from 1 to 8 percent. Parasitism in the first generation was influenced by both treatment (P = 0.0153) (unexpectedly five times more parasitism in the bagged treatment than in the unbagged treatment) and caterpillar species (P = 0.0446) (3.5 times higher in *P. quercicella*) (Fig. 7). Parasitism of first generation caterpillars was negatively correlated with principal component 1 in *P. quercicella* (r = -0.3138, n = 40, P = 0.0487), a result consistent with the slow-growth-high-mortality hypothesis, but not for *P. quercinigracella* (P = 0.9295). Parasitism of *P. quercicella* was also marginally positively correlated with total phenolics (r = 0.2713, n = 40, P = 0.0904) and marginally negatively correlated with nitrogen availability (r = -0.3043, n = 40, P = 0.0562). These results are consistent with the slow-growth-high mortality hypothesis. Parasitism in the second generation was not correlated with any measured factor.

Neither *Quercus* species (P = 0.6198) nor caterpillar species identity (P = 0.9608) affected lab survival of larvae, however generation was significant (55% survival in the first generation and 75% survival in the second generation; P = 0.0036). No principal component was correlated with lab survival for either caterpillar species in either generation (Generation 1 [*P. quercinigracella*: PC1 P = 0.4790; PC2 P = 0.3721, *P. quercicella*: PC1 P = 0.3345; PC2 P = 0.2380]; Generation 2 [*P. quercinigracella*: PC1 P = 0.9874; PC2 P = 0.8845, *P. quercicella*: PC1 P = 0.8265; PC2 P = 0.7431]).

Development time (the number of days from the second instar to pupation) varied by an average of 3.5 days for *P. quercicella* and 3.6 days for *P. quercinigracella* across plant species (Fig. 8). Only tree species was important in the model for larval development time (P = 0.0414). The greatest difference occurred between *Q. rubra* and *Q. stellata*, with *Q. rubra* having the longest development time and *Q. stellata* the shortest (*post hoc* analysis of generalized linear model; Table 7). Development time was not correlated with any principal component (P > 0.2090) or with the probability of predation (*P. quercinigracella*: P = 0.8412, *P. quercicella*: P = 0.7458) for either generation. In addition, development time was marginally negatively correlated with the probability of being parasitized in *P. quercinigracella* (r = -0.2849, n = 35, P = 0.0972) and not correlated at all in *P. quercicella* (P = 0.1328). Thus, all results regarding development time are either contradictory to the slow-growth-high-mortality hypothesis or lend no support.

Pupal mass in *P. quercinigracella* was significantly affected by tree species (P = 0.0435), with mass on *Q. velutina* and *Q. stellata* lower than that on *Q. rubra* and *Q. alba* (Table 8-9, Fig. 8). *P. quercicella* pupal mass was significantly affected by gender (P <

0.0001) (females had greater mass than males), generation (P = 0.0268) (first generation pupae were larger than those of the second), and *Quercus* species (P = 0.0267) (*Q. stellata* with the lowest mass and *Q. alba* the highest), with an interaction between *Quercus* species and generation (P = 0.0178) (Tables 10-11). For the second generation of *P. quercinigracella*, no principal component was correlated with pupal mass (PC1: P = 0.4967, PC2: P = 0.3023). *P. quercicella* pupal mass for females in the first generation was negatively correlated with principal component 1 (r = -0.4858, n = 17, P = 0.0481), while pupal mass of males was marginally positive correlated with principal component 1 (r = 0.5247, n = 13, P = 0.0656). In the second generation neither female (P > 0.1115) nor male (P > 0.1975) pupal mass was correlated with principal components. Finally, *P. quercinigracella* and *P. quercicella* mass showed no correlation with development time in either generation.

DISCUSSION

Plant traits varied significantly among tree species and generation but there was no interaction between the two. The abundance of both *P. quercicella* and predators abundance varied by tree species, however correlations with plant traits did not occur or were not consistent with the hypothesis. Mortality was affected by treatment (unbagged higher than bagged), caterpillar species (*P. quercinigracella* higher than *P. quercicella*), tree species (*Q. alba* significantly higher than *Q. rubra*), the interaction between caterpillar species and generation, and the interaction between tree species and generation. However the lack of an interaction between tree species and treatment is inconsistent with the slow-growth-high-mortality hypothesis. Finally, even though development time was affected by tree species, it did not correlate with plant traits and the probability of predation.

Variability in plant quality by Quercus *species and time of year*

A starting premise of the slow-growth-high-mortality hypothesis is that plants vary in traits that slow the growth of their insect herbivores, not enough to kill those insects but enough to increase the time over which they are vulnerable to natural enemies. In this study, plant traits differed significantly among *Quercus* species; total phenolics and nitrogen availability explained between 32.5%-37.9%-of overall plant trait variation, while percent nitrogen and water content explained 25.4% in the first generation and percent nitrogen and condensed tannins explained 20.6% in the second generation. *Quercus stellata* showed the lowest percent nitrogen but had the highest available nitrogen (the ratio of total phenolics to nitrogen content). In contrast, *Q. rubra* had the lowest available nitrogen while having the highest percent nitrogen per gram dry mass. Plant traits also differed significantly by time of year: all leaf traits declined in quality except for water content, which increased from the first generation to second. While a leaf quality decline over a season is consistent with other studies conducted on oak trees (Feeny 1970, Forkner *et al.* 2004, Mauffette and Oechel 1989), the observation that leaf water content increased from the first generation to that of the second is surprising because it is opposite that found for other North American deciduous tree species (Scriber 1977).

Natural abundance of the two leaftying species and predators by tree species

If the predictions of the slow-growth-high-mortality hypothesis hold in this system, predators should be most abundant on tree species that have the lowest leaf quality and herbivores should be the most abundant on tree species with the best overall quality foliage. However, only *P. quercicella* varied by tree species (higher abundance on *Q. alba* and *Q. rubra* than on either *Q. velutina* or *Q. stellata*), as did predators (highest on *Q. alba*). This could have been due to the fact that both *Q. velutina* and *Q. stellata* are pubescent (contain leaf hairs) while *Q. alba* and *Q. rubra* are not (KB, unpublished data). Pubescence has been shown to affect insect herbivore abundance (Lill *et al.* 2006) and predator foraging efficiency (Coll et al. 1997); previous studies, however, suggest that pubescence does not influence the abundance of some leaf-tying caterpillar species (Marquis and Lill 2010). Abundance was only measured one time in the summer and this may have caused the peak abundances of one of the leaf-tier species to be missed. Multiple abundance measurements throughout the first generation could answer this question and could also shed light on patterns of emergence and how they relate to host plant species. For example, a study on *Operophtera brumata* found that lag times between male and female emergences were drastically different on ‘alternative host’ plants (Tikkanen *et al.* 2000). If non-optimal hosts can alter the emergence between sexes, then it is reasonable to assume that it could also occur between two herbivore species. Finally, it should be noted that the abundance of these herbivores in this study were measured with both the first and third trophic levels present. There might be an interaction of both trophic levels that was not measured because no variable was experimentally manipulated.

Quercus *species, caterpillar species, and generation affected bottom-up mortality, growth, and development*

Mortality in the bagged treatment was higher for *P. quercinigracella* than *P. quercicella* during the first generation. This result could be because *P. quercinigracella* might be more sensitive to nitrogen availability and its changes (Mathavan and Pandian 1975).

In the second generation, host plant identity affected *P. quercinigracella* pupal mass (P = 0.0435). Caterpillars on *Q. velutina* and *Q. stellata* had the lowest pupal mass while those reared on *Q. alba* and *Q. rubra* had the highest mass (Fig. 8, Tables 9-11). This is an interesting and perplexing result as nitrogen availability is higher in the first two than in the last two. Altogether, *P. quercicella* females were significantly larger than males, which is consistent with a previous study (Lill and Marquis 2001). Additionally *P. quercicella* mass responded to *Quercus* species (*Q. stellata* the lowest mass) and that relationship changed with generation (individuals on *Q. stellata* having had the greatest change in mass across generations). Species size differences could have contributed to changes in digestion, ultimately resulting in mass differences (Yang and Joern 1994).

