To the Graduate Council:

I am submitting herewith a dissertation written by Milena Holmgren entitled "The Interactive Effect of Shade and Drought on Seedling Growth and Survival". I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

Louis J. Gross, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of the Graduate School

# The Interactive Effect of Shade and Drought on Seedling Growth and Survival

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Milena Holmgren
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# Abstract

The hypothesis that plants face a trade-off between shade and drought tolerance is examined. Smith and Huston (1989) had used the trade-off model to predict the growth and survival of different plant functional types along gradients of light and water availability, and showed that several natural patterns of plant distribution and succession could, in principle, be explained from this hypothesized response-model. Based on a set of assumptions on plant morphological and physiological responses to drought and shade, the authors had predicted that under drier conditions plants would become less shade tolerant, and, therefore, would grow and survive better under higher light conditions. Similarly, plants would become more sensitive to drought when exposed to low light levels. The predictions were expected to hold within a population , as well as between populations. Also, it was expected that different species would show the same basic trade-off although shade tolerant ones were expected to be more susceptible to drought.

If plants cannot simultaneously acclimate to shade and drought, they are expected to be less tolerant to shading by competitors under drier conditions. However, an array of field patterns from a variety of ecosystems shows that amelioration of drought effects under a plant canopy is one of the most important mechanisms to explain positive interactions among plants. A graphical model discusses the interplay of competition and facilitation in view of the combined response of plants to light and moisture conditions.

The assumptions of the trade-off hypothesis are tested in a shadehouse experiment. Seedlings of *Liriodendron tulipifera* (tulip poplar) were grown under

different combinations of shade (1, 5, 12, 17, 27% of ambient light) and soil water content (5-9%, 11-15%, and >20%). Physiological and growth responses were taken to test the following hypotheses: 1) leaf area ratio decreases under dry conditions 2) root/shoot dry-weight ratio increases under dry conditions, 3) whole plant light compensation point increases under dry conditions, 4) rate of carbon fixation increases with light under dry conditions, 5) the relative reduction in growth with shading increases under dry conditions. The results show that the leaf area ratio tends to decrease with photosynthetically active radiation. Under combined high irradiance and low soil water conditions, the shoot net photosynthetic rate also decreases. The estimates for the whole shoot indicate that plants under dry conditions have lower daily photosynthetic rates under high light than under low light conditions. This seems to be mainly the result of prolonged stomatal closure under combined dry and high light conditions. Thus, in this experiment, higher light levels did not compensate for the shorter period the stomata were opened. The measurements of whole shoot dark respiration rates were consistently lower for plants under dry conditions. This indicates that the reduction of the gains (daily net photosynthetic rate) under dry conditions is at least partly compensated by a reduction of the losses (dark respiration rate). Contrary to what was predicted by the trade-off hypothesis, we found that the light compensation point also tends to decrease under drier conditions. There were no evidences of an increase in the root/shoot ratio under drier conditions as predicted from the model. Overall, we do not find evidence that higher light levels compensate for the physiological and growth effects of drought in tulip poplar seedlings. Also, higher water availability did not enhance growth in the shade.

A large-scale field experiment was used to test the predictions of the trade-off hypothesis for species with different shade tolerance. In the forest area covered by the Throughfall Displacement Experiment (TDE) in Oak Ridge, TN, soil water availability is being manipulated by intercepting about 30% of the throughfall in a (80x80 m) dry-treatment plot, transporting it through a control area, and using it to irrigate a wet plot. The light conditions vary from closed understory to small gaps. In the TDE site we planted seedlings of three tree species with different shade tolerance: *Liriodendron tulipifera* (intolerant), *Quercus alba* (intermediate) and *Acer saccharum* (tolerant). The seedlings were planted during the late winter of 1993, and their growth and survival were followed during the next two growing seasons. According to the trade-off hypothesis, plant growth under dry conditions should increase with light availability. The results presented here indicate that this is not the case for tulip poplar and sugar maple. The growth of both species showed a unimodal response to light. At light transmittance over 25% for tulip poplar, and 15% for sugar maple, growth decreased at increasing light. In contrast, the growth of white oak, the most drought tolerant of the three species, was not significantly reduced with light. The observed decrease of growth of tulip poplar and sugar maple under high light is likely to be related to an increase in water stress. In both years mortality was highest in tulip poplar. During the much drier 1995 season, white oak mortality increased more than sugar maple's, apparently due to herbivory effects. The distribution patterns of naturally established seedlings are consistent with the experimental results.

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# Part 1

## General Introduction

# Introduction

The analysis of vegetation patterns along environmental gradients has a long tradition in ecology. However, studies that link these patterns to physiological and growth responses to different environmental factors are less common. We still know relatively little about the combined effects of different environmental factors on plant physiology and growth (Osmond et al., 1987; Chapin et al., 1987; and reviews in Mooney et al., 1991). Most ecophysiological work has concentrated on studying plant responses to changes in a single factor, keeping other conditions constant. Plants usually respond to an insufficient resource level by physiological and morphological changes that tend to reduce the loss or maximize the acquisition of the most limiting resource (e.g. Bloom et al., 1985; Chapin et al., 1987). For example, plants under light-limited conditions usually have a larger leaf area, while plants under nutrient or water stress can invest relatively more biomass into roots. The acclimating responses can be very specific. Under limitation of a particular nutrient, for example, roots can increase their potential to specifically absorb that nutrient (Harrison and Helliwell, 1979; Lee, 1982). However, the physiological response to shortage of one resource will usually affect the response to limitation of other resources.

In this introductory chapter, I briefly review the work that has been done on the combined effects of two or more limiting resources on plants, and explain the intended contribution of this thesis to the understanding of plant responses to simultaneously occurring light and water stress. The discussion concentrates on acclimating responses, on a shorter time scale, that do not necessarily involve adaptive changes.

# Plant responses to multiple resource limitation

## *Nutrients and light*

Photosynthetic capacity is highly correlated with nutrient availability especially nitrogen concentration (e.g. Gulmon and Chu, 1981; Field and Mooney, 1986; Evans and Terashima, 1987). The responses, however, seem to depend on species shade tolerance and light availability. For example, Thompson et al. (1992) found that photosynthetic response to nitrogen was only significant in shade intolerant species growing under weak light conditions. On the other hand, some studies report significant responses only at high light conditions (Kuppers et al., 1988). Thompson et al. (1988) found that additional nutrients increased the photosynthetic rate even under low light levels, but the nutrient effect increased with irradiance.

Plant growth response (e.g. dry weight, leaf area, height) to nutrient addition under low light conditions is very small, as is the response to increasing light under low nutrient levels even after weeks or months of experimental treatment (Steinbauer, 1932; Blackman and Wilson, 1951; Phares, 1971; Kuppers et al., 1988). Lack of a growth response to nutrient addition under low light might result in part from a reduced root surface (Mengel and Viro, 1978). Nevertheless, significant growth responses to nutrient addition under low irradiance have been reported for some shade tolerant species (Peace and Grubb, 1982; but see Corré, 1983).

The effects are more impressive when growth is not strongly limited by one of the resources. Under high irradiance, nutrient addition can increase whole plant dry weight by

three times, and under high nutrient conditions whole plant biomass can increase twice from low to high light levels (Kuppers et al., 1988). Thompson et al. (1988) found that tree seedlings growing under intermediate light and high nutrient conditions accumulated more whole plant biomass than seedlings under other resource treatment combinations. Seedling growth under low light was not responsive to nutrient supply, while seedlings under low nutrients but high light appeared to be chronically photoinhibited (Thompson et al., 1988).

The substantial responses to nutrients at high light conditions seem to result more from morphogenesis (LAR: leaf area ratio) than productivity (NAR: net assimilation rate) (Corré, 1983; Lambers and Poorter, 1992). However, nutrient enhancement can facilitate the acclimation from shade to sun through an increase in quantum yield that protects the plant against photodamage (Osmond, 1983; Ferrar and Osmond, 1986; Seemann et al., 1987; Thompson et al., 1988).

***Nutrients and water***

The effects of soil water content on nutrient availability may be as important as the direct effects of water stress on plant growth. Low soil water can significantly reduce nutrient mobility even at levels at which water uptake is not strongly reduced. Even though plants under water stress might increase allocation to roots, and/or increase the root surface area for nutrient uptake, the potential nutrient uptake during water stress can be lower than the nutrient uptake of plants under well-watered conditions (Nye and Tinker, 1977). Nutrient uptake is an active and selective process, but is affected by drought due to a reduction in

both nutrient mobility in the soil solution (by mass flow and diffusion), and permeability of roots to nutrients (Sands and Mulligan, 1990).

Nutrient addition can increase biomass production under water stress (Dodd and Lauenroth, 1979; Belesky et al., 1982), and can even enhance growth of some desert plants more than water addition (Romney et al., 1978; Gutierrez and Whindford, 1987). There has been an increased interest in the possibilities of enhancing drought tolerance by fertilization, but the results are controversial. Plants growing under conditions of high nutrient availability can exhibit a greater ability to maintain growth, stomatal conductance and photosynthesis during drought than plants growing on infertile sites (Radin and Parker, 1979; Lahiri, 1980; Radin and Ackerson, 1981; Abrams, 1988). However, fertilization may actually reduce the physiological performance of a plant under water stress (Augé et al., 1990; Kleiner et al., 1992).

Fertilization can probably increase drought tolerance only under mild water stress and high light conditions. The mechanisms could be enhanced root elongation, allowing access to deeper sources of water (McNaughton, 1991), or two physiological mechanisms that are still very controversial, but that could potentially play an important role in this (Schulze, 1991). First, under water stress, some plants accumulate solutes that increase the osmotic potential and help maintain turgor (Morgan, 1984). Although there is no proof that osmotic adjustment allows a plant to keep growing under water stress, it might have developed as a way of surviving stress (Munns, 1988). In many cases, carbohydrates and amino acids have been identified as the main contributors of osmotic adjustment. A plant will only have enough solutes if photosynthesis is possible, which

implies only a mild water stress, enough nutrient availability and enough light. Potassium accumulation has been identified as a major contributor of osmotic adjustment also (Morgan, 1992), but direct potassium additions have failed to increase osmotic adjustment (Wilson and Ludlow, 1983). The second physiological mechanism could involve abscisic acid (ABA). Plant response to ABA, recently recognized as an important signal in the response of stomata to water stress, seems to be related to the nutritional status of the plant (Schulze, 1991).

The link between water stress and nutrient limitation does not mean that water and nutrients have similar effects on plant community structure. For instance, long-term nitrogen additions on dry grasslands probably have little effect on species composition, whereas continued water additions would lead to replacement of the present community by legumes; and dual supplementation would result in displacement of the native flora by exotic, invading species (Dodd and Lauenroth, 1979). This means that a species' competitive ability for nutrients may not predict its competitive ability for soil water.

***Light and water***

Smith and Huston (1989) hypothesized that the response of plants to the combined effects of light and water is characterized by a trade-off between drought tolerance and shade tolerance. They showed that several natural patterns of plant distribution and succession could, in principle, be explained from this hypothesized response-model. The trade-off hypothesis assumes that under drier conditions plants allocate relatively more biomass to roots than to aboveground structures. As a consequence of this, the ratio of respiring

biomass to photosynthetic material would increase, and therefore the amount of light necessary to keep a positive carbon balance should be higher (whole-plant light compensation point). Also, since under low water conditions plants avoid water loss by closing their stomata, it was assumed that higher light levels could compensate for reductions in photosynthetic activity by enhancing the photosynthetic rate. Based on these assumptions, Smith and Huston (1989) predicted that under drier conditions the whole-plant light compensation point (i.e. amount of light at which photosynthesis equals respiration) would shift to higher levels, and a plant would become more shade intolerant. Similarly, plants would become more sensitive to drought when growing under low light levels. The authors used the resulting hypothetical trade-off model to predict the growth and survival of different plant functional types along gradients of light and water availability. Shade-tolerance as used by Smith and Huston (1989) accentuates the emphasis on how high the light compensation point is. In forestry, shade tolerance has been more commonly used in reference to survival in shade. Both definitions, however, are compatible. As Smith and Huston (1989) point out, the changes in light compensation point should be reflected in the patterns of growth and survival along environmental gradients of shade and water.

The experimental evidence for the hypothesized trade-offs between shade tolerance and drought tolerance has been equivocal. Some experiments have shown that plants under sunny conditions that simultaneously suffer water stress show a more rapid reduction in leaf net photosynthesis (Gamon and Pearcy, 1990; Kolb et al., 1990; Abrams, et al., 1992), or are more predisposed to photoinhibition (Gauhl, 1979; Björkman and

Powles, 1984; Ludlow and Björkman, 1984), than plants in the shade. Similar effects of drought on net photosynthesis have been reported for sun versus shade leaves (Ogren and Oquist, 1985). The interpretation of some of the previous reports should be considered cautiously, because the trade-off model is based on whole-plant responses and not responses at the leaf level.

The evidence from field patterns is also controversial. If plants become shade intolerant under dry conditions, one would not expect plant establishment to be higher in the shade. However, in ecosystems where plants are exposed to severe stress, for instance as a result of heat and desiccating conditions, the establishment of new plants is often restricted to the shady places under the canopy of other plants, called nurse plants. In addition to improving temperature and moisture conditions, nurse plants have also been shown to improve soil properties (accumulation of nutrients and organic matter), reduce the probabilities of mechanical or herbivory damage, and favor colonization by attracting seed dispersers (Hunter and Aarssen, 1988). This positive effect of plants on the establishment or growth of other plants is called facilitation. Obviously, positive and negative interactions will likely occur simultaneously. While improving some environmental conditions, nurse plants will tend to have negative effects on other factors. They can, for instance, enhance air humidity and prevent extreme temperature fluctuations, but on the other hand impede seedling emergence by litter accumulation (Barton, 1993), limit the potential growth of the newly established plants by reducing the availability of light and soil water (Franco and Nobel, 1988; 1989; Nobel, 1989), or excrete allelopathic substances (Muller, 1953; Muller and Muller, 1956; Callaway, et al.,

1991). To understand the net effect of nurse plants on establishing seedlings in a mechanistic way, it is necessary to know the combined responses of the seedlings to multiple environmental factors.

On the other hand, there are some patterns that are consistent with the predictions of Smith and Huston's model. Vance and Zaerr (1991) found that shaded seedlings of *Pinus ponderosa* were less tolerant to drought and were killed at higher soil moisture than unshaded plants. Huston (1994) considers that the $CO_2$ exchange measurements of Jarvis (1989) for a *Picea sitchensis* stand during different weather conditions (vapor pressure deficit and incident quantum flux density) are also consistent with the trade-off model. During drier days (greater vapor pressure deficit) extrapolations of the original data seem to indicate that the canopy net $CO_2$ influx is zero at higher quantum flux density. The interpretation of Huston (1994) is that the whole stand light compensation point increases during drier days. There are at least two problems with this interpretation. First, the changes in biomass allocation assumed in the trade-off model (i.e. change in root/shoot ratio, leaf area ratio) to predict changes in the whole plant light compensation point under drier conditions occur over several weeks and months. Aggregation of data recorded during days with different weather conditions can not be used as an evidence of a process that takes much longer time scales. The second problem is the positive correlation between vapor pressure deficit and incident light under natural conditions. Brighter days will tend to be drier. Therefore changes on the net $CO_2$ exchange rates can then be an artifact of the subset of conditions found.

