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Ecological Implications of Organic Mulches in Arboriculture: A Mechanistic Pathway Connecting the Use of Organic Mulches with Tree Chemical Defenses

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Abstract. In addition to the aesthetic and practical benefits of mulching, studies have shown indirect benefits of organic mulches to tree establishment and growth. These indirect benefits are associated with direct improvements on soil water and nutrient availability by mulches. The generalization of the organic mulches benefit to soil and trees has been questioned by several studies showing contradictory results under different experimental conditions and mulching materials. In addition, overall benefits for trees may be overlooked by focusing studies on some aspects of plant performance (e.g., plant growing rate) while ignoring others (e.g., plant chemical defense). This paper reviews studies showing how organic mulches can directly affect plant resource availability in the soil, presenting evidence from the literature that illustrates the influence of organic mulches on plant resource availability can also affect tree photosynthate allocation dynamics with direct consequences on plant chemical defenses. Based on the reviewed literature, presented here is a mechanistic pathway to illustrate how organic mulches can influence plant resources in the soil, and in turn how that can affect tree physiology and tree-insect interactions in urban areas.

Key Words. Growth-Differentiation Balance; Nitrogen Availability; Photosynthate Allocation; Water Availability.

Organic mulches are extensively used in urban systems to improve plant establishment and development (Acquaah 2004). Mulch is defined as "any material such as straw, sawdust, leaves, plastic film, and loose soil that is spread on the surface of the soil to protect the soil and plant roots from the effects of raindrops, soil crusting, freezing, and evaporation" (Brady and Weil 1999). This definition is based on mulch-substrate physical properties that benefit mostly soil structure and water content. Beside the physical benefits of mulching, this practice can increase or decrease the amount of inorganic N in the soil depending on the carbon (C) to nitrogen (N) ratio (Melillo et al. 1982; Herms et al. 2001; Lloyd et al. 2002; Erhart and Hartl 2003). These alterations to the soil, that directly affect tree growth, can also affect the synthesis of chemical defenses and as consequence plant-herbivore interactions.

This paper proposes a mechanistic pathway to explain how the impact of organic mulches applied to the soil surface can influence patterns of tree resource uptake, C assimilation and C allocation between growth and chemical defenses. Present here is a model that illustrates pathway connections and identifies the three most likely affected processes: (i) soil resource availability (water and N), (ii) plant C and N uptake, and (iii) plant C allocation between growth and the production of secondary compounds (Figure 1). The objective of this paper is to compile scientific evidence, pertinent for arboriculture, showing direct and indirect relationships among mulch application, soil resource availability and plant physiological responses. This review should increase awareness among arborists and scientists in the tree care industry to improve the utilization of organic mulches and promote further experimental studies in urban landscape scenarios.

CONCEPTUAL FRAMEWORK

Effect of Organic Mulches on Resource Availability

Organic mulches can affect the soil availability of two important resources for plants: water and N. Benefits of mulches to soil water content have been associated with the physical properties of mulches to buffer soil temperature (Mbagwu 1991; Bussiere and Cellier 1994). During days with high temperatures, a mulch layer protects soil surface from direct solar radiation. As a consequence, soil temperature remains cooler than air temperature and less water evaporates from the soil. Iles and Dosmann (1999) reported that 2–10 cm (0.79–4 in) of organic mulches (pine bark, pine wood, and hard wood chips) were more effective in reducing soil surface temperature [by ~2ºC (3.6ºF)] and increasing soil gravimetric water content [by ~0.2 g kg^{-1} ($3.2x10^{-3}$oz lb^{-1})] compared to inorganic mulches (pea gravel, lava rock, river rock and crushed red bricks) or bare soil. Furthermore, Appleton et al. (1990) found that, during summer days, when soil covered with fabric or plastic film to protect them from weed establishment were also mulched, soil temperature was lower and water content was higher than nonmulched soils independently of the weed control treatment. Although the influence of mulching on soil water content is frequently associated with reduction in soil temperature, De Vleeschauwer et al. (1980) showed that mulching can also improve water content by enhancing biological activity of soil macrofauna (e.g., earthworms) that increases soil porosity.