Under the slow-growth-high-mortality hypothesis one would expect that development time would change between tree species if plant traits were significantly different. Development time was significantly affected by *Quercus* species, a result consistent with the hypothesis. The greatest differences for both leaf-tier species was between *Q. rubra* and *Q. stellata*, which coincides with the pattern in available nitrogen and is consistent with another study measuring developmental rates and plant quality (Taylor 1989).While *P. quercinigracella* showed no relationship between development time and pupal mass, *P. quercicella* pupal mass was negatively correlated with development time, but only weakly so (r = -0.2801), meaning the longer a larva feeds, the smaller it would be at pupation. While a smaller larva might be difficult to find by predators and thus may avoid predation, their smaller size might also make them more vulnerable to parasitoids because smaller individuals might have less energy to dedicate to encapsulation.

The association of *Psilocorsis quercicella* pupal mass and the principal components varied by generation and gender. While males showed little or no relationship with principal components, females showed opposite trends across generations (negatively correlated with PC1 in generation 1 but positive correlated in generation 2) and both relationships were moderate (-0.4858 in generation 1 and 0.4532 in generation 2). Differences in the associations to principal components could be due to males and females utilizing compensatory feeding differently (Docherty *et* al. 1994, Raubenheimer and Simpson 1990), however there is no clear trend and warrants further investigation. Future studies should measure the digestive efficiency and the resulting pupal mass between the two genders of *P. quercicella* in conjunction with a measure of compensatory feeding.

Treatment and Quercus *species affect top-down mortality and parasitism is affected by treatment and generation*

The observed effect of bagging was expected because the unbagged individuals were exposed to predation while the bagged were not. However, generation also caused slight differences in top-down mortality, with the first generation incurring more than the second. Similarly, slightly fewer larvae of *P. quercinigracella* were removed by the third trophic level than *P. quercicella* and *Quercus* species caused additional differences.

Host plant identity was predicted to affect the probability of parasitism under the current hypothesis, but measured parasitism was low, with 3.2% individuals parasitized. Only the first generation showed differences, specifically with regards to caterpillar species and treatment. *P. quercicella* experienced more parasitism than *P. quercinigracella*, 7.5% versus 2.5% (Fig. 7). The leaf-tier species could affect the type of attacking parasitoid and hence result in a difference in parasitism, however parasitoid species identity was not recorded. In addition, because I did not measure encapsulation, there could be a difference in the immune system response between the leaf-tier species that could contribute to a difference in parasitism and development rate (Benrey and Denno 1997, Klemola *et al.* 2007).

Treatment also affected the probability of parasitism, however opposite that expected. Those individuals in the bagged treatment experienced higher parasitism (8.2%) than the unbagged treatment (1.9%). Larvae were collected in the field and, therefore, some individuals certainly were parasitized before collection. Some parasites and parasitoids have been shown to increase the risky behavior of hosts, increasing their mortality (Trail 1980). This could lead to higher mortality in the unbagged larvae which were exposed to the third trophic level, thus making it appear as if there were more parasitized individuals in one treatment over the other.

Are interactions in this system consistent with the predictions of the Slow Growth-High Mortality Hypothesis?

The only other study examining the slow-growth-high-mortality hypothesis in this system found that the development time of *P. quercicella* larva showed no response to plant quality, but rather was associated with relatedness (Lill and Marquis 2001). Here I show that host plant identity influenced both development time and mortality due to the third trophic level but that none of the measured plant traits were correlated with either of these variables. While the result that there is a generational difference in mass in response to leaf quality is consistent with Lill and Marquis (2001), I found an additional effect of gender that shows opposite correlations (females negatively correlated to PC1 and males positively correlated to PC1).

Larval mortality responded differently to *Quercus* species when exposed to the third trophic level (unbagged), possibly indicating that there was unequal foraging among arthropod predators among tree species (Tables 3-5, Fig. 4), which has been seen in other systems (Medina *et al*. 2005, Mooney *et al*. 2012, Singer *et al*. 2012). As with the leaf-tiers, the highest predator abundance occurred on *Q. alba*, which does not follow the predictions of the slow-growth-high-mortality hypothesis because *Q. alba* did not have the lowest leaf quality. Differences of surrounding foliage by tree species as they affect predator refuge could be important (Forkner and Hunter 2000). The third trophic level effect was high for both *Q. rubra* and *Q. stellata* when both leaf-tiers are pooled, but changes when each is looked at separately (Table 6, Fig. 9). This can be interpreted as differences in predator foraging preferences, with *P. quercinigracella* a more preferred prey item over *P. quercicella* when only *Q. rubra* and *Q. stellata* are considered. Lastly, even though there was a small difference between generation and leaf-tier species in effect size (0.23-0.32) (Fig. 10), parasitism only showed differences between generation and leaf-tier species and was not associated with any principal component. Therefore, we can separate parasitoids from the other predators in the third trophic level and conclude that they too, as in other systems, do not follow the slow-growth-high-mortality hypothesis (Thaler 1999, Medina *et al*. 2005, Connahs *et al*. 2011).

Conclusions

There was a difference in plant traits among tree species, which is opposite of leaf-tier mortality, at least from the bottom-up (*e.g.* high mortality and high leaf quality on *Q. stellata* and low mortality and low leaf quality on *Q. rubra*) and in leaf-tier generation (changes in per generation proportional mortality: *Q. velutina* = -3.2%, *Q. rubra* = 2.7%, *Q. stellata* = -2.2%, *Q. alba* = 2.7%) (Table 4-5, Fig. 4). Mortality due to the third trophic level (unbagged – bagged mortality) did not match the pattern of bottom-up mortality, possibly meaning unequal foraging by predators, however a one-time census for predator abundance did not match the third trophic level effect size pattern (high predator abundance on *Q. alba* but the largest third trophic level effect on *Q. rubra*) (Table 6). Additionally, because development time and the probability of predation were not correlated but some plant traits and mass were and that in most cases the effect size of the third trophic level remains small (0.0-0.30), it seems likely that plant quality acts as more of a direct defense rather than indirect, at least for *P. quercicella*.

Lastly, plant traits, measured as principal components, were for the most part uncorrelated with measures of survivorship (bottom-up and top-down), development and parasitism. However, host plant species did affect these measures and the fact that they were not correlated could indicate that the relevant factors contributing to principal components in this study were not ultimately responsible for the differences in survivorship, development, and parasitism. Hence, it does not seem likely that the hypothesis holds true in this system.

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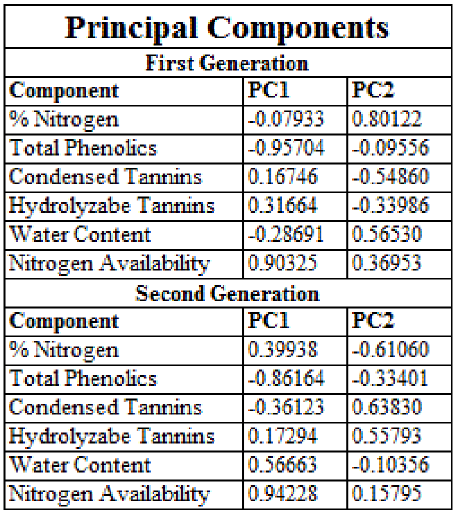
TABLES AND FIGURES

Table 1. Results from repeated measures MANOVA in SAS (9.2).

Treatment	**Value**	**F Value**	**Num DF**	**Den DF**	**Pr > F**
Tree Species	1.24497067	2.6	18	66	0.0025
Generation	0.68927697	7.39	6	20	0.0003
Tree Species * Generation	0.65641613	1.03	18	66	0.4434

Table 1. Loadings for principal components 1 and 2 both generations.