***Plant responses to light, water and nutrients***

Integration of three limiting factors in manipulative experiments is very rare. Bazzaz and Morse (1991) report the results of an experiment for two annual plants. Under high or intermediate soil water conditions, biomass increased as a function of nutrient availability but only under 50% or higher light levels. Plants under low water showed a low response to nutrient additions along the whole light gradient. The pattern of biomass accumulation was very similar for both species, but not the reproductive allocation.

Luxmoore and Millington (1971) worked with a perennial ryegrass and found the same response under intermediate water conditions (i.e., greater biomass accumulation under higher nutrient and light). But under low water conditions the perennial showed a positive response to nutrient additions at intermediate and high light levels, and reached maximum biomass at intermediate nutrient concentration and high light levels.

Kolb et al. (1990) compared the growth responses of seedlings of two tree species. Unfortunately, the levels of photosynthetically active radiation (100% and 20% of ambient) and nutrient levels (168 kg N/ha) were too high to be relevant to growth and survival of these species in the natural understory. Nevertheless the responses were interesting. Tulip poplar growth always decreased significantly more in response to impoverishment of nutrients or water at full sun than in shade. Under 20% light, which is approximately the light environment in intermediate gaps, the growth was more sensitive to reductions in moisture (-65%) than nutrients (-33%).

## Objectives of this thesis

This thesis concentrates on plant responses to the interacting effects of light and water. I seek to test some of the assumptions and predictions derived from the trade-off hypothesis of shade tolerance versus drought tolerance (Smith and Huston, 1989). The implications of the trade-off model are not only important to understand natural patterns of plant distribution and succession but also to predict the potential outcome of human-induced environmental change. In order to test the trade-off model I have used a combination of approaches. According to the trade-off model, plants cannot simultaneously acclimate to shade and drought. Therefore, plants are expected to be less tolerant to shading by competitors under drier conditions. An observation that is, at first sight, incompatible with this idea, is the fact that in dry areas the establishment of new plants is often restricted to the shady places under the canopy of other plants, called nurse plants. In **Part II**, I intend to clarify this paradox. The first section reviews an array of examples of facilitation in which amelioration of drought effects is an important mechanism. Subsequently, a graphical model is presented to discuss the interplay of facilitative and competitive effects in view of the combined response of plants to light and moisture conditions. The final section treats the applicability of the model of facilitation to patterns in general.

**Part III** seeks to experimentally test some of the assumptions of the trade-off model. In a shadehouse experiment seedlings of *Liriodendron tulipifera* (tulip poplar) were grown under different combinations of shade (1, 5, 12, 17, 27% of ambient light)

and soil water content (5-9%, 11-15%, and >20%). Physiological and growth responses were taken to test the following hypotheses: 1) leaf area/total biomass decreases under dry conditions 2) root/shoot dry-weight ratio increases under dry conditions, 3) whole plant light compensation point increases under dry conditions, 4) rate of carbon fixation increases with light under dry conditions, 5) the relative reduction in growth with shading increases under dry conditions.

**Part IV** looks for evidences of the trade-off hypothesis in the patterns of growth and survival of planted and naturally established tree seedlings. Here I report the results of a field experiment in the forest area covered by the Throughfall Displacement Experiment (TDE) in Oak Ridge, TN (Hanson et al., 1995). In the TDE site soil water availability is being manipulated by intercepting about 30% of the throughfall in a dry treatment plot, transporting it through a control area, and using it to irrigate a wet plot. The light conditions vary from closed understory to small gaps. In the TDE site I planted seedlings of three tree species with different shade tolerance: *Liriodendron tulipifera* (intolerant), *Quercus alba* (intermediate) and *Acer saccharum* (tolerant) (Baker, 1949; Fowells, 1965). The seedlings were planted during the late winter of 1993, and their growth and survival were followed during the next two growing seasons. This chapter also contrasts the experimental results with the patterns of abundance and survival found for naturally established seedlings.

In **Part V** I summarize the results and discuss future directions. This section can offer an overview of the importance that a better understanding of the combined effect of light and water has for theoretical and applied problems in plant ecology.

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# Part 2

## The interplay of facilitation and competition in plant communities

## Abstract

If plants can not simultaneously acclimate to shade and drought because of physiological trade-offs, then plants are expected to be less tolerant to shading by competitors under drier conditions. An observation that is, at first sight, incompatible with this idea, is the fact that in dry areas the establishment of new plants is often restricted to the shady places under the canopy of other plants, called nurse plants. In this paper I review some of the evidence for such facilitation in deserts, Mediterranean vegetation, tropical savannas, temperate forests and grasslands, salt marshes, dunes and tundras. Although several explanations for facilitative patterns are found, improved plant water relations for establishing seedlings under the canopy of nurse plants is one of the most often reported mechanisms. A graphical model is used to show how most of the observed patterns can be understood from the effect of plant canopies on microsite light and moisture and the physiological responses of establishing seedlings to those factors.


## Introduction

Facilitation, the positive effect of plants on the establishment or growth of other plants, has long been recognized as an important driving force in primary and secondary succession (Clements et al., 1926; Connell and Slatyer, 1977). Nonetheless, competition has received far more attention in ecological research over the last decades (see reviews by Connell and Slatyer, 1977; Connell, 1983; Schoener, 1983; Keddy, 1989; and

Goldberg and Barton, 1992). Recently, however, there has been renewed interest in the topic of facilitation (Hunter and Aarssen, 1988; Goldberg, 1990; Callaway, 1995) and the environmental conditions that make it possible. Bertness and Callaway (1994) have hypothesized that competition increases in importance towards the more productive part of the environmental gradient while facilitation is more important under harsh conditions.

Facilitative interactions have been demonstrated in a broad range of ecosystems. Most evidence comes from ecosystems where plants are exposed to severe stress, for instance as a result of heat and desiccating conditions. In such situations the establishment of new plants is often restricted to the shady places under the canopy of other plants, called nurse plants. In addition to improving temperature and moisture conditions, nurse plants have also been shown to improve soil properties (accumulation of nutrients and organic matter), reduce the probabilities of mechanical or herbivory damage, and favor colonization by attracting seed dispersers (Hunter and Aarssen, 1988). Although facilitative interactions have been more frequently found in physically stressful environments like deserts or salt marshes, they have also been described for lush vegetations such as temperate grasslands and forests, and moist tropical savannas.

Obviously, positive and negative interactions will likely occur simultaneously. While improving some environmental conditions, nurse plants will tend to have negative effects on other factors. They can, for instance, enhance air humidity and prevent extreme temperature fluctuations, but on the other hand impede seedling emergence by litter accumulation (Barton, 1993), or limit the potential growth of the newly established plants by reducing the availability of light and soil water (Franco and Nobel, 1988; 1989;

Nobel, 1989), or by excreting allelopathic substances (Muller, 1953; Muller and Muller, 1956; Callaway, et al., 1991).

To understand the net effect of nurse plants on establishing seedlings in a mechanistic way, it is necessary to know the combined response of the seedlings to multiple environmental factors. Multifactorial studies are surprisingly rare in ecophysiology (Chapin et al., 1987; Osmond et al., 1987), but some appealing hypotheses have been formulated about the simultaneous effect of interacting stresses (Bloom et al., 1985; Tilman, 1988; Smith and Huston, 1989; Chapin, 1991; Luxmoore, 1991). Smith and Huston (1989) developed a model of plant distributions along spatial and temporal gradients of light and water availabilities based on a hypothetical trade-off between shade and drought tolerances. The main idea of this trade-off is that under dry conditions, plants invest relatively more of their biomass in roots instead of leaves, and therefore become more shade intolerant. Note that such physiological trade-offs makes the occurrence of facilitation less likely. If plants become shade intolerant under dry conditions, one would not expect establishment to be as high in the shade of nurse plants as is observed.

In this paper I seek to clarify this paradox. The first section briefly reviews an array of examples of facilitation in which amelioration of water stress is an important mechanism. I then present a graphical model to discuss the interplay of facilitative and competitive effects in view of the combined response of plants to light and moisture conditions. In the final section I discuss the applicability of the model to facilitative patterns in general.

## Facilitation along environmental gradients: some field cases

Evidence for facilitative interactions comes from a variety of ecosystems. Here I present a set of examples found in deserts, Mediterranean vegetation, tropical savannas, temperate forests and grasslands, salt marshes, dunes, and tundras. Since my intention is to understand the relative importance of the reduction of water stress in the shade, I have focused on this particular mechanism. However, in many cases facilitative patterns can result from other mechanisms, such as an increase in nutrients, or a reduction in herbivory. Callaway (1995) presents an extensive review of facilitative patterns and mechanisms involved in both terrestrial and marine ecosystems.

In deserts, seedlings of succulent and non-succulent plants generally occur under the canopy of larger perennial plants. The establishment of succulent plants seems to be facilitated mainly by reduction of extreme soil temperatures (Turner al., 1966, Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991). This is crucial for succulents because they cannot prevent overheating through transpiration. Soil water content might be only slightly higher (Shreve, 1931) or even lower under the shade than in the open (Nobel, 1989), but the thermal stress is much lower close to the nurse plant. Establishment of non-succulent plants is facilitated under the shade due to a reduction of transpiration demands (Shreve, 1931; Abd El Rahman and Batanouny 1965 a,b). However, seedling growth could also be reduced by the presence of nurse plants. Simulation results predict that this is mainly a consequence of a drastic reduction in photosynthetically active

radiation and competition for soil water with the nurse plant (Franco and Nobel, 1988, 1989; Nobel, 1989). An increase in nitrogen availability under the nurse canopy can also add to the facilitative effects (Franco and Nobel, 1989), but this is not always the case (Valiente-Banuet et al., 1991b, Arriaga et al., 1993). The establishment of new plants does not leave the nurse plants completely unaffected. Competition, especially for soil water, can have a negative effect on the nurses, leading to a reduction in their growth and fecundity (Flores-Martínez et al., 1994) or to an increased branch mortality among nurse plants associated with succulents (McAuliffe, 1984a; Valiente-Banuet et al., 1991a,b).

In Mediterranean ecosystems characterized by dry summers and wet winters, the interplay of facilitative and competitive interactions seems to be more variable than in the very dry conditions of the desert. In the oak savannas close to the coast of northern California, the productivity of herbaceous plants growing under the oak canopy is lower than in open grasslands, and removal of trees has a positive effect on herbaceous production (Murphy and Crampton, 1964). In contrast, in the drier foothills of the Sierra Nevada in central California, shading increases herbaceous production, especially during dry years (Frost and McDougald, 1989). These patterns support the idea that facilitation becomes more important than competition with increasing dryness. Callaway et al. (1991), also working in Central California, showed that apparent facilitative or interfering effects under oak canopies can be found within several meters of each other. They found that nutrient inputs tend to facilitate grassland productivity, but in some trees, root allelopathic exudates seem to have an interfering effect.

In the Chilean matorral, also with a Mediterranean climate, natural patterns and experimental manipulations have shown that shrub seedlings establish mainly under shrubs as a result of a high mortality primarily from desiccation, but also from rabbit herbivory in the open surrounding grassland (Fuentes et al., 1984, 1986). Although recruitment of shrub seedlings under nurse shrubs occurs along the whole matorral range (Fuentes et al., 1986) in moister areas the establishment of shrub seedlings occurs also in the open areas (Holmgren, Segura and Fuentes, unpublished).

In the dry African savannas, herbaceous productivity is often higher under the tree canopy than in open grassland. This increase in productivity seems to be mainly a result of higher nutrient concentration under the trees (Belsky, 1994). Interestingly, the magnitude of this increase is highly correlated with moisture conditions. In the low-rainfall areas the increase in herbaceous productivity below the trees, relative to the grasslands, is much greater than at the high-rainfall sites (95 vs 52% respectively; Belsky et al., 1993). In drier sites, two mechanisms lead to lower water stress under trees: a reduction in evapotranspiration demands and a relative reduction in competition for soil water with the tree roots. Experimental results have shown that trees compete more strongly and reduce productivity of herbaceous plants only in high-rainfall sites because they concentrate their roots close to their own canopy, intensifying competition for water with the understory grasses (Belsky, 1994). In savannas, therefore, as in Mediterranean systems, the microclimatic changes under the nurse plant have stronger effects in the drier areas.

Facilitative interactions are also important to explain the distribution and successional dynamics of forests. In the mountains of southwestern USA, the lower altitude limits of some pine species seem to be controlled by water stress. With decreasing elevation, pine seedlings increasingly occur in microsites with relatively low light, but lower soil temperature and higher soil moisture. Seedlings of some species are nearly restricted to this type of microsites beneath nurse trees (Barton, 1993). In early successional communities of deciduous forest in eastern USA, Berkowitz, et al. (1995) experimentally show that surrounding vegetation could strongly inhibit tree seedling growth in productive sites, but had little effect or actually improved it on harsh sites, especially during drought periods. Comparing gaps of different sizes, Sipe and Bazzaz (1995) found that tree seedling survival was substantially reduced in large gaps. This pattern could result from water stress. Large gaps have higher levels of photosynthetically active radiation and temperature, but lower soil moisture in the top soil layers (Kozlowski et al., 1991).

Indications of facilitation have also been found in humid forested regions, originally covered by rain forests and now transformed into pastures with large isolated trees still remaining. These isolated trees function as a nursery for tree seedlings, many of them rainforest species, that are not found in the surrounding open places (Guevara et al., 1992). Trees are probably facilitating seedling colonization by providing perching sites for seed-depositing birds and bats, and by modifying the microclimatic conditions (Guevara et. al, 1992). Light reduction under the tree might also reduce competition with

the shade intolerant grasses and facilitate the establishment of the more shade tolerant tree seedlings (Huston, 1982).

The arid Patagonian steppe is a mosaic of shrubs each tightly surrounded by a dense ring of grasses and scattered tussocks interspaced with bare soil (Soriano et al, 1993). Experimental manipulations suggest that small shrubs that are able to establish on bare soil, can initially facilitate the recruitment of grasses by a reduction in evapotranspiration demands under the shrub canopy (Aguiar and Sala, 1994). However, once the ring has been formed, strong competition for soil moisture with the established grasses overshadows the positive effect of the shrub canopy (Aguiar and Sala, 1994).

Under certain circumstances even taller grasses can act as the necessary shelter for the establishment of grass seedlings. In a limestone grassland of northern Switzerland, Ryser (1993) found that the roots of the focal plant stabilize the soil, preventing the seedling roots from being uprooted by frost heave and exposed to desiccation during the dry spring days. Seedling survival of species particularly vulnerable to this environmental impact was significatively lower in gaps than under the shelter of neighboring plants (4% versus 40%). Positive effects on seedling establishment from the presence of other plants have also been reported for the chalk grasslands (Schenkeveld and Verkaar, 1984). Again, the effect of already established plants on new seedlings depends on environmental conditions. In the chalk grasslands of England, Hillier (1990) found that on the drier south-facing slopes, established plants enhanced the survival of some species, while on

the moister north-facing slopes, seedling establishment was strongly dependent on the availability of open gaps.

In salt marshes, plants can also be exposed to severe desiccating conditions due to high radiation, low water availability and high salinity. Here, winter annual species can either have negative or positive associations with perennial shrubs. In the latter case, the effects of shade in reducing salinity and increasing water availability more than compensate for the effects of reduced photosynthetically active radiation and root interference (Callaway, 1994). Experimental manipulations have demonstrated that alleviation of the stress produced by salinity can shift the nature of the interspecific interactions from facilitative to competitive (Bertness and Shumway, 1993; Bertness and Hacker, 1994; Bertness and Yeh, 1994, Shumway and Bertness, 1994).