Despite the numerous studies reporting positive benefits of organic mulches on soil water content, other studies have also

reported negative or no effect of mulching on plant water availability (Watson and Kupkowski 1991; Erhart and Hartl 2003, Gilman and Grabosky 2004, Cook et al. 2006). These contradictory results reflect the variability in application methods and mulch material. For example, Gilman and Grabosky (2004) reported that hydric stress on balled-and-burlapped oak trees increased proportionally to mulch depth, after two weeks of planting. This study shows that under conditions of low precipitation and/or low irrigation rate, mulch can intercept significant amounts of water, reducing soil water-recharging rates (Gilman and Grabosky 2004). Depending on the environmental conditions, this negative effect of mulch on soil water content could be aggravated by applying mulch layer thicker than recommended by the International Society of Arboriculture [5–10 cm (2–4 in)] (ISA 2004) and by using mulching substrates with high water holding capacity, such as farmyard manure compost (Cook et al. 2006).

Organic mulches also influence the availability of N in the soil. In general, organic matter increases soil labile N through leaching and decomposition (Lambers et al. 1998; Aerts and Chapin 2000). During decomposition, decaying plant material is broken down and incorporated in the soil as particulate organic matter (POM). Nitrogen is released from POM as soluble organic N. Then, soil microorganisms may mineralize the dissolved organic N to ammonia (NH_4^+), which may be further oxidized to nitrate (NO_3^-). Ammonia and nitrate are considered the main sources of N used by plants in most ecosystems (Chapin 1995; Aerts and Chapin 2000). In non- or infrequently-fertilized systems, decomposition of plant material provides more than 90% of N supplied to plants (Lambers et al. 1998). For example, in Sitka spruce (*Picea sitchensis*) stands, system productivity of second rotation increased when branches and leaves from previous harvest episodes were left on site (Proe et al. 1996). The improvement in tree growth was attributed to the contribution of decomposing tree residues to the soil nutrient pool. The contribution was estimated to meet uptake requirements of second rotations for up to nine years (Proe et al. 1996).

Decomposition rate of decaying organic matter is highly controlled by environmental conditions, soil microbial activity and the organic matter chemical composition (Vitousek et al. 1994). Regarding organic matter chemical composition, studies have shown negative relationships between decomposition rates and the proportions of lignin:N and phenols:N ratios in decaying organic matter (Melillo et al. 1982; Vitousek et al. 1982; Northup et al. 1995; Aerts and De Caluwe 1997). Furthermore, the proportion of C:N in the organic matter has been found to be the most consistent predictor of organic matter decomposition rate (Seneviratne 2000). Specifically, plant residues with high percentages of N (> 2%), such as composted organic materials, show linear relationships with the amount of N released to the soil during decomposition (Seneviratne 2000). This pattern though, was better explained by the C:N proportion in the organic matter, rather than total N.

As in decaying organic matter, decomposition rate of organic mulches is also influenced by the substrate C:N ratio. Lloyd et al. (2002) compared the effect of two mulches made out of shredded wood pallets (C:N > 100:1) and composted yard-waste (C:N < 20:1) on soil N dynamics. They found that mulched soils with yard-waste compost had higher levels of total N, labile N and mineralization rate compared to sites mulched with shredded wood pallets. In the same study, microbial organisms immobilized up to 83% of the total pool of N in the soils after mulching with shredded wood pallets. These results support the study of Sønsteby et al. (2004) where the amount of both ammonia and nitrate, were lower on mulched soil with bark chips (C:N ~135:1) compared to nonmulched soils.