Principal Components

First Generation

Component	**PC1**	**PC2**
% Nitrogen	-0.07933	0.80122
Total Phenolics	-0.95704	-0.09556
Condensed Tannins	0.16746	-0.54860
Hydrolyzabe Tannins	0.31664	-0.33986
Water Content	-0.28691	0.56530
Nitrogen Availability	0.90325	0.36953

Second Generation

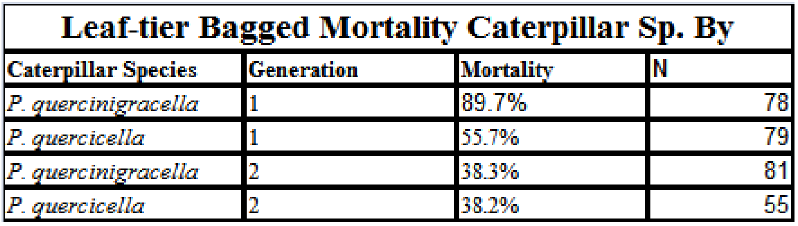
Component	**PC1**	**PC2**
% Nitrogen	0.39938	-0.61060
Total Phenolics	-0.86164	-0.33401
Condensed Tannins	-0.36123	0.63830
Hydrolyzabe Tannins	0.17294	0.55793
Water Content	0.56663	-0.10356
Nitrogen Availability	0.94228	0.15795

Table 3. Wald Z and Post hoc analysis of the response mortality in a generalized linear model in R stats, package (“lme4”).

Factor	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Caterpillar Sp.	-4.865533	0.7855326	-6.1939285	**<0.001**
Treatment	-0.497719	0.195104	-2.551	**0.011**
Generation X Caterpillar Sp.	2.458014	0.452754	5.429	**<0.001**

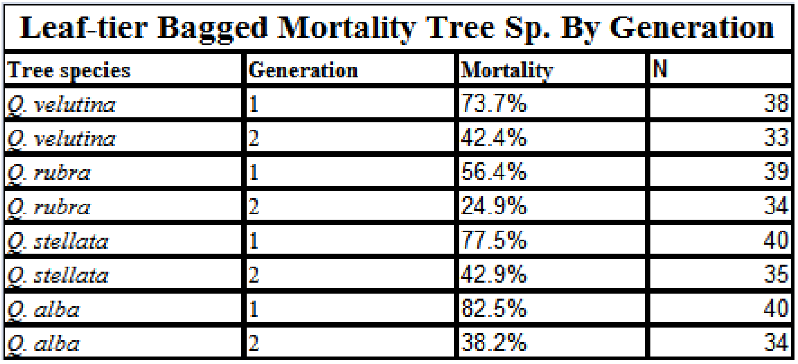
	Q. velutina		***Q. rubra***		***Q. stellata***		***Q. alba***	
Factor	**p (Up Bound)**	**p (Low Bound)**	**p (Up Bound)**	**p (Low Bound)**	**p (Up Bound)**	**p (Low Bound)**	**p (Up Bound)**	**p (Low Bound)**
Q. velutina	-	-	0.3632	0.3632	0.0934	0.0935	**0.0098**	**0.0098**
Q. rubra	0.3631	0.3632	-	-	**0.0119**	**0.0120**	**0.0006**	**0.0006**
Q. stellata	0.0934	0.0935	**0.0119**	**0.0120**	-	-	0.3950	0.3950
Q. alba	**0.0098**	**0.0098**	**0.0006**	**0.0006**	0.3950	0.3950	-	-
Generation	0.6611	0.6611	0.6852	0.6852	0.0432	0.0433	**0.0003**	**0.0003**
Generation X *Q. velutina*	-	-	0.5076	0.5076	0.1865	0.1866	**0.0087**	**0.0087**
Generation X *Q. rubra*	0.5075	0.5076	-	-	0.0525	0.0526	0.0012	0.0012
Generation X *Q. stellata*	0.1865	0.1866	0.0525	0.0526	-	-	0.2102	0.2103
Generation X *Q. alba*	**0.0087**	**0.0087**	**0.0012**	**0.0012**	0.2102	0.2103	-	-

Table 4. Leaf-tier bagged mortality by caterpillar species, generation, and tree species.



Leaf-tier Bagged Mortality Caterpillar Sp. By

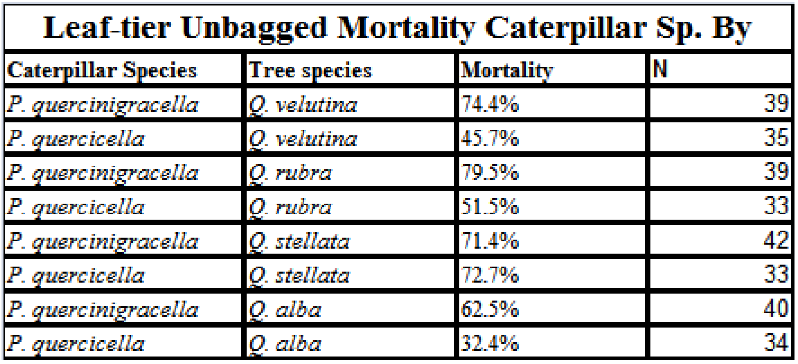
Caterpillar Species	Generation	Mortality	N
P. quercinigracella	1	89.7%	78
P. quercicella	1	55.7%	79
P. quercinigracella	2	38.3%	81
P. quercicella	2	38.2%	55



Leaf-tier Bagged Mortality Tree Sp. By Generation

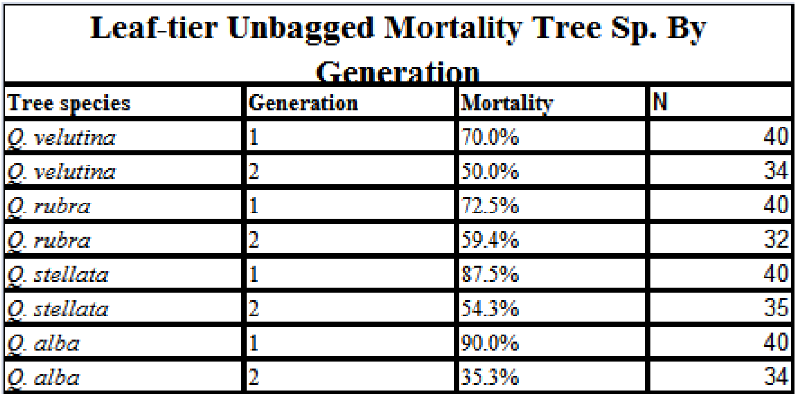
Tree species	Generation	Mortality	N
Q. velutina	1	73.7%	38
Q. velutina	2	42.4%	33
Q. rubra	1	56.4%	39
Q. rubra	2	24.9%	34
Q. stellata	1	77.5%	40
Q. stellata	2	42.9%	35
Q. alba	1	82.5%	40
Q. alba	2	38.2%	34

Table 5. Leaf-tier unbagged mortality by tree species, generation, and caterpillar species.