Desiccation and nutrient deficiency are the primary causes of poor seedling establishment in coastal dunes (Maun, 1994). Severe moisture stress results from the combination of very low water-holding capacity of the sand, exposure of the root system by wind action and high soil temperatures. Under these extreme conditions, the shade provided by nurse plants significatively increases seedling survivorship because of improved moisture conditions (Fuller, 1914; McLeod and Murphy, 1977; De Jong and Klinkhamer, 1988). Experimental manipulations have not only shown that seedlings under the nurse shade can survive, but also that artificial watering can increase seedling survival and growth, especially in open areas (De Jong and Klinkhamer, 1988).

Tundras are characterized by slight precipitation but also low potential evaporation. Although the climate is considered humid (Walter, 1985) it has been shown that also in tundras shrubs can facilitate the growth of herbs by reducing the impact of desiccating winds (Carlsson and Callaghan, 1991).

Summarizing, these cases illustrate that an increase in growth or survival under the nurse shade seems to be a rather general phenomenon in harsh environments. Facilitative effects are stronger in drier sites and drier years. Moreover, several field experiments support the causal link of moisture conditions to seedling establishment in dry environments. Many factors can contribute to lower water stress in the shade: a) lower transpiration demands (due to lower vapor pressure deficit and thermal stress), b) increased soil water availability (because of lower evaporation, reduced salinity, or improved water-holding capacity), c) improved conditions for root growth (due to enhanced soil stability and structure, increased soil moisture, or reduced soil temperatures). Obviously the relative importance of these factors will depend on the particular ecosystem.

## A conceptual model

In this section I derive a graphical model to show that much of the interplay of facilitation and competition can be understood from two components: 1) the growth and survival of

plants in relation to water and light availabilities; and 2) the effect of plant canopies on microsite light and moisture.

***Plant growth responses***

A simple way to visualize the growth response of a plant to the level of two environmental factors is by plotting its zero-isocline in the resource plane (Fig. 1). This line indicates the resource levels at which growth is zero, and consequently demarcates the area in the resource space where growth is possible. The most naive approach to construct the isocline, is to assume that growth simply requires a fixed minimum critical light level ($l_0$) and moisture level ($m_0$). This results in a rectangular isocline (Fig. 1 a).

However, isoclines with more or less rounded shapes could be more realistic, because of the trade-offs at the leaf and whole plant levels discussed by Smith and Huston (1989) and incorporated as assumptions of their model. Under low light conditions, plants invest proportionally more biomass in leaves and aboveground parts which increases the transpiration surface relative to the amount of roots, and consequently the susceptibility to dry conditions. Thus, under low light levels, plants would require higher levels of moisture to grow and survive. Therefore, the horizontal part of the isocline is expected to bend upwards to the left (Fig. 1b). In contrast, under drier conditions plants invest relatively more in roots while reducing the transpiring leaf area. This would increase the amount of respiring material relative to the amount of photosynthetically active biomass, and consequently would increase the light compensation point for the whole plant (amount of light at which photosynthesis equals respiration). Consequently, the vertical

part of the isocline is expected to bend off to the right at low moisture conditions (Fig. 1b).

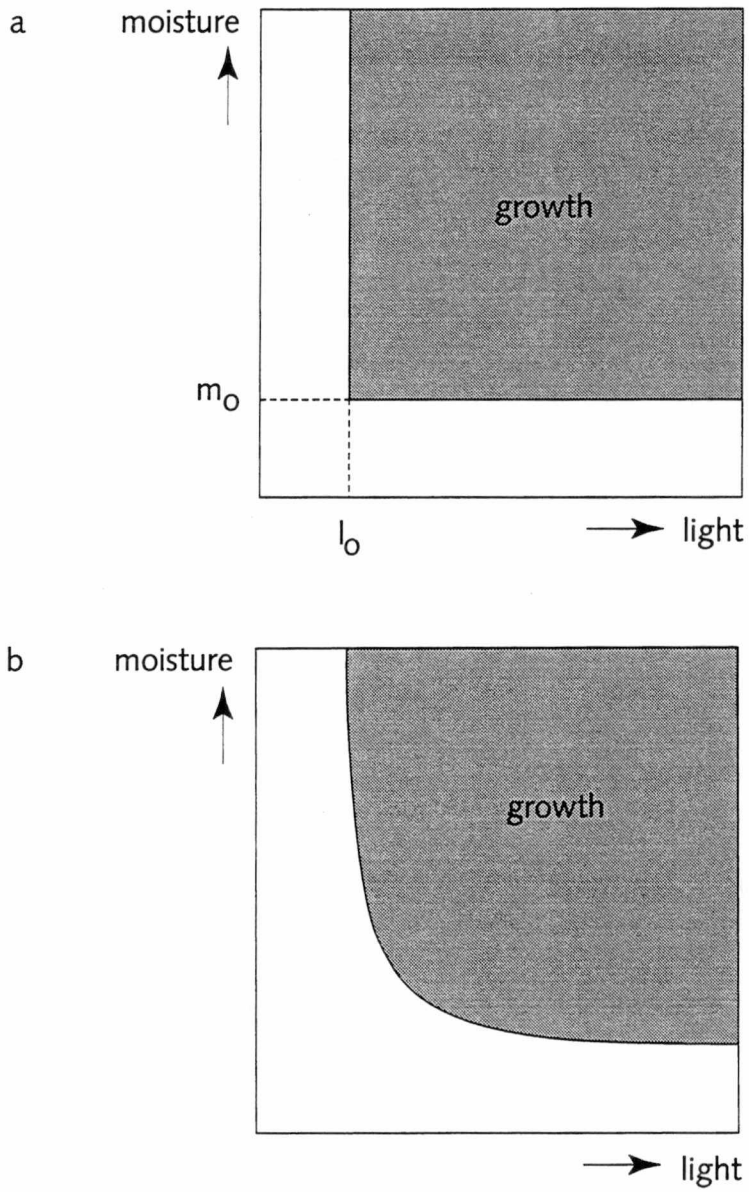


Figure 1. Plant growth response to light and moisture showing a positive net plant growth in the shaded region delimited by the zero-growth isoclines. The simplest assumption with respect to the shape of the isocline (panel a) is that plants can grow if both light and moisture exceed a critical minimum level ($l_0$ and $m_0$ respectively). However, a rounded isocline (panel b) is more realistic for plants facing a physiological trade-off between drought and shade tolerance.

When we depict not only the 0-isocline, but also the growth rate, the picture becomes three dimensional (Fig. 2). If one assumes that the growth response to one factor can be described by a saturation curve, the response to two factors has the shape of a quarter bell.

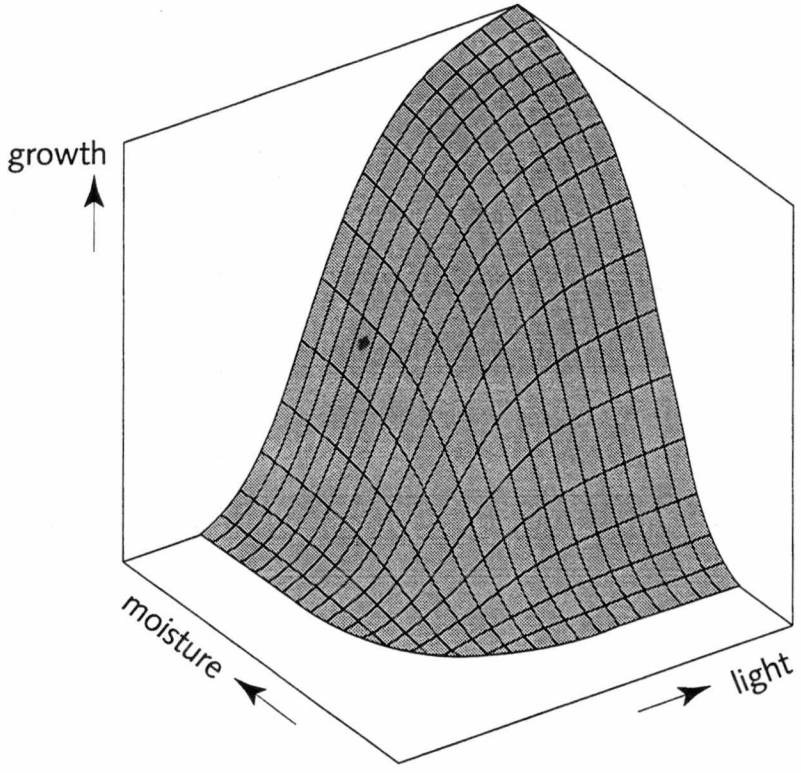


Figure 2. Plant growth as a function of light and moisture conditions assuming a physiological trade-off between drought tolerance and shade tolerance. The projection of the shaded area on the horizontal plane is equivalent to the isocline representation of Figure 1 b.

***Canopy effect on light and moisture***

Light is obviously reduced by the presence of a plant canopy. The effect of a plant canopy on the moisture environment that a seedling experiences is more complicated. Any large plant that provides a canopy, takes up soil water and therefore reduces the overall soil water available (Joffre and Rambal, 1988). However, for at least two reasons, the

moisture environment for an establishing seedling is likely to be influenced more by other mechanisms. First, its shallow root system is initially dependent mainly on the soil water of the most superficial soil layers. For some established trees and shrubs, this may not be an important rooting zone. Second, the water status of a seedling is not only dependent on soil water but also on its transpiration demands and thermal stress. Many studies have shown that under the canopy, soil and air temperatures are lower, wind velocity is less and the air humidity is higher than in the open (Geiger, 1965; Larcher, 1983; Chen et al., 1995). Because of these microclimatic changes the transpiration demands are lower in the shade, but also evaporation from the superficial soil layer will be less (Larcher, 1983). In fact evaporation and transpiration rates tend to follow the same patterns (Abd El Rahman and Batanouny, 1965b). This reduced evaporation generally helps maintain higher water availability in the shaded top soil layers for longer periods of time (Fuller, 1914; Shreve, 1931; Parker and Muller, 1982; Joffre and Rambal, 1988; Bradshaw and Goldberg, 1989; Vetaas, 1992; Barton, 1993). In some cases, however, upper horizon water conditions may slightly improve or even decline under the nurse plant (Shreve, 1931; Nobel, 1989). Even when soil water conditions do not necessarily improve under the shade, the reduction in transpiration demands and thermal stress improve the seedling water relations. This combination of atmospheric and soil water conditions represent the microsite moisture. Thus, the microsite for a seedling under the nurse plant has its own microclimate with more favorable moisture conditions but less light than in nearby open areas. This implies that in a given area with otherwise homogeneous topographical, soil and precipitation conditions, microsite moisture decreases while microsite light increases

from the canopy to the open places. It is difficult to infer a priori the precise form of this relationship in any specific case. Therefore, I simply assume a straight line as a default (Fig. 3). The slope of this line represents the decrease in microsite moisture going from the shade to the open. This slope depends critically on the general climatic conditions. In very wet areas, moisture will be high irrespective of the radiation exposure, whereas in drier situations, light availability and microsite moisture conditions will be more negatively correlated.

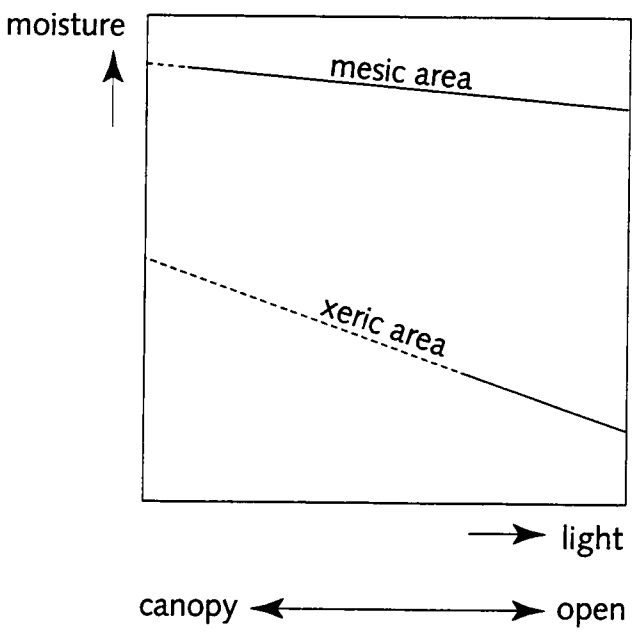


Figure 3. Hypothesized correlation between microsite light and moisture conditions for establishing seedlings along a gradient from shade under the canopy to unprotected open places. In mesic areas moisture conditions will be relatively good even in the open. In drier areas, however, the canopy of the overstory reduces the evapotranspiration demands which results in enhanced moisture conditions for establishing plants (higher slope). Under xeric conditions plants do not produce a dense canopy and deep shade does not occur.
Therefore the dashed left-hand part of the microclimatic gradient is unlikely to be found in nature.

Note that zero light does not occur in practice. Therefore, the (dotted) left part of the depicted gradients is irrelevant for all practical purposes. The maximum shade that occurs in an area depends on the number of leaf layers shading the grounded surface (leaf area index). Deep shade is more likely to be found in mesic, productive, environments (Whittaker and Likens, 1975; Larcher, 1983). Therefore, in dry areas where vegetation is sparse, the relevant part of the gradient is further restricted to the right (light) side.

***Implications for facilitation and competition***

The consequences of the interplay of microclimatic gradients and physiological trade-offs can be explored by combining the above graphical relationships. A first impression can be obtained from an overlay of the zero growth isocline with the microclimatic gradients (Fig 4).

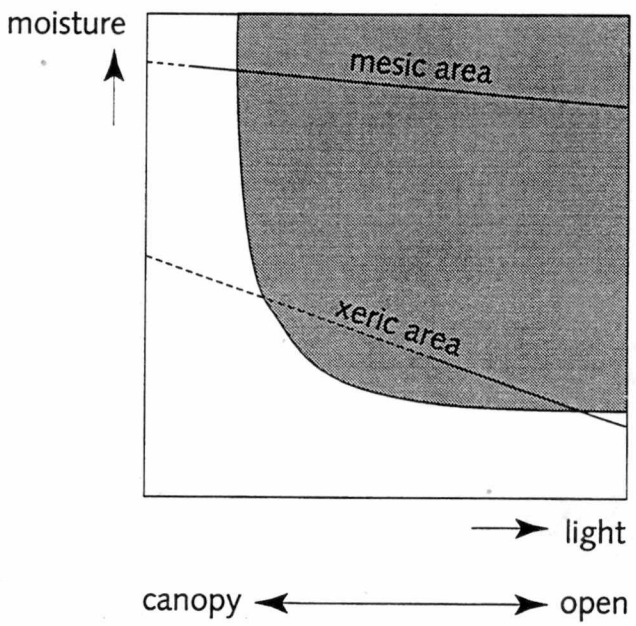


Figure 4. Overlay of the plant growth response (Fig. 1b) and the microclimatic gradients of light and moisture (Fig. 3). In dry areas water stress inhibits growth in the open, and seedling establishment will be restricted to shady sites.