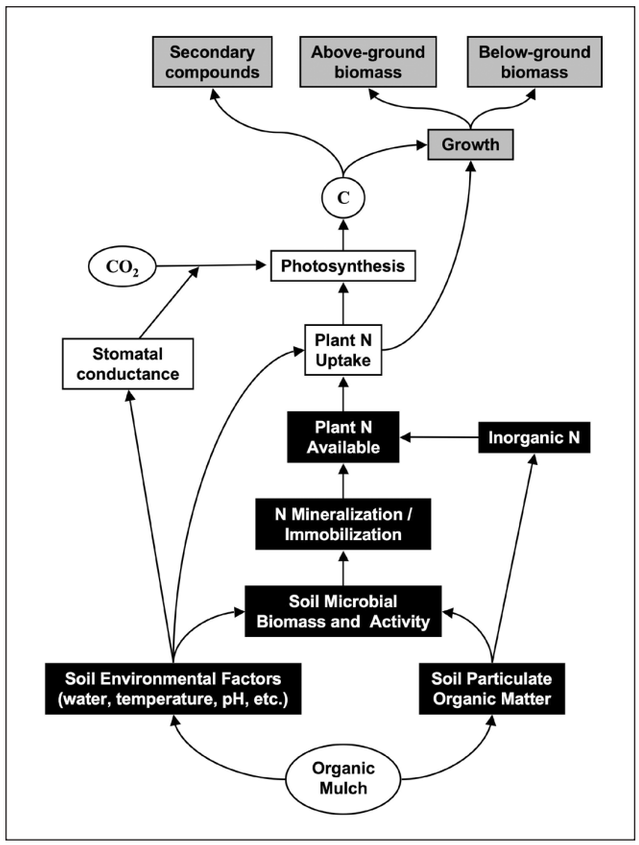

Figure 1. Conceptual model illustrating the effect of organic mulches on plant nitrogen (N) and carbon (C) uptake, and C allocation. White circles represent main inputs and transitional forms of C in the mode. Black squares represent processes associated with soil N availability and soil environmental conditions. White squares represent plant processes associated with resource acquisition. Gray squares represent plant processes associated with photosynthate allocation.

The association between organic matter C:N ratio and the amount of N released during decomposition can be explained using a metabolic approach. Overall, soil microorganisms require one atom of N for the consumption of a substrate containing 20 atoms of C (Davet 2004). During decomposition of organic matter with C:N ratio higher than 20, microorganisms have to supplement their N demand by absorbing N from the soil solution (i.e., immobilization), which in many cases results in competition with surrounding plants. In contrast, when the organic matter C:N ratio is lower than 20, excess N is excreted by the soil microorganisms in the form of inorganic N (i.e. mineralization) becoming available for the plants (Lambers et al. 1998; Davet 2004). This proportion of C to N can vary between 20 and 35 depending on the soil microbial community (Smith 1982).

Besides mulch chemical composition, soil conditions can also influence decomposition rates and consequently soil N availability. Microbial biomass and activity are sensitive to changes of soil

pH, temperature, moisture and aeration (Davet 2004). However, the responses to change in these variables fluctuate among decomposer community. For example, fungi are able to develop and reproduce in a pH range of 3.5 to 8.5 while most bacteria cannot survive at a pH lower than 6.5 (Davet 2004). In addition, extremes in temperature and soil moisture reduce decomposition rates of organic matter because they decrease metabolic activities of microorganisms (Swift and Anderson 1989; Barrett and Burke 2000).

Extant nutrients in the soil may also affect mulch decomposition by providing nutrients needed by microbes during decomposition (Torn et al. 2005). However, some contrasting results have been reported between studies comparing organic matter decomposition rates in fertilized and nonfertilized soil. Torn et al. (2005) and Hobbie (2005) reported positive and significant correlation between litter decomposition rate and soil nitrogen availability in nonfertilized soil. This correlation however, was not detected when soil at the same study site was N-fertilized. Three potential explanation for these conflicting patterns are: (1) decomposition process was not N limited (Torn et al. 2005), (2) decomposition was more limited by poor C quality (e.g., high lignin content) than by N availability (Hobbie 2000), and (3) there was an inhibitory effect of supplied N on microbial synthesis of lignolytic enzymes (Hobbie and Vitousek 2000; Torn et al. 2005). More studies are needed to understand what is causing the inconsistent effects of soil N content on mulch decomposition between fertilized and nonfertilized soils.