Leaf-tier Unbagged Mortality Caterpillar Sp. By

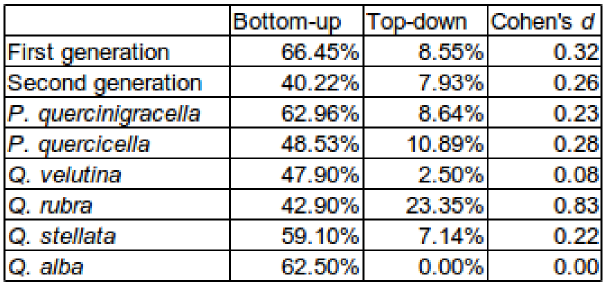
Caterpillar Species	Tree species	Mortality	N
P. quercinigracella	*Q. velutina*	74.4%	39
P. quercicella	*Q. velutina*	45.7%	35
P. quercinigracella	*Q. rubra*	79.5%	39
P. quercicella	*Q. rubra*	51.5%	33
P. quercinigracella	*Q. stellata*	71.4%	42
P. quercicella	*Q. stellata*	72.7%	33
P. quercinigracella	*Q. alba*	62.5%	40
P. quercicella	*Q. alba*	32.4%	34



Leaf-tier Unbagged Mortality Tree Sp. By Generation

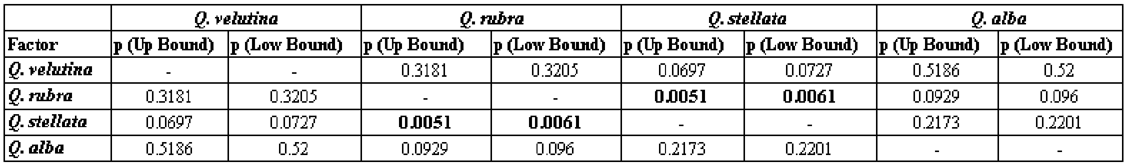
Tree species	Generation	Mortality	N
Q. velutina	1	70.0%	40
Q. velutina	2	50.0%	34
Q. rubra	1	72.5%	40
Q. rubra	2	59.4%	32
Q. stellata	1	87.5%	40
Q. stellata	2	54.3%	35
Q. alba	1	90.0%	40
Q. alba	2	35.3%	34

Table 6. Average bottom-up and top-down mortality with Cohen’s *d* as effect size.



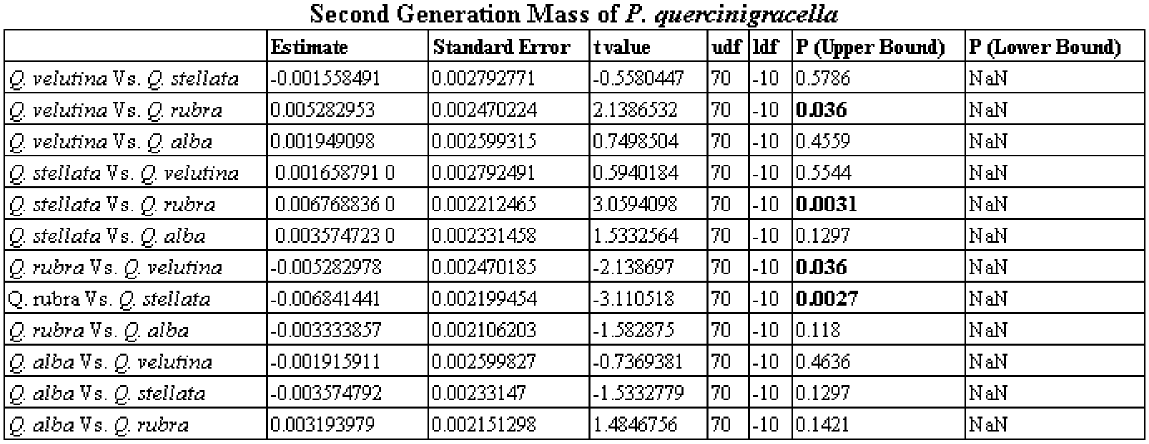
	Bottom-up	Top-down	Cohen's *d*
First generation	66.45%	8.55%	0.32
Second generation	40.22%	7.93%	0.26
P. quercinigracella	62.96%	8.64%	0.23
P. quercicella	48.53%	10.89%	0.28
Q. velutina	47.90%	2.50%	0.08
Q. rubra	42.90%	23.35%	0.83
Q. stellata	59.10%	7.14%	0.22
Q. alba	62.50%	0.00%	0.00

Table 7. Posthoc analysis of days from second instar to pupation of both caterpillar species on four species of oak in a generalized linear model in R stats, package ("lme4"). The only significant difference occurs between *Q. stellata* and *Q. rubra*. Significance calculated both conservatively (ldf "lower degrees of freedom") and anti-conservatively (udf "upper degrees of freedom").



	Q. velutina		***Q. rubra***		***Q. stellata***		***Q. alba***	
Factor	**p (Up Bound)**	**p (Low Bound)**	**p (Up Bound)**	**p (Low Bound)**	**p (Up Bound)**	**p (Low Bound)**	**p (Up Bound)**	**p (Low Bound)**
Q. velutina	-	-	0.3181	0.3205	0.0697	0.0727	0.5186	0.52
Q. rubra	0.3181	0.3205	-	-	**0.0051**	**0.0061**	0.0929	0.096
Q. stellata	0.0697	0.0727	**0.0051**	**0.0061**	-	-	0.2173	0.2201
Q. alba	0.5186	0.52	0.0929	0.096	0.2173	0.2201	-	-

Table 8. Generalized linear model with post hoc analysis on the second generation of *P. quercinigracella* mass in R stats, package ("lme4"). Significance calculated both conservatively (ldf "lower degrees of freedom") and anti-conservatively (udf "upper degrees of freedom").



Second Generation Mass of *P. quercinigracella*

	Estimate	**Standard Error**	**t value**	**udf**	**ldf**	**P (Upper Bound)**	**P (Lower Bound)**
Q. velutina Vs. *Q. stellata*	-0.001558491	0.002792771	-0.5580447	70	-10	0.5786	NaN
Q. velutina Vs. *Q. rubra*	0.005282953	0.002470224	2.1386532	70	-10	**0.036**	NaN
Q. velutina Vs. *Q. alba*	0.001949098	0.002599315	0.7498504	70	-10	0.4559	NaN
Q. stellata Vs. *Q. velutina*	0.001658791 0	0.002792491	0.5940184	70	-10	0.5544	NaN
Q. stellata Vs. *Q. rubra*	0.006768836 0	0.002212465	3.0594098	70	-10	**0.0031**	NaN
Q. stellata Vs. *Q. alba*	0.003574723 0	0.002331458	1.5332564	70	-10	0.1297	NaN
Q. rubra Vs. *Q. velutina*	-0.005282978	0.002470185	-2.138697	70	-10	**0.036**	NaN
Q. rubra Vs. *Q. stellata*	-0.006841441	0.002199454	-3.110518	70	-10	**0.0027**	NaN
Q. rubra Vs. *Q. alba*	-0.003333857	0.002106203	-1.582875	70	-10	0.118	NaN
Q. alba Vs. *Q. velutina*	-0.001915911	0.002599827	-0.7369381	70	-10	0.4636	NaN
Q. alba Vs. *Q. stellata*	-0.003574792	0.00233147	-1.5332779	70	-10	0.1297	NaN
Q. alba Vs. *Q. rubra*	0.003193979	0.002151298	1.4846756	70	-10	0.1421	NaN