In humid (mesic) areas growth is possible along the entire gradient with the exception of the deep shade. In the dry (xeric) areas, however, growth is also limited at the high-light end of the gradient because of increased water stress in the open unprotected sites. Here, seedling growth is only possible in the shade of nurse plants. As argued, deep shade may be rare in xeric areas. Therefore this facilitative effect of nurse-plants can actually dominate the field patterns of seedling establishment under dry conditions.

Intersection of the microclimatic gradients with the seedling growth response to light and moisture (Fig. 5) gives a more detailed view of the balance of competitive and facilitative effects of nurse canopies on seedlings.

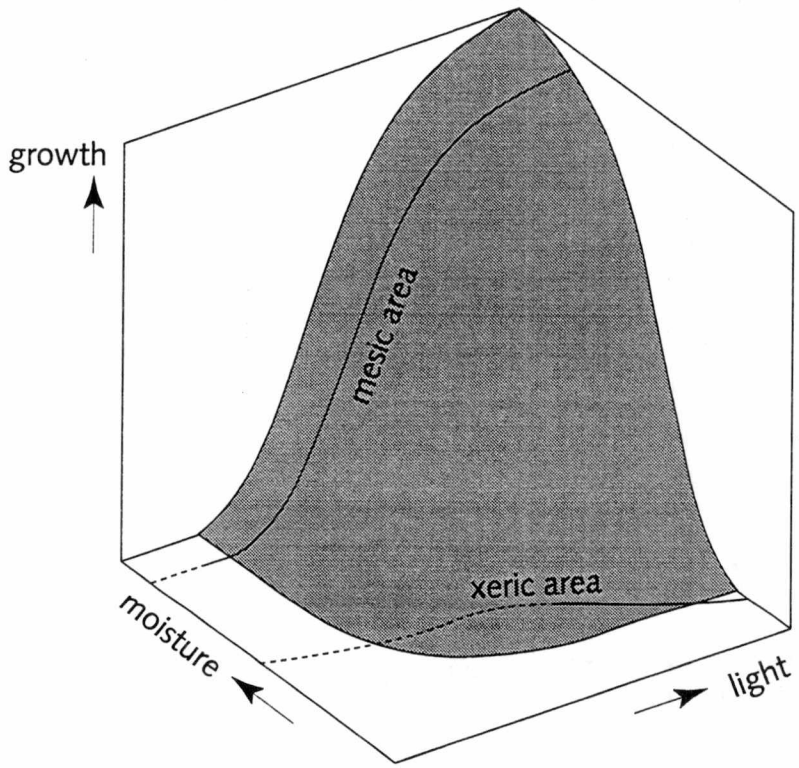


Figure 5. Intersection of the hypothesized correlation between microsite light and moisture (Fig. 3) with the seedling growth (Fig. 2) as a function of those factors. It shows the resulting variation in growth along a gradient from the shade to the open in moist and dry areas.

In very mesic areas, overall growth rates are much higher than under xeric conditions. Under such climatic conditions, water stress might never really important, even in the open, and growth simply declines with shade. In more xeric areas, however, the decrease of microsite moisture towards the open becomes important. The net effect of the interplay of shading and enhanced water relations along the gradient from the open to the canopy can be more clearly seen if the growth along the gradient is projected in the light-growth plane (Fig. 6). Growth in xeric areas shows an unimodal response along the gradient from shade to light. On the high-light side of the gradient, seedling growth declines with the distance from the established 'nurse' vegetation. Obviously, this is what is commonly referred to as facilitation.

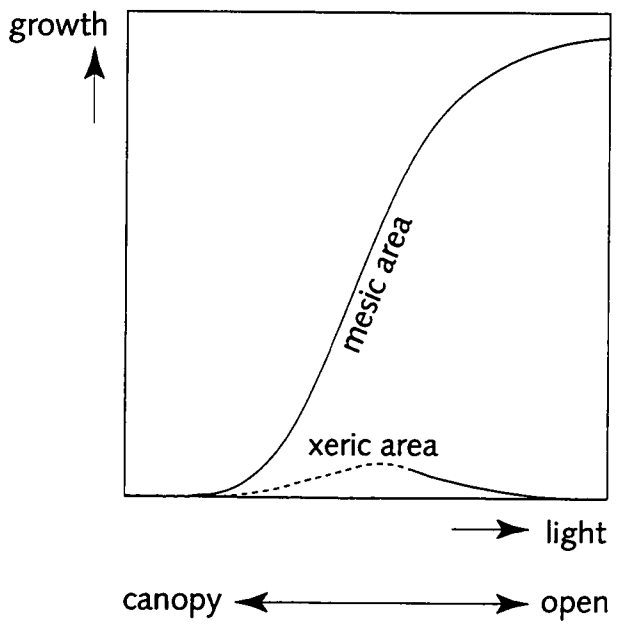


Figure 6. Growth of establishing plants along a gradient from shady to open places, obtained by projecting the intersections shown in Figure 5, on the light-growth plane. The negative slope on the right-hand side of the growth response in xeric areas implies facilitation, as growth decreases with the distance from the canopy of nurse plants. Because very shady conditions (dashed) may be absent in dry areas, facilitation may actually be the only obvious pattern with respect to seedling establishment.

Note that the graphs have focused on the growth response of a single hypothetical species. In practice, communities consist of many species with different responses to environmental conditions. Drought tolerant plants will often prevail in the open while shade tolerant plants are found under the canopy. Also plant communities in xeric areas will have more drought tolerant species while lush forests in mesic areas will harbor more shade tolerant species. Because of the discussed physiological trade-offs, shade tolerant species would tend to be relatively sensitive to water stress. This suggests that even in mesic areas facilitation through improvement of microsite moisture conditions may occur. Water stress is less extreme than in xeric areas, but on the other hand more species will tend to be rather intolerant to dry conditions. In terms of growth isoclines (Fig. 4), such shade tolerant, but drought intolerant species will have an isocline that reaches further to the left (shady) side of the graph, but does not extend as much to low moisture levels as the depicted isocline does. As a result even a moderate decline in microsite moisture on a gradient from the canopy to the open in mesic areas may result in a noticeable reduction of the seedling performance. Indeed, reports of facilitative patterns come predominantly, but not exclusively from xeric areas.

## Discussion

The graphical model presented here focuses on the effects of shade and dry conditions to clarify the interplay of facilitation and competition. As demonstrated by the presented collection of field studies, desiccating conditions are thought to play a role in many

reported cases of facilitation over a wide array of different plant communities. Nonetheless, other factors than moisture are often found to explain facilitative patterns. Enhanced nutrient conditions (Muller, 1953; Franco and Nobel, 1989; Callaway et al., 1991; Belsky, 1994; Maun, 1994) and protection from herbivores (Ellison and Houston, 1958; Turner, et al., 1969, Atsatt and O'Dowd, 1976; Jaksic and Fuentes, 1980; Fuentes et al., 1984, 1986; McAuliffe, 1984b, 1986) under the nurse canopy are frequently reported. The graphical model could also be applied to these mechanisms. The same graphs would be defendable after changing the text on the vertical axis from moisture to nutrients, or (inverting the axis) to herbivory losses. Rather than adjusting the model to analyze other specific mechanisms, we extend the basic idea to a more general mechanistic framework for understanding the balance of facilitation and competition. In short, the main point is that nurse plants affect various factors simultaneously and the effect on seedlings depends on their physiological and growth responses.

In practice there will always be a complex gradient of various resources and disturbances going from the open to the canopy. Over this gradient, some factors (e.g. nutrients, moisture) will change for the better while others (e.g. light, allelopathic exudates) change for the worse. The net effect of these correlated changes will depend on the combined response of plants to all factors involved. If a factor that improves under the canopy happens to be the only 'limiting factor', that is, if the effect of the simultaneous change in other factors is nil, the net effect of the canopy will obviously be facilitative. However, in reality the matter will usually be more complicated. Rarely will the impact of one environmental factor be independent of the value of others. As argued,

physiological trade-offs may cause plants under water stress to be less tolerant to shade, leading to the curved (Fig. 1a) rather than the rectangular (Fig. 1b) isocline. Similarly, plants will be less capable of compensating for herbivory losses when their productivity is low due to shading, and might be less shade tolerant at low nutrient levels. Also, plants with a better nutrient status are probably more tolerant to water stress under relatively high light and not extremely dry conditions due to changes in the potential for osmotic adjustment (Morgan, 1984; Munns, 1988) and the response to abscicic acid (Schulze, 1991).

The general pattern is that when one environmental factor becomes unfavorable the requirements for other factors increase if growth is to be maintained. Since some factors will usually change for the better, while others change for the worse under the nurse canopy, the implication is that positive effects of nurse canopies will always tend to be counteracted by negative ones. Reduced herbivory losses, improved microsite moisture or enhanced nutrient conditions only lead to an overall positive effect of the canopy on seedlings if the benefits exceed the costs of growing under the canopy.

Extending the graphical model, the discussed interactive effects of various environmental factors imply that isoclines in the multi-dimensional environmental factor space will tend to be curved rather than rectangular. Whether facilitation occurs depends on the way in which the various factors change over a gradient from the canopy to the open. In the presented model for light and water, facilitation occurs only if the environmental line declines more steeply than the growth isocline at the right side (Fig. 4). Thus in order to lead to facilitation, the increase in microsite moisture under the

canopy should exceed the increase in moisture demand when plants acclimatize to shade by investing less in roots and more in leaves. Phrased in general terms the condition for facilitation to occur is that improvement of an environmental factor (e.g. water, nutrients, herbivory) under the canopy exceeds the increased 'demand' for that factor caused by deterioration of another factor (e.g. light). Especially when factors like herbivory, water or nutrient limitation pose an important constraint to plant recruitment, the effect of an improvement of these factors under the nurse canopy may often outweigh the limited costs of reduced light levels.

Obviously, the net effect of nurse canopies on the understory may shift from facilitative to competitive or vice versa when conditions change. Many studies show, for instance, that facilitative effects are stronger on the drier sites and in drier years (Parker and Muller, 1982; Fuentes et al., 1984; Frost and McDougald, 1989; Hillier, 1990; Belsky et al., 1993, Berkowitz et al., 1995), and experimental addition of water has been shown to enhance seedling survival and growth much more in open areas than under the canopy (De Jong and Klinkhamer, 1988; Shumway and Bertness, 1992). Also experimental manipulations in salt marshes have shown that alleviation of the stress can switch the effects of the interaction from facilitative to competitive (Bertness and Shumway, 1993; Bertness and Hacker, 1994; Bertness and Yeh, 1994; Shumway and Bertness, 1994). In addition, the net effect of plants on other plants can change dramatically over time as a result of growth. Newly established plants can eventually shade out the former nurse, and their extending root system allow uptake from limited sources that were previously available only to the nurse plant (Conard and Radosevich, 1982; McAuliffe, 1984a;

Valiente et al., 1991a,b). Moreover, competition with other small plants in the shade can increase because of the common exploitation of limited resources in the top soil layers (Aguiar and Sala, 1994).

Clearly, the net effect of one plant on another plant can easily shift from negative to positive and vice versa. The terms facilitation and competition refer to the net effect of changes in the environment of a plant caused by the presence of other plants. In practice, however, competition and facilitation are often discussed almost as if they were completely exclusive processes acting in plant communities. Addressing the intertwined positive and negative aspects of plant-plant interactions explicitly may prove a fruitful way to enhance our understanding of the highly variable nature.

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# Part 3

## Interactive effects of shade and drought on seedlings of tulip poplar: is there a trade-off in tolerance?

## Abstract

Seedlings of tulip poplar (*Liriodendron tulipifera* L.) were grown under different combinations of shade (1, 5, 12, 17, and 27% of ambient light) and soil water content (5-9%, 11-15%, and >20%). The experiment was designed to test the assumptions that plants face a trade-off between shade and drought tolerance. Shoot dark respiration rates and light compensation points decreased under drier conditions. Under well watered conditions (predawn $\Psi_{leaf}$ around -0.1 MPa), estimated daily shoot carbon gain ($\mu mol\ g^{-1}d^{-1}$) increased 76% in plants growing under 27% of ambient light versus plants under 5%. In contrast, under dry conditions (predawn $\Psi_{leaf}$ around -1 MPa) rates of carbon fixation decreased with increasing light availability. Daily xylem sap flow patterns indicate that this was associated with a strong reduction in stomatal conductance in plants growing in dry soil and high light conditions. At dry conditions, plants under 5% of ambient light transpired for around 7 h and 30 m while plants at 27% transpired for only 2 h and 15 m a day. Overall, I do not find evidence that higher light levels compensate for the physiological and growth effects of drought in tulip poplar. Also, higher water availability did not enhance growth in the shade.


## Introduction

The analysis of vegetation patterns along environmental gradients has a long tradition in ecology. Studies that link these patterns with physiological and growth responses to

different environmental factors are, however, less common. We know relatively little about the combined effects of different environmental factors on plant physiology and growth (Osmond et al., 1987; Chapin et al., 1987; and reviews in Mooney et al., 1991). Most ecophysiological work has concentrated on studying the response of plants to changes in a single factor, keeping the other conditions constant. However, the levels of various resources usually change simultaneously along gradients in nature. Since the combined response to two or more resources cannot be predicted simply from responses to separate resources, the vast body of research on single factor effects is an insufficient basis for understanding natural patterns in practice.

Smith and Huston (1989) hypothesized that the response of plants to the combined effects of light and water is characterized by a trade-off between drought tolerance and shade tolerance. They showed that several natural patterns of plant distribution and succession could, in principle, be explained from this hypothesized response-model. The trade-off hypothesis was based on a set of physiological and energetic constraints that affect the ability of a plant to: 1) tolerate low levels of a resource while maintaining the ability to grow rapidly at high levels of the same resource; and 2) simultaneously use different types of resources when levels of both resources are low. As a consequence of these two trade-offs, the competitive ability of different types of plants is expected to shift along environmental gradients (Huston and Smith, 1987).

The first trade-off, related to growth rate and tolerance to low levels of a single resource, has been strongly supported by empirical results along gradients of light, nutrients and water (Grime and Hunt, 1975; Mooney et al., 1978; Chapin, 1980; Ellison et

al., 1993; Kitajima, 1994). The second trade-off, relating the simultaneous tolerance to low levels of two resources, has been studied less. Smith and Huston (1989) based their trade-off hypothesis on some expected physiological responses of plants to light and water. They assumed that under drier conditions plants allocate relatively more biomass to roots than to aboveground structures. As a consequence of this, the ratio of respiring biomass to photosynthetic material would increase, and therefore the amount of light necessary to keep a positive carbon balance should be higher (whole-plant light compensation point). Also, since at low water conditions plants avoid water loss by closing their stomata, it was assumed that higher light levels could compensate for reductions in photosynthetic activity by enhancing the photosynthetic rate. Based on these assumptions, Smith and Huston (1989) predicted that under drier conditions the whole-plant light compensation point (i.e. amount of light at which photosynthesis equals respiration) would shift to higher values, and plants would demonstrate more shade intolerant behavior. Similarly, plants would become more drought intolerant when growing under low light levels. The trade-off model focuses on plant responses during acclimation to shade and drought. The predictions are expected to hold within a population (for individuals growing in different conditions of light and water), as well as between populations (for populations growing in different conditions of light and water). Also, it is expected that different species should show the same basic pattern, although some type of species (or plant functional types) might be more susceptible to either drought or shade. The authors used the resulting hypothetical trade-off model to predict the growth and survival of different plant functional types along gradients of light and

water availability. This model represents a significant contribution to the efforts in plant ecology to explain natural patterns on the basis of responses of individual plants to their environment.