In agro-forestry systems, mulching with blends of organic residue with contrasting C:N ratios is recommended as an alternative to enhance soil N content without adding fertilizer. Some advantages of this practice include: reduction of leaching losses, prolongation of nutrient availability and synchronization of nutrient release with plant demands (Myers et al. 1994; Fortuna et al. 2003). Schwendener et al. (2005) studied the effect of mixing high-C:N cacao litter with low-C:N leguminous litter on decomposition and soil N dynamics in a cacao agro-forest system. In this study, legume leaves decomposed faster than cacao leaves without affecting the decomposition rate of cacao leaves during the time of the experiment (96 days). In addition, total soil N and microbial activity increased proportional to the amount of legume litter in the mulch mixture. These results suggest that N availability of mulched soils with high C:N substrates (> 20) can be improved by adding low C:N (< 20) organic material to the mulch.

Resource Acquisition

Changes of soil water and N availability by mulching can have a direct effect on the amount of C and N acquired by plants. Several studies have documented that acquisition of N by plants is directly related to the abundance of inorganic N in the soil (Min et al. 1999; Aerts and Chapin 2000). As mentioned before, most plants incorporate the majority of N in the inorganic forms (NH_4^+ and NO_3^-). Higher concentrations of NH_4^+ and NO_3^- in the soil can trigger the synthesis of nitrate reductase and glutamine synthase in plants (Oaks 1994). These enzymes are indispensable for the assimilation of NO_3^- and NH_4^+, respectively.

A close relationship between N acquisition and C acquisition has been well documented (Field and Mooney 1986). In forest systems, net primary productivity (NPP) of individual trees and entire forest stands are positively correlated with soil N availability (Oren et al. 1985; Aerts 1989; Aerts and Decaluwe 1989; Sampson et al. 2006). The enhancement in productivity occurs mostly because of the increase in total foliar mass. At stand level and when levels of available soil N increase, plants allocate more resources to leaf production (Millard and Proe 1991). In this way, trees can optimize the acquired N for C assimilation (Field 1983). Although NPP can also be enhanced by an increase in leaf photosynthetic ratio (Farquhar 1978; Shadchina and Beloivan 1993), studies with woody plants of different taxa have reported no significant effect of N-fertilization on specific leaf photosynthetic ratio (Laitinen et al. 2000; Merilo et al. 2006).

Depending on the soil type, low soil water recharging rate promoted by thick layers of organic mulches can also limit C acquisition. Levels of C assimilation are determined by the amount of CO_2 entering the leaves through the stomatal aperture. Two dominant factors controlling stomatal conductance among plant species are: (1) the availability of water in the soil and (2) the particular water use efficiency of each species (Marshall and Zhang 1994; Korol et al. 1999). Chapin (1991) proposed a physiological mechanism to explain how water stress can affect stomatal conductance. Under water stress conditions, the biosynthesis of abscisic acid in the roots is transferred to the leaves. This phytohormone is responsible for decreasing the stomatal aperture and reducing the water loss. Consequently, both transpiration and C uptake rates are constrained.

Resource Allocation

In terms of resource allocation, the model (Figure 1) has a particular focus on a plant's ability to allocate photosynthate between growth and production of secondary compounds. Evidence in the literature suggests that manipulation of nutrient dynamics in the soil can influence patterns of photosynthate allocation between growth and the production of secondary compounds (Herms and Mattson 1992; McKinnon and Quiring 1998; Glynn et al. 2003). For example, Wilkens et al. (1996) found that dry mass of tomato plant was positively correlated to the amount of fertilizer applied. However, the foliar concentration of two phenolics (rutin and chlorogenic acid) showed a parabolic relationship, with the highest concentrations of each at intermediate levels of fertilization. This pattern has been associated with plant defense hypotheses such as the Growth-Differentiation Balance (GDB) hypothesis because, in many cases, secondary compounds serve as natural defenses against pathogens and insect herbivores. Loomis (1953) and Herms and Mattson (1992) described the physiological mechanisms associated with the patterns of C allocation between growth and secondary compounds under different levels of resource availability. They contend that: (i) the assimilation of photosynthate to biomass and the synthesis of secondary metabolites are negatively correlated because both are dependent upon the same C pool of photosynthates. That (ii) under conditions of high resource availability, plant photosynthates are preferentially allocated to biomass accumulation. Finally, (iii) any condition slowing biomass accumulation more than C acquisition through photosynthesis (e.g., moderated levels of water or N availability) will increase the pool of photosynthates available for the synthesis of secondary compounds.