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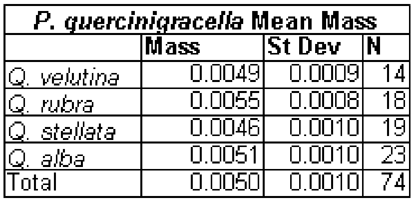
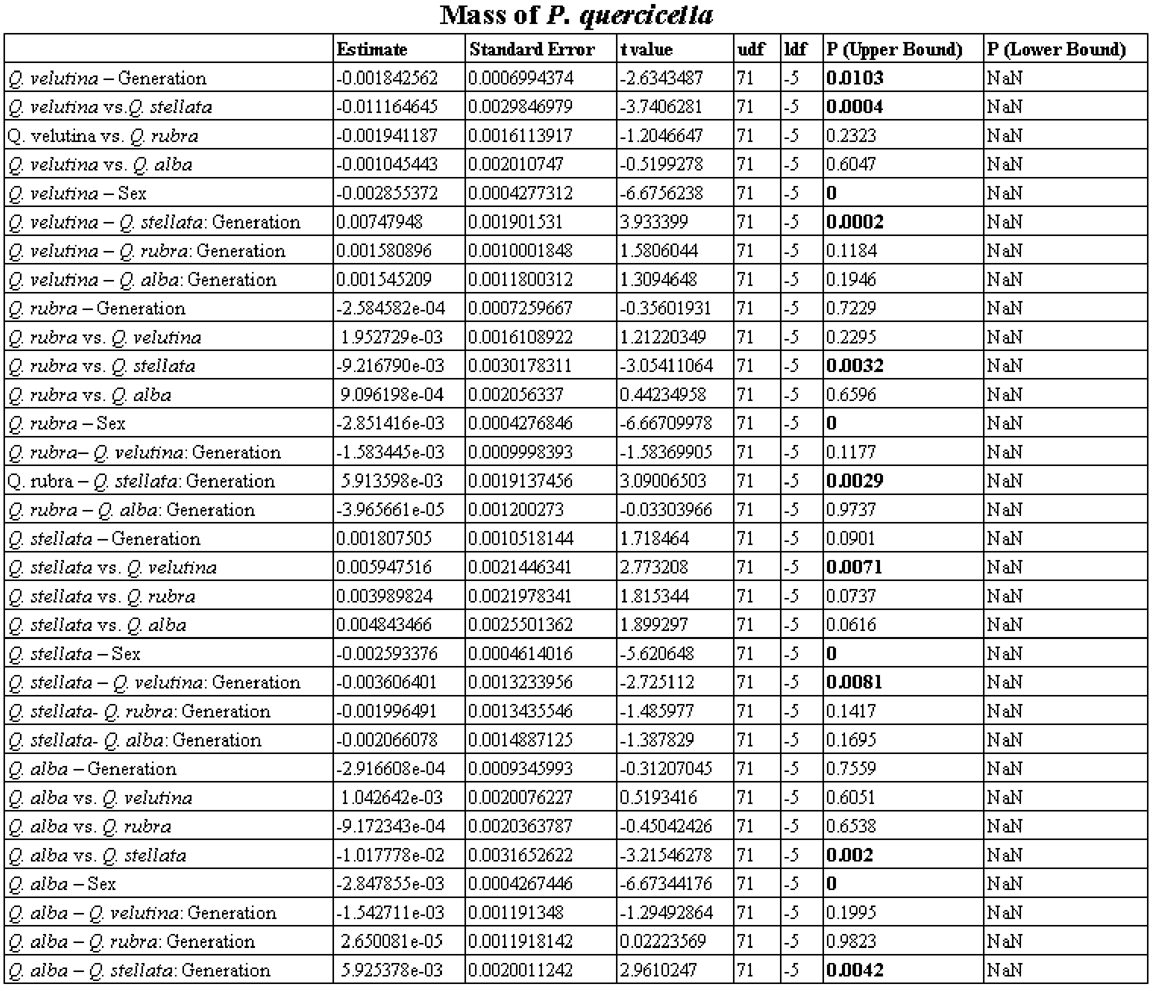
Table 9. *P. quercinigracella* mass in the second generation (grams).



P. quercinigracella Mean Mass

	Mass	St Dev	N
Q. velutina	0.0049	0.0009	14
Q. rubra	0.0055	0.0008	18
Q. stellata	0.0046	0.0010	19
Q. alba	0.0051	0.0010	23
Total	0.0050	0.0010	74

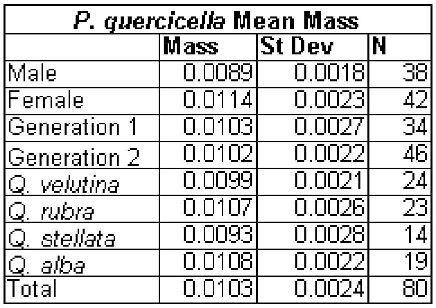
Table 10. Post hoc analysis on a generalized linear model of *P. quercicella* mass in all generations and *Quercus* species in R stats, package ("lme4").Significance calculated both conservative ("upper bound") and anti-conservative ("lower bound") p values.



Mass of *P. quercicella*

	Estimate	**Standard Error**	**t value**	**udf**	**ldf**	**P (Upper Bound)**	**P (Lower Bound)**
Q. velutina – Generation	-0.001842562	0.0006994374	-2.6343487	71	-5	**0.0103**	NaN
Q. velutina vs.*Q. stellata*	-0.011164645	0.0029846979	-3.7406281	71	-5	**0.0004**	NaN
Q. velutina vs. *Q. rubra*	-0.001941187	0.0016113917	-1.2046647	71	-5	0.2323	NaN
Q. velutina vs. *Q. alba*	-0.001045443	0.002010747	-0.5199278	71	-5	0.6047	NaN
Q. velutina – Sex	-0.002855372	0.0004277312	-6.6756238	71	-5	**0**	NaN
Q. velutina – *Q. stellata*: Generation	0.00747948	0.001901531	3.933399	71	-5	**0.0002**	NaN
Q. velutina – *Q. rubra*: Generation	0.001580896	0.0010001848	1.5806044	71	-5	0.1184	NaN
Q. velutina – *Q. alba*: Generation	0.001545209	0.0011800312	1.3094648	71	-5	0.1946	NaN
Q. rubra – Generation	-2.584582e-04	0.0007259667	-0.35601931	71	-5	0.7229	NaN
Q. rubra vs. *Q. velutina*	1.952729e-03	0.0016108922	1.21220349	71	-5	0.2295	NaN
Q. rubra vs. *Q. stellata*	-9.216790e-03	0.0030178311	-3.05411064	71	-5	**0.0032**	NaN
Q. rubra vs. *Q. alba*	9.096198e-04	0.002056337	0.44234958	71	-5	0.6596	NaN
Q. rubra – Sex	-2.851416e-03	0.0004276846	-6.66709978	71	-5	**0**	NaN
Q. rubra– *Q. velutina*: Generation	-1.583445e-03	0.0009998393	-1.58369905	71	-5	0.1177	NaN
Q. rubra – *Q. stellata*: Generation	5.913598e-03	0.0019137456	3.09006503	71	-5	**0.0029**	NaN
Q. rubra – *Q. alba*: Generation	-3.965661e-05	0.001200273	-0.03303966	71	-5	0.9737	NaN
Q. stellata – Generation	0.001807505	0.0010518144	1.718464	71	-5	0.0901	NaN
Q. stellata vs. *Q. velutina*	0.005947516	0.0021446341	2.773208	71	-5	**0.0071**	NaN
Q. stellata vs. *Q. rubra*	0.003989824	0.0021978341	1.815344	71	-5	0.0737	NaN
Q. stellata vs. *Q. alba*	0.004843466	0.0025501362	1.899297	71	-5	0.0616	NaN
Q. stellata – Sex	-0.002593376	0.0004614016	-5.620648	71	-5	**0**	NaN
Q. stellata – *Q. velutina*: Generation	-0.003606401	0.0013233956	-2.725112	71	-5	**0.0081**	NaN
Q. stellata- *Q. rubra*: Generation	-0.001996491	0.0013435546	-1.485977	71	-5	0.1417	NaN
Q. stellata- *Q. alba*: Generation	-0.002066078	0.0014887125	-1.387829	71	-5	0.1695	NaN
Q. alba – Generation	-2.916608e-04	0.0009345993	-0.31207045	71	-5	0.7559	NaN
Q. alba vs. *Q. velutina*	1.042642e-03	0.0020076227	0.5193416	71	-5	0.6051	NaN
Q. alba vs. *Q. rubra*	-9.172343e-04	0.0020363787	-0.45042426	71	-5	0.6538	NaN
Q. alba vs. *Q. stellata*	-1.017778e-02	0.0031652622	-3.21546278	71	-5	**0.002**	NaN
Q. alba – Sex	-2.847855e-03	0.0004267446	-6.67344176	71	-5	**0**	NaN
Q. alba – *Q. velutina*: Generation	-1.542711e-03	0.001191348	-1.29492864	71	-5	0.1995	NaN
Q. alba – *Q. rubra*: Generation	2.650081e-05	0.0011918142	0.02223569	71	-5	0.9823	NaN
Q. alba – *Q. stellata*: Generation	5.925378e-03	0.0020011242	2.9610247	71	-5	**0.0042**	NaN

Table 11. *P. quercicella* mass in generations, gender, and tree species (grams).