In this paper I seek to experimentally test some of the assumptions on which the trade-off model of shade and drought tolerance is based, namely that: 1) leaf area/total biomass decreases under dry conditions 2) shoot/root ratio decreases under dry conditions, 3) whole plant light compensation point increases under dry conditions, 4) rate of carbon fixation increases with light under dry conditions, 5) the relative reduction in growth with shading increases under dry conditions. Here I concentrate on the expected responses within a particular species along gradients of light and water availability.

To test these assumptions I set up field and shade-house experiments with tree seedlings of different species. This paper presents the results of a shade-house experiment with seedlings of *Liriodendron tulipifera* (tulip poplar). Tulip poplar frequently colonizes new open gaps in the eastern North American deciduous forests. It is a fast growing species that is usually classified as shade intolerant (Baker, 1949; Fowells, 1965; Wallace and Dunn, 1980), and commonly occupies mesic sites, which in part results from its reported sensitivity to drought (Roberts et al., 1979; Chason and Huston, 1990).

# Methods

### *Experimental design*

Two-year-old seedlings of tulip poplar were grown under five levels of light (1%, 5%, 12%, 17%, and 27% of ambient) and three ranges of soil water content (5-9%, 11-15%, >20%) from May 20 to October 6 of 1994. These light and soil water levels were chosen to represent the natural gradients found in the understory of the Throughfall Displacement Experimental (TDE) Site during the growing seasons of 1992 and 1993. The TDE is a large-scale field experiment designed to describe the physiological and ecological effects of drought (Hanson et al., 1995), in which I am also testing the trade-off model by following the growth and survival of seedlings along natural gradients of light and experimental gradients of soil water availability. The shade-house experiment described in this paper was conducted at 9 km from the TDE site, at the Global Change Field Research Facility on the National Environmental Research Park, Oak Ridge, TN, USA.

Leafless bare-root seedlings (30 cm tall) were obtained from Tennessee (Hillis Nursery Company, Inc., McMinnville, TN). On May 10, 1994 each seedling was planted in a plastic pot (28 cm wide x 31 cm deep) containing a Paleudult type, A horizon, forest soil (compacted at 1.21 g/cm) over a 5-cm layer of gravel at the bottom to help drainage. The seedlings leafed out under 27% light and well watered conditions, and on May 20, 1994 were transferred to the different light treatments. An insecticide application (Malathion 50) to all seedlings was necessary on May 31 to control an outbreak of aphids.

Five shade-houses, one per light treatment, were built using an aluminum frame covered with neutral shade clothes of different densities (polypropylene, PAK Unlimited, Inc.), and the resulting reduction in photosynthetically active radiation (PAR) confirmed with a quantum radiometer (LI 185A, Li-Cor Inc, Lincoln, NE). The roof and upper part of the walls were covered with transparent plastic to exclude rainfall. The pots were placed on 80 cm-tall tables. Each shade-house had four plants in each of the three water treatments, except for the 1%-light shade-house where only two plants grew under the lowest (5-9%) and highest (>20%) soil water ranges. Since there was only one shadehouse per light treatment the design was pseudoreplicated. Daily air temperatures inside each shadehouse were recorded with a minimum-maximum thermometer hanging from the roof.

***Soil water measurements***

Volumetric soil water content ($^{v}/_{v}$) was recorded every other day using a time domain reflectometer (TDR) (Trase system 1, model 6050X1, Soilmoisture Equipment Co., Santa Barbara, CA), and a 24-cm pair of waveguides permanently inserted in each pot. When the soil water content dropped below the minimum value of the treatment range, sufficient water was added to return soil water content to upper range. Multiple TDR readings before and after watering helped determine the amount of water necessary for each plant. Every TDR reading was subsequently converted to pre-dawn leaf water potential ($\Psi_{leaf}$) using a TDR-leaf water potential curve (n=40, $r^2$=0.73):

$$\Psi_{leaf} = -27.25\ (TDR)^{-1.73} \qquad (1)$$

This curve was made in late September after the maximum range in soil water content had been reached in each shadehouse. Estimations of pre-dawn leaf water potential were made for all the treatment combinations using a pressure chamber (model 1000, PMS Instrument Co., Corvalis, OR), and TDR readings were taking immediately after. The above formula was used to transform each TDR reading taken during the experiment, and calculate an average predawn leaf water potential for each plant (in MPa units).

***Gas exchange measurements***

Gas exchange (net photosynthesis and dark respiration) of the whole aboveground portion of a plant was measured in a 40-L custom chamber connected to a closed-path infra-red gas analysis system (LI 6200, Li-Cor Inc., Lincoln, NE). The glass chamber (32x32x40 cm) had two fans placed on the upper and lower part of two opposing walls, and a light sensor on the top (LI 190SA, Li-Cor Inc., Lincoln, NE). The chamber was placed on top of a sealed wooden platform to isolate the upper portion of the plant from the soil. This plate consisted of two halves sealed around the plant stem and placed on top of the pot. Isolating foam was used around the stem and also between the wooden plate and the chamber edges to get an air-tight seal (Fig. 1).

To take the measurements, the plant was removed from the shade-house while protected with shade cloth of the same density, and carried to the chamber location. Net

photosynthesis was first measured at the same light level that the plants had experienced in the shade-house and then under step-wise decreasing light conditions until stable negative values of carbon exchange were recorded. Irradiance was then gradually increased to saturating light levels (PAR > 1200 μmol $m^{-2}s^{-1}$). Photosynthetically active radiation (PAR) levels were changed by covering the chamber with shade cloth of different densities.

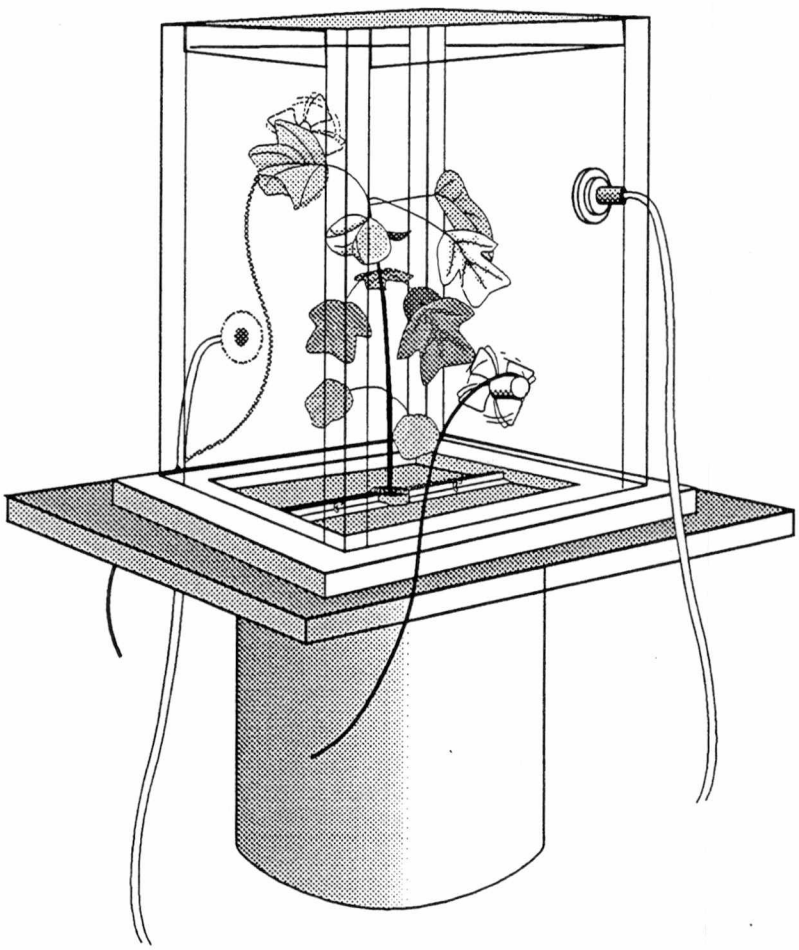


Figure 1. Drawing of the custom cuvette and gas-exchange system used for the measurements.

Twenty plants were measured between 11:00 and 15:00 from late July to early September. Light compensation point (LCP) was estimated by fitting a linear regression (typical $r^2$= 0.9) using measured net photosynthetic $CO_2$ assimilation values (A) up to 100 μmol $m^{-2}s^{-1}$ of PAR.

Shoot dark respiration rates (i.e., leaves and stem) were measured on eight seedlings (one at low water and one at high water treatment from the shade-houses with 5, 12, 17 and 27% of ambient light) during the morning of September 21. The seedlings were moved to a dark room the evening before, and kept there during the measurements. Respiration rate of each plant was calculated as an average of approximately 10 30s-observations.

***Xylem sap flow measurements***

Xylem sap flow sensors (model SGA 5 and 10) using the constant heating method (Dynamax, Inc., Houston, TX) were installed on a subsample of seedlings growing at 5% and 27% of ambient light. In each of these two shade-houses, two seedlings (one at low and one at high water treatments) were monitored for four days (from October 1 to 4). Then all the seedlings were well watered and followed for another four days.

***Carbon gain***

Carbon gain was estimated for seedlings at low and high soil water treatment growing under 5% and 27% of ambient light between October 1 and 4. The hourly net shoot photosynthesis was estimated by plotting hourly PPFD readings on the light response

equation fitted for a seedling growing under the same conditions. PPFD readings consisted of an average of 60 readings (one per minute) taken at ambient conditions, and multiplied by the fraction of light that passed the shade cloth. Daily net photosynthesis was calculated by adding the hourly estimates during the period the plant was transpiring, which was indicated by the xylem sap flow sensors. To estimate the daily net shoot carbon gain, the shoot dark respiration losses were subtracted from the daily net photosynthesis. Respiration losses were estimated by multiplying the shoot dark respiration rates by the number of hours the plant was not photosynthesizing. The respiration rates were standardized to $20^0$C (assuming a $Q_{10}$ of 2). Dark respiration rates initially increase during the first hours of dark and then decrease towards dawn. Therefore my estimates using early morning measurements and assuming a constant rate likely underestimate the daily dark respiration rates.

***Plant growth analysis***

Measurements of above-ground plant biomass were taken on a subsample before the plants were planted, after each gas exchange measurement, and at the final harvest. The stem diameter was measured with calipers at the base of the apical bud and close to the stem base. Stem height was measured from soil level to the base of the apical bud. The width of each leaf was measured at the widest point, and leaf area was estimated using a linear regression based on a subsample of leaves (n=111, $r^2$=0.99) measured on an area meter (LI3100, Li-Cor, Inc.):

$$\log(area) = [\,1.9348 \log(width)] - 0.2434 \qquad (2)$$

Stem volume was estimated as a truncated cone. To calculate the increment in stem and total aboveground biomass during the course of the experiment, I estimated the initial stem dry weight of the experimental seedlings using a linear regression based on a subsample of seedlings in which the stem volume and dry weight were measured (n=50, $r^2$=0.84):

$$dry\ weight = 0.3283\ (volume) + 1.0087 \qquad (3)$$

In early October, plants were removed from the pots, and the roots were manually separated and washed free of remaining soil using fine strainers to reduce material loss. Clean roots were deep frozen in plastic bags until separated into three diameter classes (<1mm, 1-2 mm, and >2 mm). All plant tissue was dried at 70$^0$C and leaves, petioles, stem and the three root categories weighed.

***Statistical analysis***

I used two-way factorial designs for the analysis of growth responses including light (4 levels) and soil water (3 levels) as main effects. Seedlings were considered as experimental replicates. However, since there was only one shadehouse per light treatment the design was really pseudoreplicated. The experimental design was also imbalanced because at 1% of light there were only two levels of water replicated twice. In order to simplify the data analysis, the responses at 1% of light were not included in the ANOVAs, but compared with the responses at 5% only using t-tests. Transformations of the original variables (e.g. log, or arcsin(sqrt)) were done in order to homogenize

variances or normalize residuals. Differences between levels of each factor were tested using generalized contrasts.

## Results

### *Biomass allocation*

There were no significant differences in most growth parameters between plants grown under the low and intermediate water treatments (Fig. 2). There were also no significant differences between plants from the two lowest light treatments (1 and 5% of ambient light), nor between the three higher ones (12, 17, and 27%) (Fig 2).

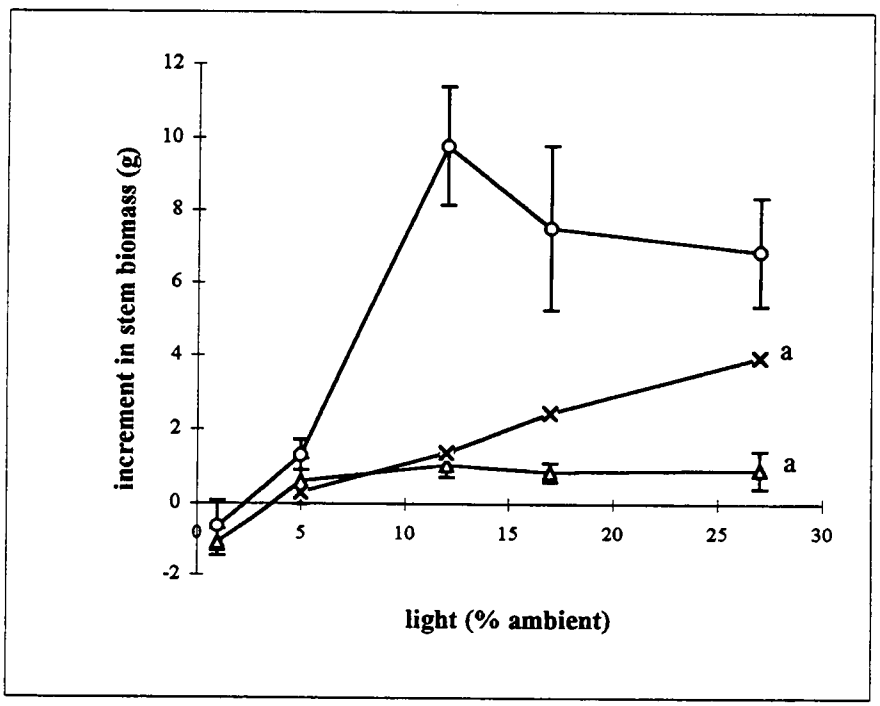



Figure 2. Seasonal increment in shoot biomass (g) at increasing light conditions for three soil water treatments: low (Δ), intermediate (x), and high (○ ).

There was a significant interaction effect between light and water in biomass production (Table 1). This pattern was consistently found for final biomass (total, aboveground, and roots) and the increment in stem biomass. Light availability increased biomass production only under high soil water conditions (Table 2). Soil water availability increased biomass production only at light levels greater than 5% (Table 3).