Alternatively, during the 1980s, a number of studies suggested that forest stands with "vigorous" trees (i.e., trees with high growing rates) are more resistant to herbivory (Larsson et al. 1983; Mitchell et al. 1983; Christiansen et al. 1987) and pathogen out-

breaks (Matson and Waring 1984; Oren et al. 1985; Waring et al. 1987). This hypothesis was based on studies that examined mountain pine beetle outbreaks (Dendroctonus ponderosae). In these studies, stand wood production per unit of leaf area increased after thinning and fertilizing. Contrary to the GDB hypothesis, Waring and Pitman (1985) proposed that trees prioritize photosynthate allocation as follows: new foliage > new roots > storage > diameter growth > chemical defenses. Under this assumption, trees growing under dense canopy are more susceptible to herbivores because they receive lower levels of photosynthetic active radiation and overall produce less photosynthate. Therefore, the amount of photosynthate available for synthesis of chemical defenses become limited and trees become more susceptible to herbivores. Waring and Pitman (1985) and Waring et al. (1992) recommended stand fertilization and thinning as pest control management strategies.

Because of forest fertilization studies, fertilization has been adopted in urban landscapes as a managements practice to improve pest resistance properties on urban trees (see Herms 2002). This recommendation, clearly contradicts Lorio's (1986) point of view of a physiological trade-off between photosynthate allocation to growth or to synthesis of chemical defenses. Lorio (1986) used the GDB hypothesis to explain how the synthesis of oleoresin [principle defensive chemicals against bark beetles (Ruel et al. 1998)] can be reduced during periods of rapid growth, creating an opportunity for bark beetle attack. Lorio's proposition was supported by studies using a variety of botanical taxa (Bryant et al. 1987, Bryant et al.1988, Hunter and Shultz 1995, Villalba et al. 2002). These studies showed that nutrient enhancement delayed long-term induced chemical defenses and improved the palatability of foliage to herbivores.

IMPLICATIONS FOR ARBORICULTURE

The International Society of Arboriculture recommends applying 5 to 10 cm of organic mulches around trees to improve aesthetics and edaphic conditions in the landscape (ISA 2004). The reviewed literature in this paper supports this recommendation. This study also concludes that organic mulches can directly affect soil water and N availability with indirect consequences for plant photosynthate allocation. Plant physiological response is species specific and depends on mulch material, and on soil properties such as fertility, water holding capacity and pH. However, the information compiled in this paper also illustrates general physiological and ecological consequences for plants after altering edaphic conditions through mulching. These general consequences are illustrated in the conceptual model (Figure 1).

It is also suggested that the controversy between Waring's and Lorio's points of view (i.e., photosynthate allocation priority versus photosynthates trade-off between growth and chemical defenses) is present in urban systems. Furthermore, that the experimental evidence supporting the use of fertilizer to enhance tree pest resistance is scarce and inconclusive. In fact, evidence suggests fertilization enhances insect performance by redirecting the resources allocated to defense and/or by increasing the palatability of the host plant (Herms 2002). These contradictory results reveal the necessity for additional studies that will help us understand the implication of mulching on tree physiological responses that affect their ecological, aesthetic, and economic value.