***P. quercicella* Mean Mass**			
	Mass	**St Dev**	**N**
Male	0.0089	0.0018	38
Female	0.0114	0.0023	42
Generation 1	0.0103	0.0027	34
Generation 2	0.0102	0.0022	46
Q. velutina	0.0099	0.0021	24
Q. rubra	0.0107	0.0026	23
Q. stellata	0.0093	0.0028	14
Q. alba	0.0108	0.0022	19
Total	0.0103	0.0024	80

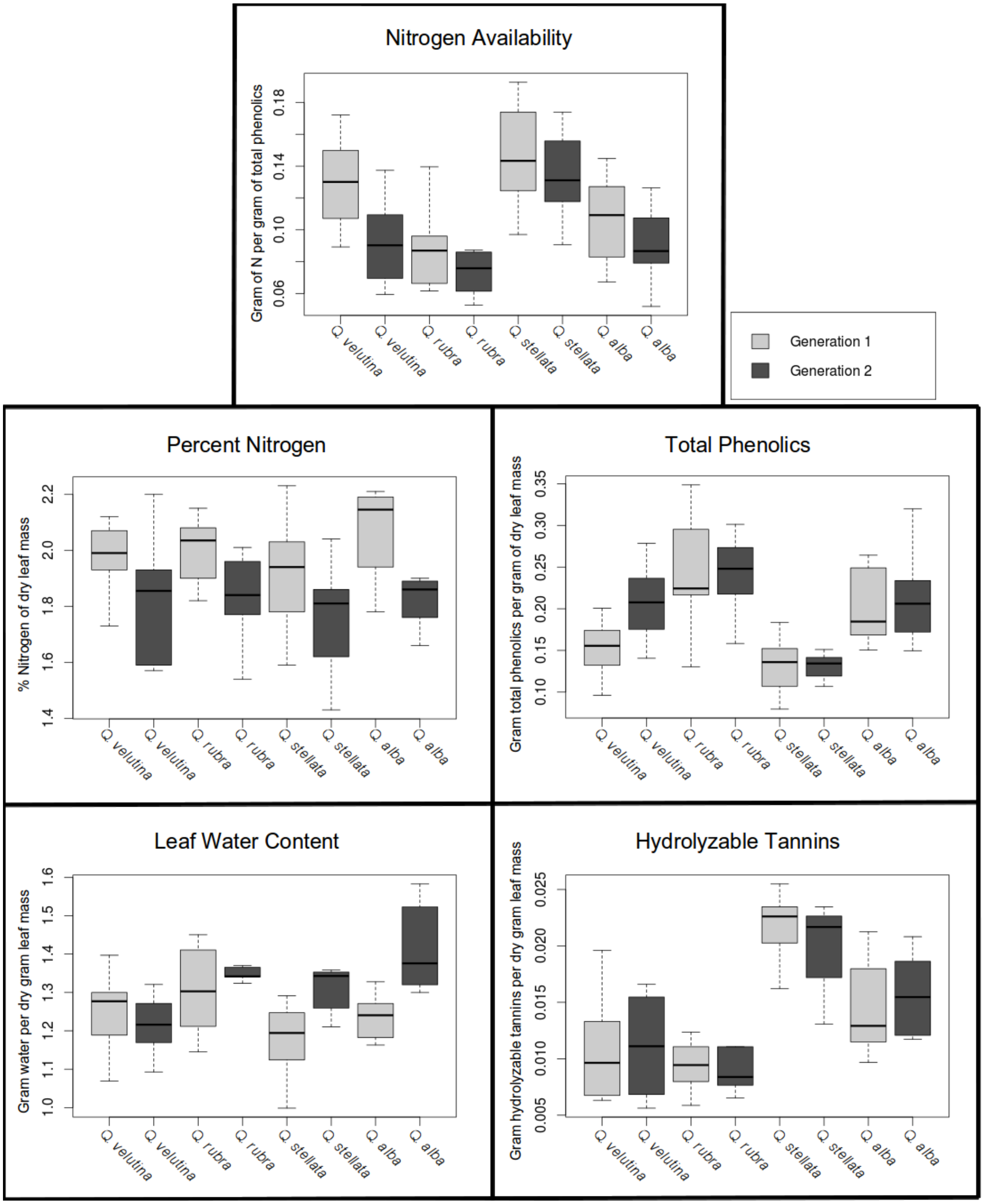


Figure 1. Plant traits by tree species and generation.

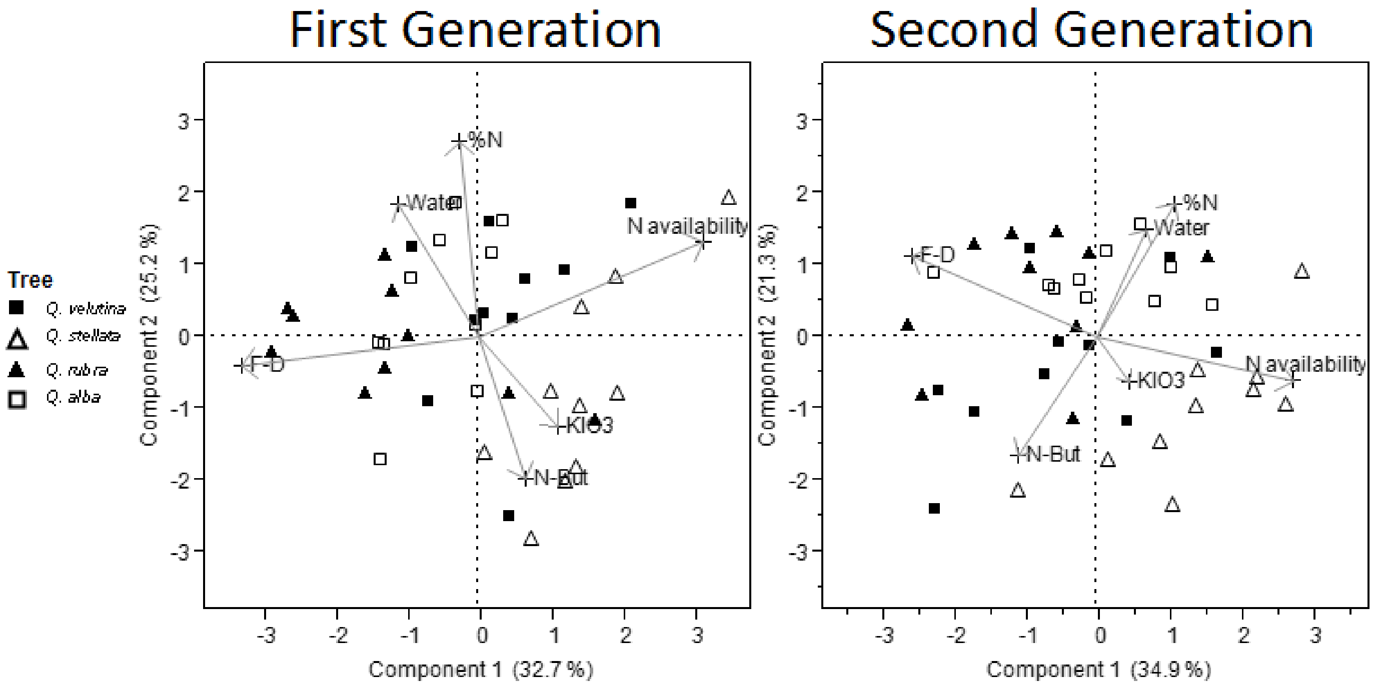


Figure 2. Principal components analysis ordination of plant traits against the first two principal components in both generations. (%N – percent nitrogen, N availability – nitrogen availability, Water – water content, F-D – total phenolics, KIO3 – hydrolysable tannins, N-But – condensed tannins).