Table 1. Results of two-way factorial ANOVA's for final harvest of tulip poplar seedlings grown under light (5%, 12%, 17%, 27%) and soil water ranges (low, intermediate, and high). Data are p-values (≤).

| | light | water | interaction |
|---|---|---|---|
| total biomass (log) | .0001 | .0001 | .007 |
| aboveground biomass (log) | .0005 | .0001 | .03 |
| belowground biomass (log) | .0001 | .0001 | .005 |
| stem biomass increment | .001 | .0001 | .007 |
| leaf area ratio | .001 | .012 | .57 |
| specific leaf area | .0007 | .015 | .36 |
| leaf weight ratio | .25 | .07 | .64 |
| shoot/root | .03 | .53 | .54 |
| root≤ 1mm/total root biomass (arcsin( | .054 | .02 | .48 |

Table 2. Light effects on final biomass of tulip poplar seedlings. Seedlings were grown under four light levels (5%, 12%, 17%, 27%) and three soil water ranges (LW: low, IW: intermediate, HW: high). Data are p-values testing the null hypothesis defined in the heading. Contrasts are presented for different water levels because the interaction effects between water and light were significant (see Table 1).

| | | null hypothesis | | |
|---|---|---|---|---|
| | | 5 = 12 | 12 = 17 | 17 = 27 |
| total biomass | LW | .99 | 1 | 1 |
| | IW | .75 | .97 | .90 |
| | HW | .001 | .95 | .99 |
| aboveground biomass | LW | .99 | 1 | .99 |
| | IW | .95 | .96 | .99 |
| | HW | .006 | .96 | .99 |
| belowground biomass | LW | .99 | .99 | 1 |
| | IW | .31 | .99 | .64 |
| | HW | .002 | .96 | .96 |
| stem biomass increment | LW | 1 | 1 | 1 |
| | IW | .99 | .99 | .98 |
| | HW | .0006 | .88 | .99 |

Table 3. Water effects on final biomass of tulip poplar seedlings. Seedlings were grown under four light levels (5%, 12%, 17%, 27%) and three soil water ranges (LW: low, IW: intermediate, HW: high). Data are p-values testing the null hypothesis (Ho) defined in the heading. Contrasts are presented for different light levels because the interaction effects between water and light were significant (see Table 1).

| | Ho | light | | | |
|---|---|---|---|---|---|
| | | 5 | 12 | 17 | 27 |
| total biomass | LW = IW | .99 | .99 | .69 | .06 |
| | LW = HW | .70 | .003 | .026 | .001 |
| aboveground biomass | LW = IW | .99 | 1 | .90 | .35 |
| | LW = HW | .99 | .006 | .054 | .004 |
| belowground biomass | LW = IW | .96 | .97 | .52 | .03 |
| | LW = HW | 1 | .014 | .071 | .011 |
| stem biomass increment | LW = IW | 1 | 1 | .97 | .66 |
| | LW = HW | .99 | .0004 | .011 | .034 |

The results can then be summarized in two soil water treatments: low water (original low and intermediate soil water treatments), which was equivalent to a seasonal $\Psi_{leaf} < -0.2$ MPa, and high water with a seasonal $\Psi_{leaf} > -0.2$ MPa (see Appendix 1); and two light treatments: low light (1 and 5%) and high light (12, 17 and 27%), resulting in 4 treatment combinations (LL/LW: low light-low water, LL/HW: low light-high water, HL/LW: high light-low water, HL/HW: high light-high water). The growth and physiological

characteristics of the plants in the four treatment combinations are summarized in Table 4 (complete data set can be found in Appendix 2).

Table 4. Final biomass and gas exchange parameters for tulip poplar seedlings. Seedlings were grown under low light (LL: 1 and 5% of ambient), high light (HL: 12, 17, and 27%), low soil water (LW: original low and intermediate water treatments), and high soil water (HW). $\Psi_{leaf}$ : predawn leaf water potential, lcp: light compensation point. Data are means and standard errors.

| | LL | | HL | |
|---|---|---|---|---|
| | LW | HW | LW | HW |
| Water conditions | | | | |
| season $\Psi_{leaf}$ (MPa) | -0.3 ± 0.04 | -0.1 ± 0.00 | -0.4 ± 0.02 | -0.1 ± 0.00 |
| season TDR (%) | 15.9 ± 0.6 | 24.9 ± 0.2 | 14.6 ± 0.4 | 22.8 ± 0.4 |
| Growth | | | | |
| total biomass (g) | 7.0 ± 0.8 | 8.9 ± 1.6 | 12.9 ± 1.4 | 36.7 ± 3.7 |
| shoot biomass (g) | 4.8 ± 0.6 | 6.5 ± 1.4 | 7.6 ± 0.7 | 22.9 ± 2.0 |
| root biomass (g) | 2.2 ± 0.3 | 2.3 ± 0.4 | 5.2 ± 0.8 | 13.8 ± 2.1 |
| Gas Exchange | | | | |
| lcp ($\mu$mol $m^{-2}s^{-1}$) | 9.8 ±1.5 | 16.0 ± 3.8 | 27.9 ± 5.8 | 31.1 ± 3.2 |
| dark respiration ($x10^{-4}$)($\mu$mol $g^{-1}s^{-1}$) | 27.7 | 69.8 | 19.5 ± 3.3 | 45.9 ± 8.7 |

At low light, there were no differences in the final biomass (above-ground, below-ground and total) between low and high water treatments (Table 4), indicating that water addition did not reduce the negative effects of shade. In contrast, at high light conditions, the reduction in biomass due to drier conditions was over 60%. Similarly, higher light levels had relatively minor effects on growth under low water conditions. At dry conditions,

biomass was almost twice as high under high light as under low light (Table 4), but under moist conditions, the difference between the high and low light plants was a factor of four. Thus, the shading effects on growth are stronger under moist conditions than at dry conditions.

Leaf area ratio (LAR: total leaf area/total biomass) decreased at high light (Fig. 3a; Table 5) and also under dry conditions (Fig. 3a; Table 6). This was the result of a decrease in the specific leaf area (SLA: leaf area/leaf biomass) (Fig. 3b), as the proportion of total biomass allocated to leaves remained practically constant (LWR: leaf biomass/total biomass) (Fig. 4c).

Table 5. Light effects on biomass allocation of tulip poplar seedlings. Seedlings were grown under four light levels (5%, 12%, 17%, 27%) and three soil water ranges (LW: low, IW: intermediate, HW: high).

| | 5 = 12,17,27 | 12 = 17 | 17 = 27 |
|---|---|---|---|
| leaf area ratio | .001 | .69 | .78 |
| specific leaf area | .001 | .80 | .98 |
| leaf weight ratio | .98 | .75 | .27 |
| shoot/root | .07 | .97 | .56 |
| root≤ 1mm/total root | .09 | .99 | .81 |

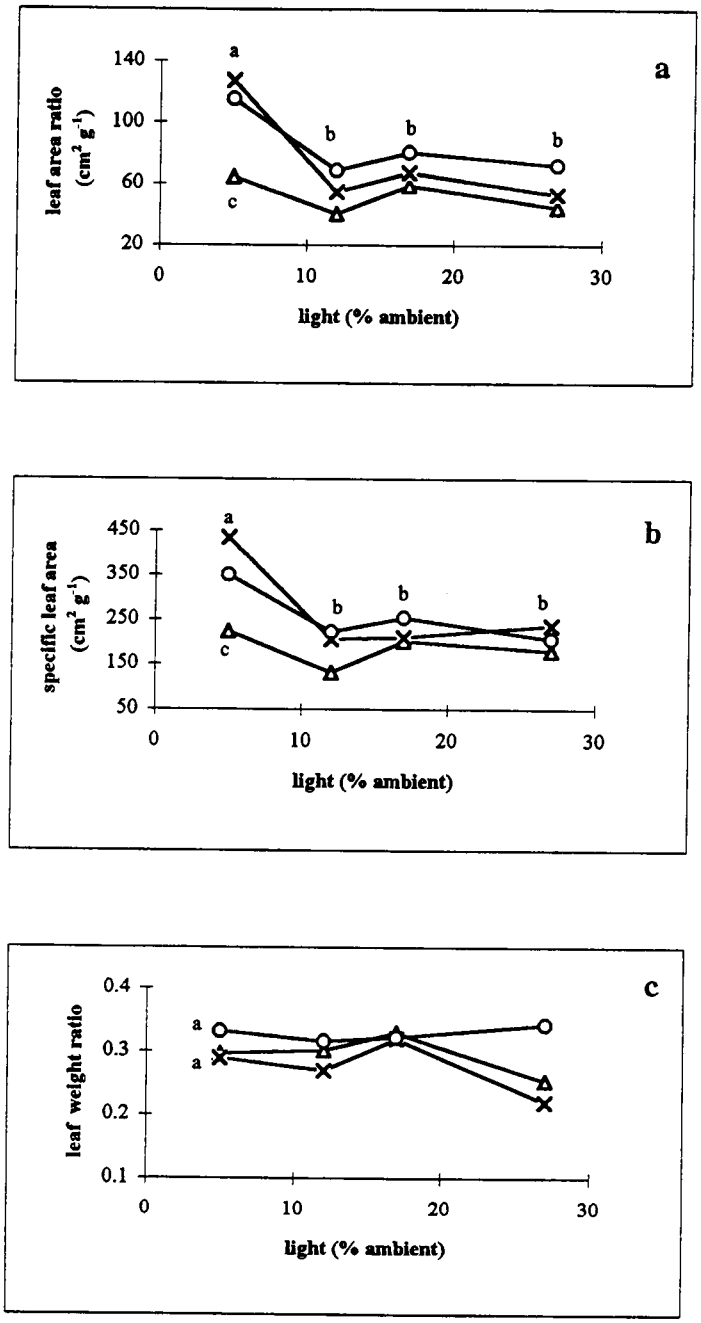



Figure 3. Leaf area ratio and its components under three soil water treatments: low (△), intermediate (x), and high (○ ). a) leaf area ratio, b) specific leaf area, c) leaf weight ratio. Letters indicate significant differences (see Tables 5 and 6)

Table 6. Water effects on biomass allocation of tulip poplar seedlings. Seedlings were grown under four light levels (5%, 12%, 17%, 27%) and three soil water ranges (LW: low, IW: intermediate, HW: high). Data are p-values (≤) for the null hypothesis defined in the heading.

| | LW = IW | LW = HW |
|---|---|---|
| leaf area ratio | .09 | .01 |
| specific leaf area | .02 | .06 |
| leaf weight ratio | .65 | .36 |
| shoot/root | .76 | .93 |
| root≤ 1mm/total root | .15 | .69 |

Shoot/root ratio can change with plant ontogeny, and therefore plant size. In this experiment, however, shoot/root ratio was not correlated with final whole plant biomass (linear regression, $r^2$=0.05). It tended to decrease at higher light levels (Fig. 4a: Table 5), but was unaffected by the water treatments (Table 6). The allometric approach, in which root mass is plotted against shoot mass on log scales, suggests that there were no effects of soil water on relative root growth (Table 7). This is particularly clear under high light conditions (>12% of ambient) because of the little scatter. The slope of the regression in high water (>-0.2 MPa) is not statistically different than the slope in low water (<-0.2 MPa). On the other hand, there was a significant increase in root production at increased light conditions (Table 7). More interesting was the allocation change to fine roots. The proportion of root biomass allocated to roots less than 1 mm in diameter peaked at the intermediate water level (Fig. 4b).

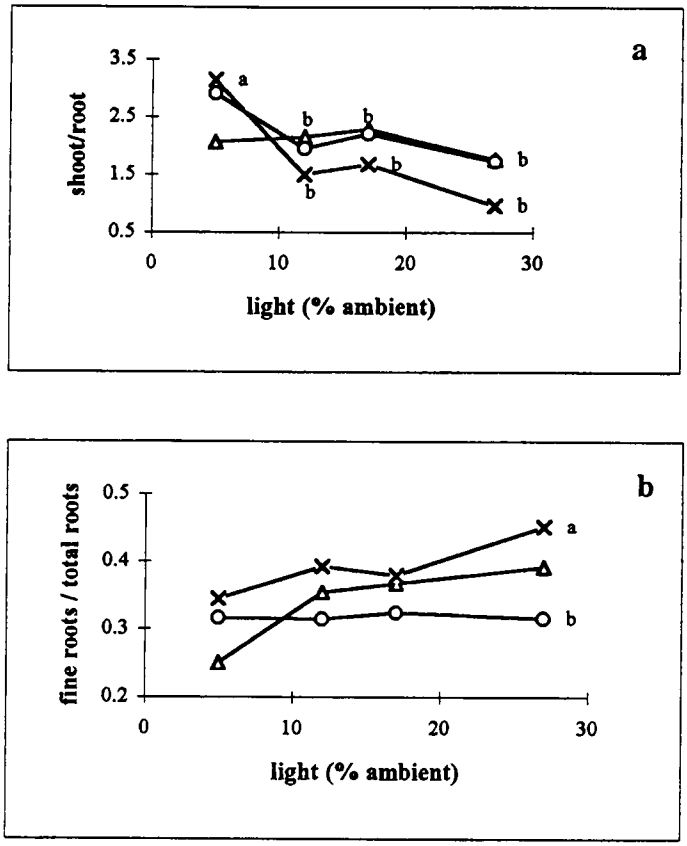



Figure 4. Biomass allocation to a) shoot/root, and b) roots < 1mm/total root biomass under three soil water treatments: low (△), intermediate (x), and high (○).

Table 7. Allometric relationships between root and shoot mass for tulip poplar seedlings. Seedlings were grown under low light (LL: 1 and 5% of ambient), high light (HL: 12, 17, and 27%), low soil water (LW: seasonal $\Psi_{leaf}$<-0.2 MPa), and high soil water (HW: seasonal $\Psi_{leaf}$>-0.2 MPa). Data are results of linear regressions: log(root) = a + b log(shoot).

| treatment | a ± se | slope ± se | p (≤) | $r^2$ | n |
|---|---|---|---|---|---|
| LL/LW | 0.03 ± 0.40 | 0.36 ± 0.59 | 0.56 | 0.06 | 7 |
| LL/HW | 0.23 ± 0.37 | 0.19 ± 0.49 | 0.72 | 0.04 | 5 |
| HL/LW | -0.24 ± 0.14 | 1.04 ± 0.16 | 0.001 | 0.64 | 24 |
| HL/HW | -0.53 ± 0.39 | 1.20 ± 0.29 | 0.002 | 0.63 | 12 |

*Gas exchange*

Shoot light compensation point was higher for plants raised under higher light levels (Fig. 5, Table 4), and also tended to be higher for plants raised under wetter conditions (Table 4). A multiple linear regression was used to relate the estimated light compensation point (lcp) with the experimental light (p=0.01) and plant water potential (p=0.1) conditions ($r^2$=0.36, p=0.02):

$$lcp = 18.9 + 0.7 * (light) + 16.7\ (pwp) \qquad (4)$$

In addition, there was a positive correlation of light compensation point with temperatures during the measurements (p=0.01), but not with $CO_2$ concentrations.