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Résumé. En plus des bénéfices esthétiques et pratiques des paillis, des études ont démontré des bénéfices indirects provenant des paillis organiques, et ce sur la reprise des arbres et leur croissance. Ces bénéfices indirects sont associés à des améliorations directes sur la disponibilité en eau et en éléments minéraux par les paillis. La généralisation des bénéfices au sol et aux arbres par les paillis organiques a été questionnée par plusieurs études qui montraient des résultats contradictoires sous différentes conditions expérimentales et différents paillis. De plus, l'ensemble des bénéfices pour les arbres peuvent avoir été occultés par des études ciblées sur certaines aspects de la performance de la plante (ex.: taux de croissance de la plante) qui en occultaient d'autres (ex.: défense chimique de la plante). Dans cet article, nous faisons une revue des études qui démontrent comment les paillis organiques peuvent directement affecter la disponibilité en ressources du sol pour la plante. Nous présentons des faits provenant de la littérature qui illustrent que l'influence des paillis organiques sur la disponibilité en ressources pour la plante peut aussi affecter les dynamiques d'allocation des photosynthate de l'arbre, et ce avec des conséquences directes sur les défenses chimiques de la plante. En se basant sur cette revue de littérature, nous présentons un cheminement mécanistique pour illustrer comment les paillis organiques peuvent influencer les ressources pour la plante dans le sol, et en retour comment cela peut affecter la physiologie de l'arbre et l'interaction arbre-insectes en milieux urbains.

Zussamenfassung. Zusätzlich zu den ästethischen und praktischen Vorteilen von Mulchen, haben Studien auch indirekte Vorteile von organischen Mulchen für die Baumetablierung und Wachstum gezeigt. Diese indirekten Vorteile stehen mit den direkten Einflüssen auf Bodenwasser und Nährstoffverfügbarkeit von Mulchmaterialien in Verbindung. Die Verallgemeinerung von organischen Mulchen und ihrem Beitrag zu Boden und Bäumen wurde in verschiedenen Studien hinterfragt und man ist dort auch zu widersprüchlichen Ergebnissen gekommen unter verschiedenen Bedingungen und Mulchmaterialien. Zusätzlich können die allgemeinen Vorteile des Mulchens für Bäume leicht übersehen werden, wenn auf Studien fokussiert wird, die Telaspekte von Leistung (z.B. Wachstumsrate) hervorheben und andere (z.B. chemische Verteidigung der Pflanzen) außer Acht lassen. In dieser Studie geben wir einen Überblick über Studien, wie organische Mulche direkt die Verfügbarkeit der Ressourcen im Boden beeinflusst. Wir präsentieren Nachweise aus der Literatur, die verdeutlicht, dass der Einfluss von organischen Mulchen auf Pflanzenverfügbarkeit von Nährstoffen auch die Photosynthese beeinflussen kann, mit direkten Konsequenzen für die chemische Verteidigung der Pflanze. Basierend auf diesem Literaturüberblick präsentieren wir hier einen mechanischen Weg zur Illustration, wie stark organische Mulche die Pflanzenverfügbarkeit von Nährstoffen im Boden beeinflussen und wie das wiederum die Baumphysiologie und Baum-Insekten-Interaktionen in städtischen Gebieten verändern kann.

Resumen. Además de los beneficios estéticos y prácticos del mulching, los estudios han mostrado los beneficios indirectos de los mulches orgánicos para el establecimiento y crecimiento de los árboles. Estos beneficios indirectos están asociados con el mejoramiento de la disponibilidad de agua y elementos del suelo por los mulches. La generalización de los beneficios de los mulches orgánicos al suelo y los árboles ha sido cuestionada por varios estudios que muestran resultados contradictorios bajo diferentes condiciones experimentales y materiales de mulching. Además, los beneficios para los árboles pueden ser pasados por alto al enfocarse en algunos aspectos del comportamiento de la planta (por ej. tasa de crecimiento de la planta) e ignorando otros (por ej. defensa química de la planta) En este reporte, se revisan estudios mostrando cómo los mulches orgánicos pueden afectar directamente la disponibilidad de recursos en el suelo. Se presentan evidencias de la literatura mostrando que la influencia de los mulches orgánicos en la disponibilidad de recursos para la planta puede también afectar las dinámicas fotosintéticas con consecuencias directas en las defensas químicas de la planta. Con la revisión de literatura, se presentan un sendero mecanicista que ilustra cómo los mulches orgánicos pueden influir en los recursos para la planta en el suelo, y cómo pueden afectar la fisiología del árbol y las interacciones árbol-insecto en áreas urbanas.