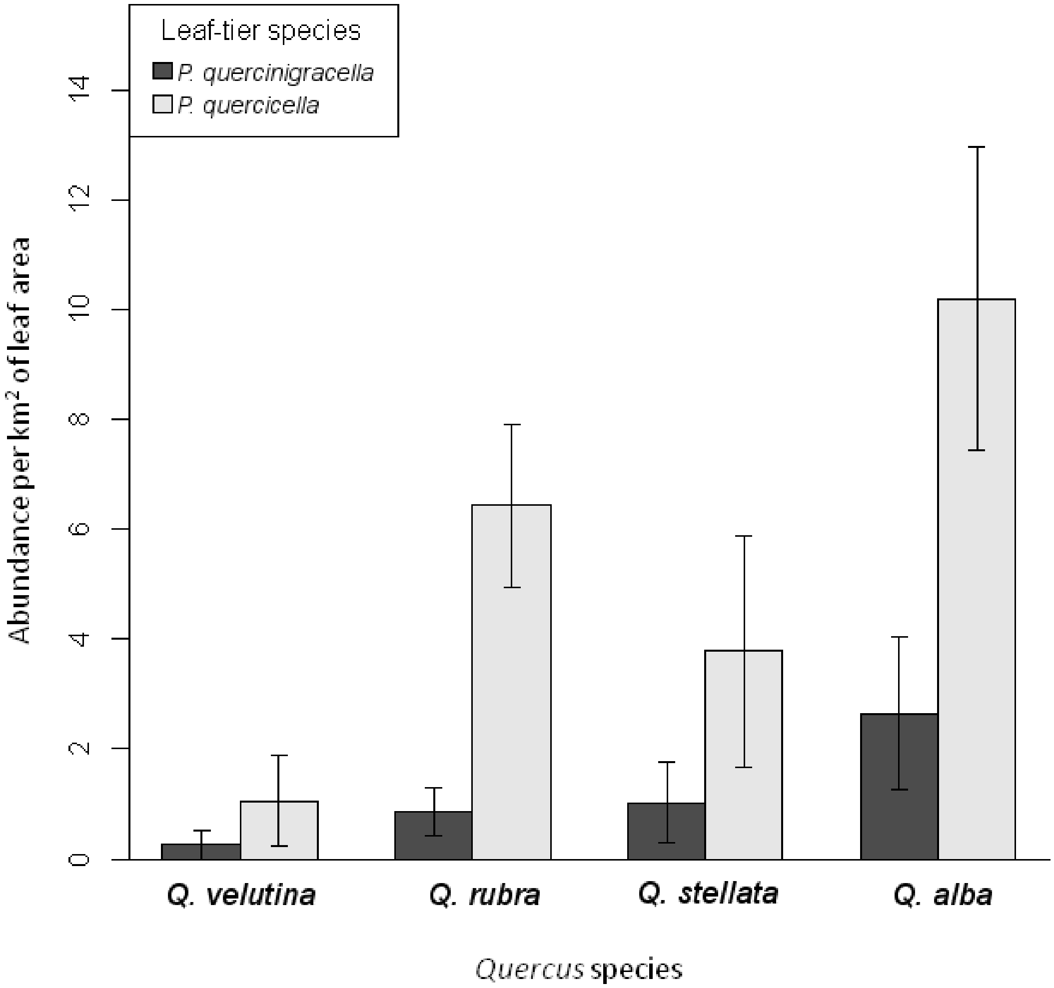
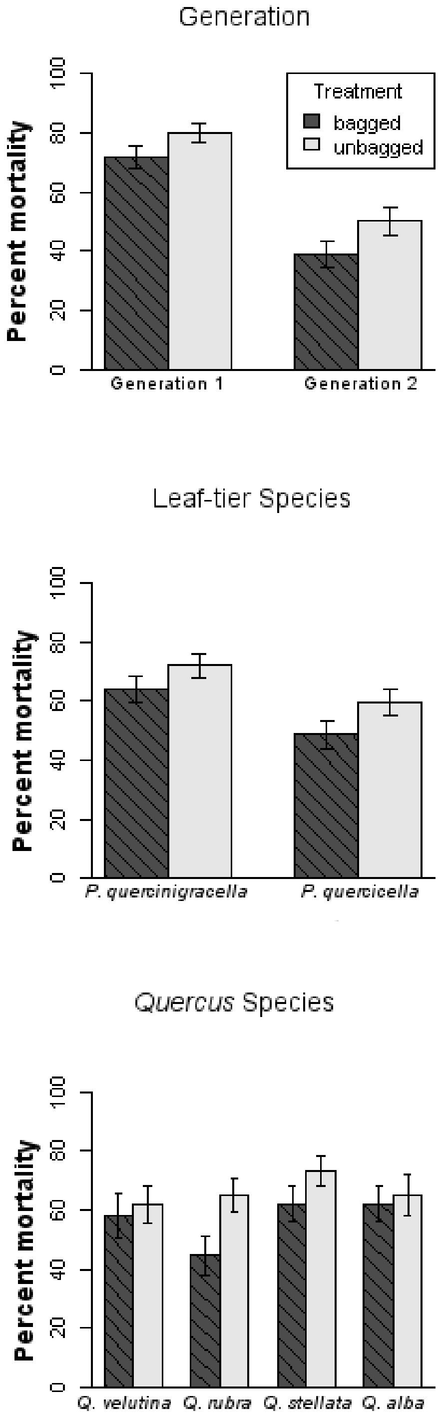


Figure 3. Abundance per km^2 of leaf area of each leaf-tier species on the four species of oak. *P. quercinigracella*'s abundance was not affected by tree species (P = 0.2121), however *P. quercicella*'s abundance was (P = 0.0073); the biggest differences in *P. quercicella* abundance were between *Q. alba* and *Q. velutina* (P = 0.0009), *Q. alba* and *Q. stellata* (P = 0.0183), and *Q. rubra* and *Q. velutina* (P = 0.0464). Error bars are standard error.



Generation

Leaf-tier Species

Quercus Species

Figure 4. Mortality in the field of leaf-tiers exposed to both the first and third trophic levels (unbagged vs. bagged). Error bars are standard error.

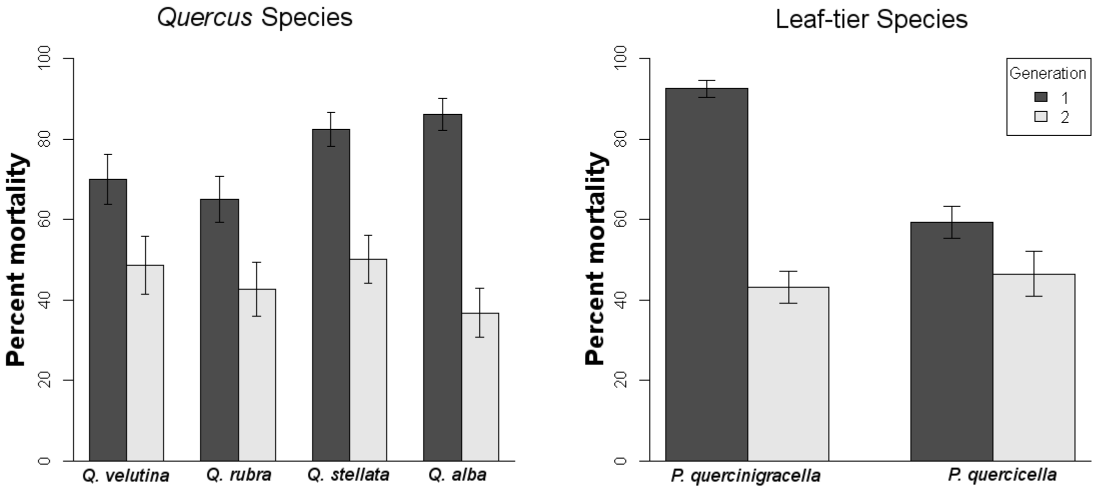


Figure 5. Mortality of leaf-tying caterpillars across two generations. There was a significant difference between caterpillar species and generation (P < 0.0001). Error bars are standard error.