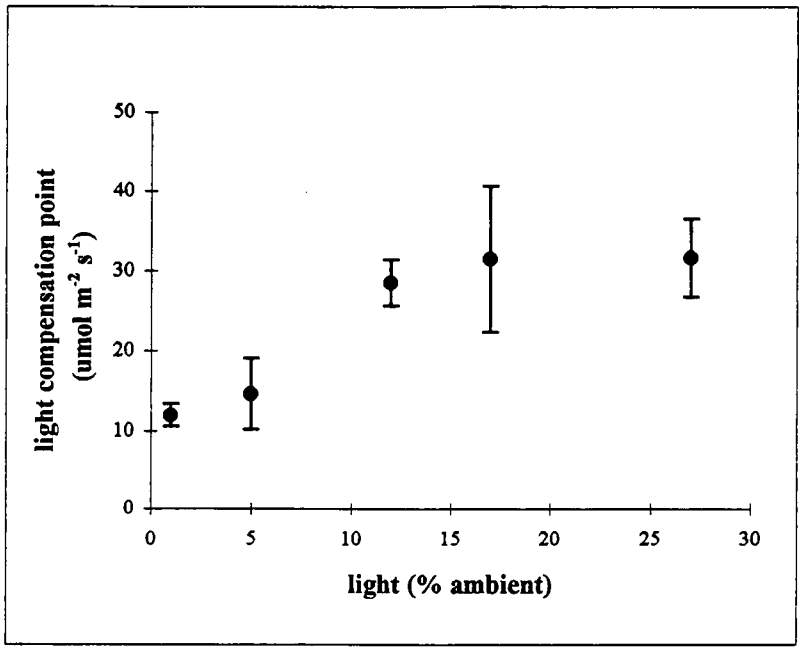



Figure 5. Light compensation point of tulip poplar seedlings grown under different light levels. Data are means and standard errors.

There was no strong correlation between light compensation point and total leaf area (Pearson p=0.20). Since plant leaf area was highly correlated to aboveground biomass (Pearson r=0.92, p<0.001), and total plant biomass (Pearson r= 0.87, p<0.001), then we can probably expect that the light compensation point was not strongly influenced by plant size.

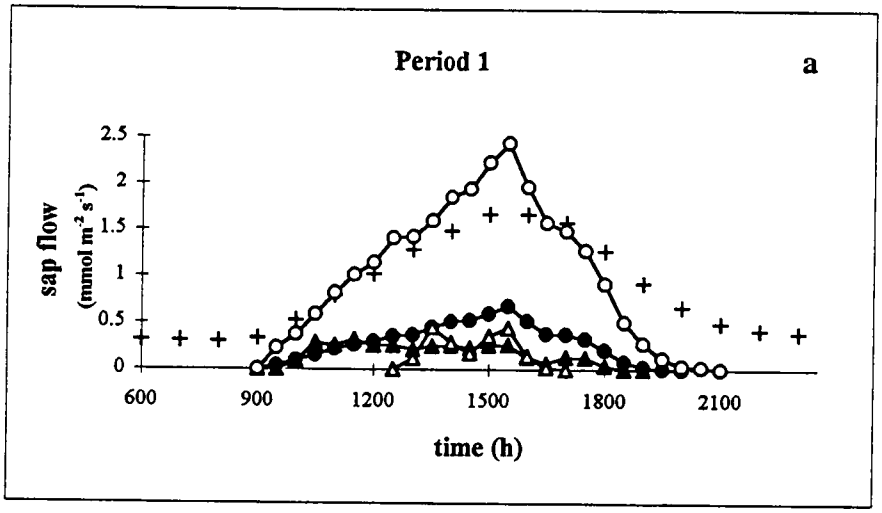
Dark respiration rates (both per unit of leaf area and per unit of biomass) were lower under dry conditions for plants raised at all light levels (Table 4; Pearson r= -0.75, p=0.02). Standardizing the respiration rates at 20$^0$C (assuming a $Q_{10}$ of 2) did not affect these results.

***Xylem sap flow patterns***

The sap flow pattern of well-watered plants closely followed the diurnal changes in ambient vapor pressure deficit, especially at high light conditions. Under moist conditions, seedlings started transpiring around 9:50 am (eastern time zone, day light savings time) and kept transpiring for about 9 hours (Fig. 6a, Table 8). In contrast, seedlings under water stress started transpiring later, especially in high light conditions (Fig. 6a, Table 8). These low-water seedlings had a shorter period of activity, especially in high light conditions (Table 7).

Also, the reduction in daily transpiration of low-water seedlings was stronger under high light conditions. Transpiration expressed per plant leaf area (g $m^{-2}$ $d^{-1}$) or plant biomass (g $g^{-1}d^{-1}$) was reduced approximately 60% at low light, versus 90% at high light (Table 8). After watering, the sap flow pattern of plants that had been previously

under water stress changed: the flow started earlier in the day (around 10:00 am) and plants maintained transpirational water loss for about 8 hours (Fig. 6b, Table 8).



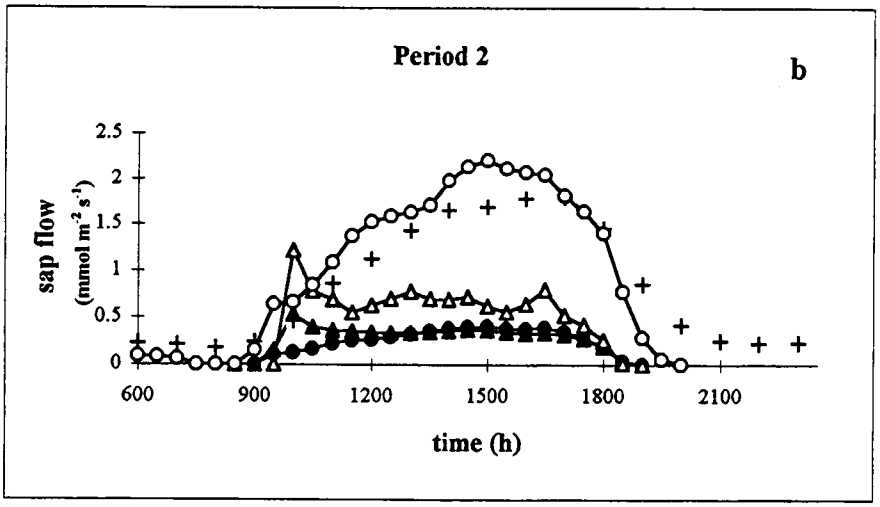




Figure 6. Daily xylem sap flow patterns. a) seedlings at 5% light/low water (▲), 5% light/high water (● ), 27% light/low water (△), 27% light/high water (○ ) and the vapor pressure deficit at ambient conditions (kpa). b) shows the same seedlings after watering. Each curve is an average of measurements taken on one seedling during four days.

Table 8. Xylem sap flow activity for tulip poplar seedlings growing under low light (LL: 5% of ambient), high light (HL: 27%), low soil water content ($\Psi_{leaf}$ <-0.9 MPa), and high soil water content ($\Psi_{leaf}$ = -0.1 MPa) before and after watering. After watering all seedlings had a $\Psi_{leaf}$ close to -0.1 MPa. Data are means of four days.

| | LL | | HL | |
|---|---|---|---|---|
| | LW | HW | LW | HW |
| Start time (h) | | | | |
| before | 10:37 | 9:45 | 13:45 | 9:52 |
| after | 9:52 | 9:22 | 10:00 | 8:37 |
| Duration (h) | | | | |
| before | 7:30 | 9:00 | 2:15 | 9:45 |
| after | 8:22 | 8:52 | 8:00 | 10:07 |

***Daily carbon gain***

Daily estimates of shoot net photosynthesis and carbon gain are shown in Table 9. Under low light conditions, net photosynthesis was not affected by soil water level. But in high light conditions, the seedling with low water availability had a much lower daily net photosynthesis than the plant under high water conditions. Moreover, under low soil water conditions, daily net photosynthesis in high light was also smaller than in low light. In fact, the estimates of daily shoot carbon gain (photosynthesis minus dark respiration) indicate that the plant under low water and high light conditions had a negative assimilation balance. This was largely the result of the extremely short period of photosynthesis at low water and high light levels (two hours), a much shorter active period than observed under low light or high water conditions (Table 9).

Table 9. Estimates of daily net shoot photosynthesis, dark respiration and carbon gain. Same codes as for Table 2.

| | LL | | HL | |
|---|---|---|---|---|
| | LW | HW | LW | HW |
| Water conditions | | | | |
| mean $\Psi_{leaf}$ (MPa) | -0.9 | -0.1 | -1.0 | -0.1 |
| mean TDR (%) | 7.0 | 25.5 | 6.7 | 19.2 |
| Net photosynthesis | | | | |
| $\mu$mol $m^{-2}d^{-1}$ (x $10^4$) | 3.0 | 3.0 | 0.7 | 10.1 |
| $\mu$mol $g^{-1}d^{-1}$ | 358.0 | 508.7 | 109.4 | 872.6 |
| Dark respiration | | | | |
| $\mu$mol $m^{-2}d^{-1}$ (x $10^4$) | 1.3 | 2.0 | 0.8 | 2.1 |
| $\mu$mol $g^{-1}d^{-1}$ | 160.2 | 347.4 | 121.7 | 186.2 |
| Carbon gain | | | | |
| $\mu$mol $g^{-1}d^{-1}$ | 197.7 | 161.3 | -12.3 | 686.3 |
| Transpiration | | | | |
| g $m^{-2}d^{-1}$ | 111.3 | 210.9 | 64.9 | 818.8 |
| g $g_{plant}^{-1}d^{-1}$ | 1.0 | 2.5 | 0.3 | 4.1 |

## Discussion

The results show that mesic conditions do not increase the growth of tulip poplar seedlings under low light levels, and also that higher light levels only slightly increase plant growth at low water conditions. These results fall short of supporting the intuitively convincing trade-off between shade and drought tolerance suggested by Smith and

Huston (1989). To understand the discrepancy between these specific results and the general prediction of the trade-off model, I examine the effects of a reduction in water availability on plant physiology and growth, and discuss how these effects could potentially be compensated by an increase in light availability.

The relative growth rate of a plant (g $g^{-1}d^{-1}$) depends on the whole plant carbon balance, which is the result of photosynthetic inputs, respiratory losses, exudatory processes and volatile losses (Lambers and Poorter, 1992). If the exudatory processes and volatile losses are neglected, we can then express plant growth as a function of the photosynthetic inputs: whole-plant photosynthetic rate, $p$ (μmol C $m^{-2}d^{-1}$) multiplied by the leaf area ratio, *LAR* (leaf area/total biomass, $m^2g^{-1}$), minus the whole plant respiration rate, $r$ (μmol C $g^{-1}d^{-1}$).

Summarizing, the physiological assumptions behind the trade-off model are that at dry conditions whole plant photosynthesis decreases relative to whole plant respiration due to: *1)* a reduction in leaf area ratio and shoot/root ratio, and *2)* prolonged stomatal closure reducing the period of photosynthetic activity. It is expected that by enhancing the photosynthetic rate during periods of activity, higher light levels could compensate for the resulting potential decrease in net carbon gain under dry conditions. A specific prediction of the trade-off model between shade and drought tolerance is that the whole plant light compensation point should increase under dry conditions.

The results do not support the hypothesis that the shoot/root ratio decreases under drier conditions. However, it is the leaf area ratio rather than the shoot/root ratio that really defines biomass production of a woody plant. Indeed, under dry conditions, the leaf

area ratio was lower. This was not a consequence of a decrease in biomass allocated to leaves, but rather of a reduction in the specific leaf area (leaf area/leaf weight). Such reductions in leaf area ratio at dry conditions have been frequently reported (e.g. Kozlowski et al., 1991).

The recorded xylem sap flow patterns confirm the expectation that plants under dry conditions transpire for shorter periods of time (which is an indication of a reduction in stomata conductance). If the rest of the factors in the growth equation do not change, the resulting drought related reduction in carbon fixation (by a reduction in *LAR* and/or photosynthetic rate, *p*) should lead to a growth reduction. However, under dry conditions the respiration rates also tend to decrease. The measurements of whole shoot dark respiration rates were consistently lower for plants under dry conditions. Thus, both the gain and the loss components of the growth equation decrease under dry conditions. Interestingly, the results show that the shoot light compensation point decreased under drier conditions. Since there were no changes in shoot/root ratio with decreasing soil water availability, and the root respiration rates also tend to decrease at drier conditions (Nicolas et al., 1985) then we may assume that the whole plant light compensation point also decreases under drier conditions. Thus, contrary to the predictions of Smith and Huston (1989) dry plants need less light to maintain a positive net carbon balance than moister plants. The low respiration losses of dry plants are a likely explanation for this pattern. The reduction of dark respiration under dry conditions is consistent with the results of several other studies (Bunce and Miller, 1976; Dougherty and Hinckley, 1981; Kramer, 1983; Lambers, 1985; Amthor, 1990; Mulkey et al., 1993). There have been

some reports of increases in dark respiration rates in drier conditions, but the increases have been transitory. For example, Brix (1962) found that under increasing water stress leaf dark respiration rates of loblolly pine seedlings initially decreased, but then significantly peaked followed by an ultimate decline.

A main assumption of the trade-off model is that an increase in light availability under dry conditions can increase the daily net photosynthetic inputs. My results, and those of numerous other studies, show that at high light levels the leaf area ratio tends to decrease (i.e. Loach, 1970). Therefore a compensatory effect of light on carbon fixation would have to be expected from an increase in the photosynthetic rate. In fact, under well watered conditions, the estimates of daily net photosynthetic rate were higher at high light conditions. But this is not the case when plants are exposed to high light levels and dry conditions simultaneously. Several studies have shown that plants under high light conditions and water stress show a more rapid reduction in leaf net photosynthesis (Gamon and Pearcy, 1990; Kolb et al., 1990; Abrams et al., 1992) or are more predisposed to photo-inhibition (Gauhl, 1979; Björkman and Powles, 1984; Ludlow and Björkman, 1984) than plants in the shade. Similar effects of low water on net photosynthesis have been reported for sun versus shade leaves (Ogren and Oquist, 1985).

The estimates for the whole shoot indicate that plants under dry conditions and high light have lower daily photosynthetic rates than plants under low light conditions (both per units of leaf area or biomass). Thus, in this experiment, higher light levels did not compensate for the shorter period the stomata were opened. It is interesting to realize that this happens despite the fact that plants at high light open the stomata later in the day,

concentrating the photosynthetic activity in periods of higher photosynthetically active radiation. Note that the estimates of carbon gain at high light and dry conditions were actually negative during those four days. This suggests that the small increase in growth found at higher light levels under dry conditions was achieved at the beginning of the experiment before the soil water content dropped to low levels.

The results also show that under low light conditions (1 and 5% of ambient) plant growth does not significantly benefit from an enhancement in soil moisture. As the xylem sap flow patterns show, at low light plants transpired for approximately the same period of time under low and high soil water conditions, which is an indication of the period the stomata are open. Also the estimations of daily net photosynthesis ($\mu mol\ m^{-2}d^{-1}$) were quite similar for both soil water conditions. If the daily net photosynthetic rate is expressed in units of shoot biomass ($\mu mol\ g^{-1}d^{-1}$), then the plant under high soil water conditions had a higher photosynthetic rate. However, since under high soil water conditions the respiration rates ($\mu mol\ g^{-1}d^{-1}$) were also higher, the carbon gain (photosynthesis minus respiration) of plants at low and high soil water conditions was very similar.

These results indicate a problem with the trade-off model for shade and drought tolerance, namely the implicit assumption that light and water conditions of a plant vary independently. In reality, an increase in light will usually lead to an increase in air temperature and leaf temperature. In this experiment, for instance, the shade-house with 17% of ambient light was an average $0.6^0C$ warmer than the shadehouses with 5% and 12%, and the shade house with 27% of light was $1^0C$ warmer than the ones at 5% and

12%. An increase in air temperature at higher light conditions will tend to increase the vapor pressure deficit, which increases the transpiration demands. Therefore, water-stress will tend to increase with light, and vice-versa, shading can enhance the plant water relations under dry conditions. Indeed, in arid ecosystems the distribution of small, shallowly rooted plants is frequently associated with the shade of taller plants (Callaway, 1995), and there is strong evidence that in a wide range of plant communities, shade of these so-called nurse plants enhances the growth and survival of smaller plants indeed by improvement of their plant-water relations (Part 2 of this thesis).