Figure 6. Total mortality of leaf-tiers in bagged and unbagged treatments. Hatched portion highlights difference between top-down and bottom-up mortality (9.5% difference) (P = 0.0110).

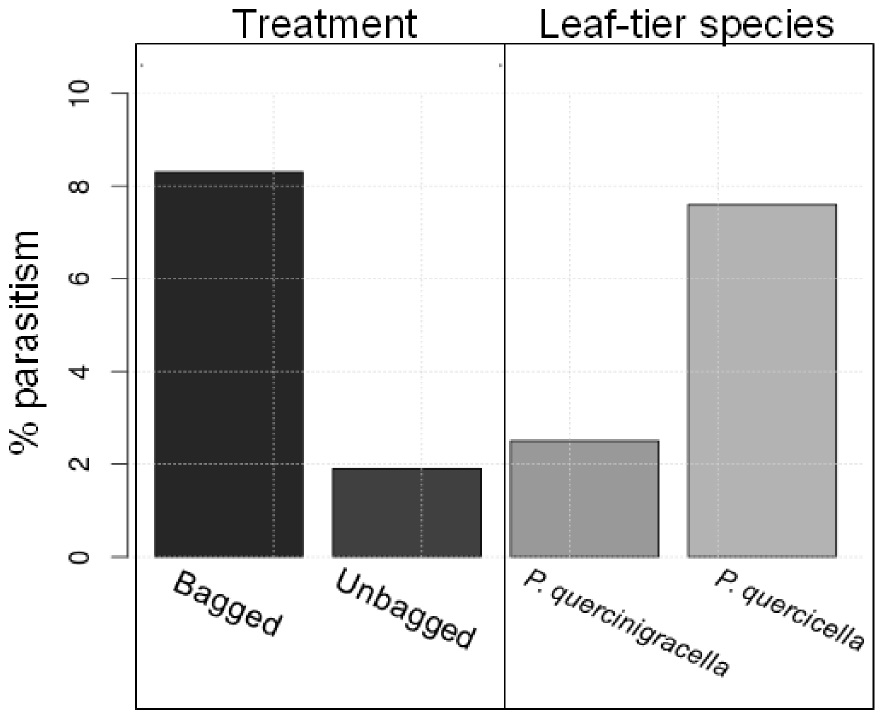


Figure 7. First generation parasitism of both leaf-tier species inside and outside bags (P = 0.0153) and parasitism between the two leaf-tier species (P = 0.0446).

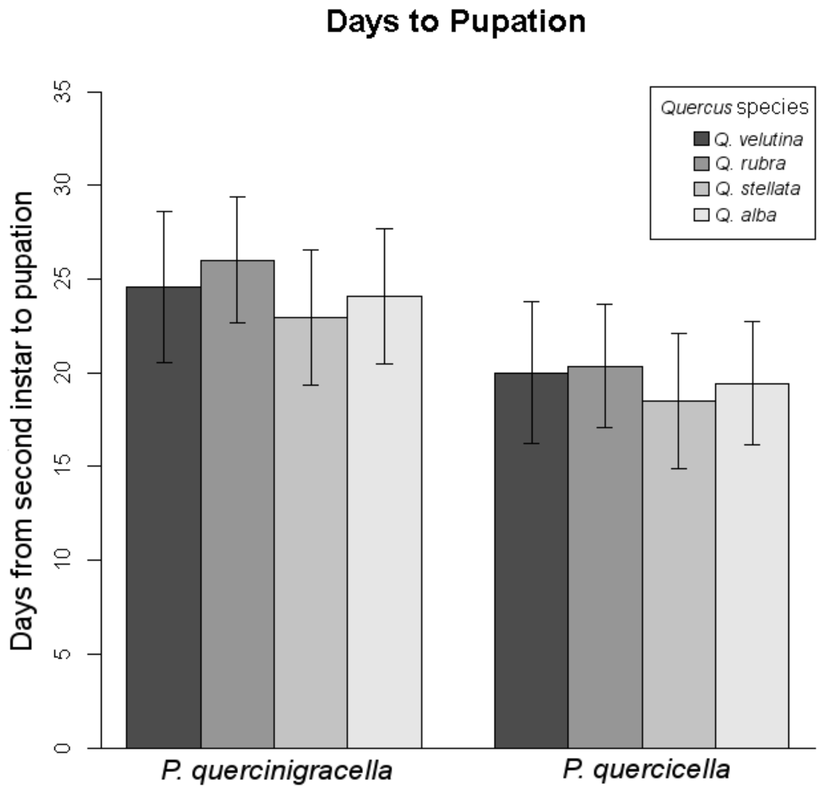


Figure 8. Days to pupation for each leaf-tiers species on four species of *Quercus*. Error bas are standard deviation.

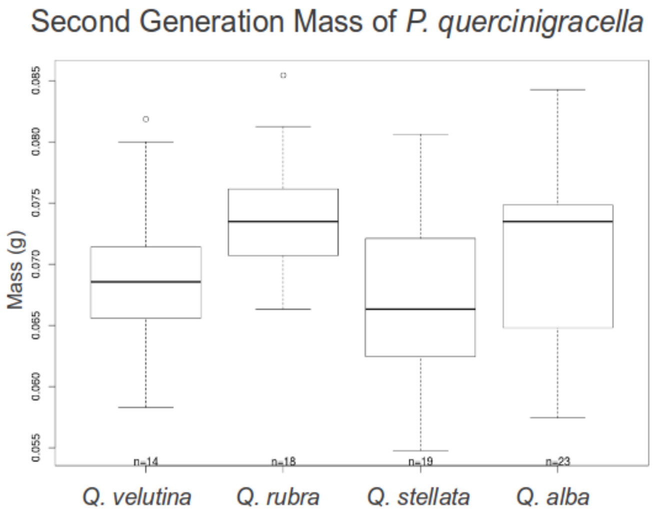


Figure 9. Pupa mass of *P. quercinigracella* on the four species of *Quercus* in the second generation.

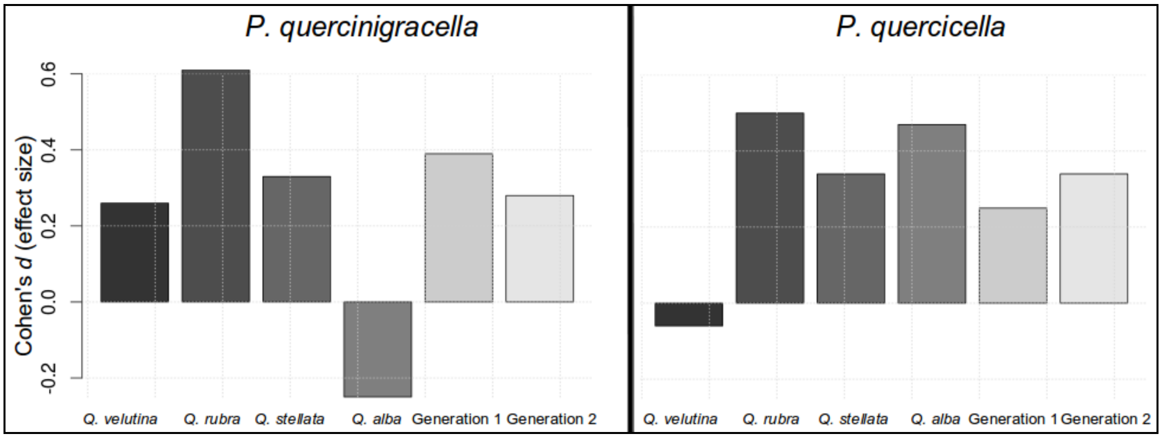


Figure 10. Cohen’s *d* of top-down effects for both species of caterpillar across tree species and generations