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# Part 4

## Drought and Shade Effects on Tree Seedling Establishment in a Throughfall Displacement Experiment

# Introduction

The accumulation of greenhouse gases in the atmosphere is expected to increase average global temperatures and alter regional patterns of precipitation. Specifically, the conditions at the middle and high latitudes are expected to become warmer and, as a result of elevated evapotranspiration, potentially drier as well. As a consequence, the productivity, distribution, and species composition of plant communities are expected to change substantially (Solomon 1986; Pastor and Post, 1988). The deciduous forests of the southeastern United States could be particularly vulnerable to the precipitation changes, because evapotranspiration demand is already high and predicted to increase as temperatures rise.

Our ability to understand and predict the long term effects of environmental changes of that magnitude is very limited. One of the primary reasons for this is that we still know relatively little about the combined effects of different environmental factors on plant physiology and growth (Osmond et a., 1987; Chapin et al., 1987; and reviews in Mooney et al., 1991). This is a major problem, as the levels of various resources usually change simultaneously in nature. Global atmospheric change, for instance, could affect plant growth through enhanced $CO_2$ levels, but also through increases in temperature, altered availability of water, and probably nutrients (Melillo et al., 1990). The effect of a change in these factors on plant productivity, and therefore on the density of plant canopy, will probably change the availability of light for the understory.

Smith and Huston (1989) hypothesized that the response of plants to the combined effects of light and water is characterized by a trade-off between drought and shade tolerance. Based on a set of physiological constraints, Smith and Huston (1989) predicted that at drier conditions plants should become less shade tolerant, and therefore grow and survive better at higher light conditions. Similarly, plants would become more sensitive to dry conditions when exposed to low levels of light. The authors used this hypothetical trade-off model to predict the growth and survival of different plant functional types along gradients of light and water availability. In particular, they predicted that the most shade tolerant species should be the most sensitive to drought effects. This implies that the predicted increase in drought in the deciduous forests of the southeastern United States should be expected to affect especially the shade tolerant species.

The Throughfall Displacement Experiment (TDE) is a large-scale field experiment designed to study the physiological and ecological effects of drought that could result from global warming. The long-term effects on species composition and abundance will strongly depend on the susceptibility of seedlings to drought because seedling survival is usually a critical step in the regeneration of plant populations. In order to test the predictions of the trade-off model of shade versus drought tolerance, I have followed the patterns of growth and survival of tree seedlings along the natural gradients of light and experimental gradients of soil water availability present in the Throughfall Displacement Experiment. I chose three common species of the eastern North American deciduous forest: *Liriodendron tulipifera* (tulip poplar), *Quercus alba* (white oak), and *Acer saccharum* (sugar maple). Often these species are considered to

represent a gradient of shade tolerance, from intolerant (tulip poplar) to very tolerant (sugar maple) (Baker, 1949; Fowells, 1965; Hicks and Chabot, 1985). Distributional patterns along natural gradients of soil water availability, as well as descriptions of physiological responses to water stress, indicate that these three species also represent a gradient of drought tolerance. Tulip poplar is a fast growing species that frequently colonizes new open gaps (Orwig and Abrams, 1994), and occupies mesic sites (Day and Monk, 1974) which in part could result from its sensitivity to dry conditions (Roberts et al., 1979; Chason and Huston, 1990). Sugar maple is a slow growing species that usually dominates old-growth stands (Clebsch and Busing, 1989), and although it tends to be more abundant in moist sites, it can also invade the understory of drier uplands (Adams and Anderson, 1980). White oak is usually considered more drought tolerant than sugar maple (Abrams, 1990).

## Methods

### *Study site*

The Throughfall Displacement Experiment (TDE) is located on a south-east facing slope at the top of the Walker Branch Watershed (35° 58' and 84°17'W) near Oak Ridge, TN, USA. The Walker Branch Watershed has been intensively studied over the past 30 years (Johnson and Van Hook, 1989). The soils are primarily Paleudults, infertile and highly permeable (Garten, 1993). The vegetation composition is typical of an upland oak forest in East Tennessee (Hutchinson et al., 1986; Hanson et al., 1995).

Three treatment plots (80x80 m) subdivide the experimental site. In the dry plot, throughfall precipitation is intercepted over 33% of the ground area by transparent plastic troughs suspended from 1.5 to 3 m above the forest floor. The water is then transferred by gravity flow across an ambient plot and distributed onto the wet treatment plot (Fig. 1). The experiment was fully installed in August 1993 and has been under way since (for a complete description see Hanson et al., 1995).

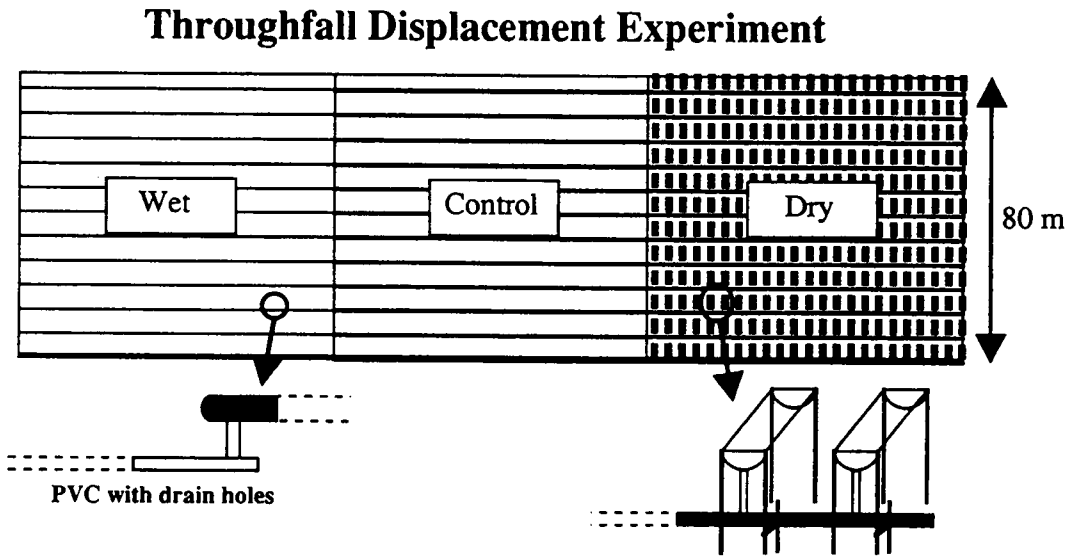


Figure 1: Schematic diagram of the experimental design in the Throughfall Displacement Experiment. It shows the collection troughs and distribution pipe network (after Hanson et al., 1995).

***Natural seedling distribution***

Naturally established seedlings of tulip poplar, white oak and sugar maple were counted in the spring (May) and summer (August) of 1993 before the throughfall experiment was

initiated. All plants smaller than 15 cm were counted in 216 plots of $1m^2$ distributed uniformly along three topographic levels (top, middle, bottom).

***Experimental plantings***

One-year old, bare-rooted seedlings of tulip poplar (n=100), sugar maple (n=100), and white oak (n=200) were obtained from Tennessee (Hillis Nursery Company, Inc., McMinnville, TN) and planted during late autumn and winter of 1993. Twice as many white oaks were planted because its establishment is usually very difficult (P. Hanson, personal communication). Groups of seedlings were planted in 49 plots of approximately $4m^2$. Each seedling plot contained two seedlings of tulip poplar, two of sugar maple, and four seedlings of white oak. Since soil water in the area tends to decrease markedly from the lower slope towards the ridge, the seedling plots were distributed on three slope levels (upper, intermediate, and bottom) in each of the three treatment plots (dry, ambient and wet). These 'seedling plots' covered roughly the same locations where naturally established seedlings had been sampled earlier that year.

***Soil water measurements***

Volumetric soil water content ($\theta_v$) was measured using a time domain reflectometer (TDR) (Trase system 1, model 6050X1, Soilmoisture Equipment Co., Santa Barbara, CA) and a pair of 35-cm waveguides permanently inserted in the intersections of a grid system that subdivides the study site into (8x8 m)- grid subplots. A total of 310 sampling locations across the experimental site are monitored approximately twice a

month. To estimate the soil water conditions experienced by each planted seedling, an average TDR value was calculated using the measurements from the four closest grid intersections. This TDR mean was weighted by the inverse of the distance from the seedling to each grid intersection, and then corrected for the coarse fraction content. The coarse fraction had been sampled in each grid intersection (Hanson et al., 1995), so I calculated an average for each (8x8 m)- grid subplot. The corrected TDR mean was then:

$$CTDR = \frac{TDR_w}{1 - CF} \qquad (1)$$

where:

CTDR = corrected TDR mean

$TDR_w$ = weighted TDR mean

CF = mean coarse fraction (in decimals)

To convert the soil water content estimates to matric potential I used the following moisture retention curve ($r^2$=0.86; Hanson et al., 1995):

$$\Psi_s = -45.57 * 2.29^{(-0.38 * CTDR)} \qquad (2)$$

To test how well the readings on the grid intersections were describing the soil water environment of the experimental seedlings, I simultaneously sampled two locations near the center of each seedling plot on a day when all intersections on the grid system were sampled. Since the correlation between the two data sets was very high (linear regression $r^2$= 0.9 ), I used the bimonthly TDR readings taken on the grid intersections for analysis of seasonal variability (Hanson *et al.* 1995). In summary, every sampling date a TDR

mean was estimated for each seedling plot, transformed to a soil water potential value, and then included in a seasonal average (February to September) for each growing season.

### *Light measurements*

In 1994, the fraction of diffuse light reaching every seedling was estimated with a light sensor during homogeneously overcast conditions (LAI-2000, LI-COR Inc., Lincoln, NE). Readings were simultaneously taken at the center of a nearby open area (approximately 0.5 km) and at the top of each seedling. In this study diffuse light transmittance was chosen as an indicator of the light conditions that could be related with growth patterns on a large number of seedlings. Transmittances of direct and diffuse radiation are highly correlated (Ross, 1976; Canham, et al., 1990).

### *Plant growth and survival*

Non-destructive measurements of leaf area were taken three times during the spring and summer of 1994 (April, June, and August) and twice in 1995 (May, and July). The width of each leaf was measured at the widest section. Leaf area was estimated using a linear regression between the logarithms of leaf area and width based on a subsample of leaves for which the area was measured on an area meter (LI3100, LI-COR Inc., Lincoln, NE). All of the established relationships had very little scatter:

| | Equation | n | $r^2$ |
|---|---|---|---|
| tulip poplar | log(leaf area) = 1.93 log(width) - 0.24 | 111 | 0.99 |
| white oak | log(leaf area) = 1.63 log(width) + 0.21 | 125 | 0.95 |
| sugar maple | log(leaf area) = 1.73 log(width) - 0.14 | 140 | 0.93 |

Stem diameter and height were measured during the last sampling session of each year. Stem diameter was measured with calipers at 5 cm from the stem base. Stem height was measured from soil level to the base of the apical bud.

Mortality was recorded throughout the season, in September of each year, and checked once again in the next growing season. A plant was considered dead when there was no green tissue left. Mortality related to mechanical damage (broken stems) was not included in the analysis of drought-related mortality.

***Statistical analysis***

Light and soil water potential were analyzed as a factorial design with topographic level (top, middle, and bottom) and experimental treatment (dry, control, and wet) as main factors. Thus the experimental design had nine 'treatment' combinations. Seedling plots were considered as replicates of each treatment combination. General contrasts were used for testing differences between levels of each factor. The limitations imposed by the pseudoreplication of this field experiment were discussed by Hanson et al. (1995).

For each species, seedling mortality was related to light and soil water using logistic regression. Deviance differences were compared against a $\chi^2$ distribution.

The relationship between growth, light transmittance, and seasonal soil water potential was described using stepwise regressions and Pearson correlations. Scatter plots of growth parameters against light suggest an optimum response to light. The pattern is especially clear for the upper boundary of the cloud of points. Maximum growth seems reduced both at deep shade and at high light (i.e. Fig 3 in Result section). To test the significance of the left and the right side of a triangular envelope marking the upper limit of the cloud of data points I used two approaches.

I first used a permutation approach. To delimit the cloud of points I visually chose three points on the x-axis (light transmittance): low light with low growth, intermediate light with maximum growth, and high light with low growth. These three points were used to estimate two lines enclosing the data set on both right and left sides. Usually one or two points were left beyond these boundaries. Then, by randomizing the pairwise linkage of x (i.e. light transmittance) and y (i.e. leaf area) values, a total (T) of 1000 permuted versions of a scatter-plot were produced. For each permuted set the number of points above the positively sloped line, representing the left side of the envelope, and the number of points above the declining right side of the envelope are scored. The number ($n_l$) of permuted sets in which the number of points beyond the left side of the envelope is smaller than or equal to the number of points above this line in the original data-set indicates the significance ($p_l$) of the left side of the envelope as a delimiter of the cloud of points:

$$p_l = \frac{n_l+1}{T+1} \qquad (3)$$

Similarly, the significance of the right hand side of the envelope ($p_r$) follows from the number of permuted sets ($n_r$) which the number of points above that line is less or equal than in the original data-set.

The second method concentrated attention on the maximum response. The light gradient was subdivided into 2%-increment light intervals. The maximum growth in each interval was then plotted against light. This method reduced most of the variability of the original data set. Then I visually chose the possible inflexion point, which was the maximum growth at intermediate light levels. Maximum points that were too high relative to the rest of the data set were considered as potential outliers and not included in the analysis. Two sets of linear regression were fitted: one among the points lower than the inflexion point, and one among the points higher than the inflexion point.

## Results

### *Light and soil water in the TDE Site*

The 1994 growing season was very wet. The upper slope of the dry experimental plot was the driest area. There, the average seasonal (February-September) soil water potential reached -0.43 MPa (Table 1), but some seedling plots reached even -0.7 Mpa. There was a significant interaction between topographic position and experimental plot (Table 2).In the dry plot, the seasonal soil water potential of the upper section was significantly lower than the ones for the middle and down slope positions (Table 3). Also, the upper and middle positions of the dry plot were significantly drier than the equivalent topographic

positions in the control and wet treatment. However, the bottom slope was not statistically different in any of the experimental plots (Table 3). The seasonal average soil water potentials in the control and wet experimental plots did not drop below -0.03 MPa (Table 1), and there were no significant differences between both plots at any topographic position.

Table 1. Seasonal soil water potential (MPa) during both growing seasons in the three experimental plots (wet, control, dry) at three topographical positions (top, middle, bottom). Data are means and stand errors using the estimates for each seedling plot.

| | 1994 | | | 1995 | | |
|---|---|---|---|---|---|---|
| | Wet | Control | Dry | Wet | Control | Dry |
| Top | -.018 ± .002 | -.035 ± .019 | -.435 ± .080 | -.375 ± .027 | -.520 ± .036 | -.663 ± .015 |
| Middle | -.033 ± .008 | -.024 ± .004 | -.205 ± .050 | -.456 ± .035 | -.478 ± .029 | -.624 ± .033 |
| Bottom | -.013 ± .002 | -.038 ± .026 | -.100 ± .055 | -.343 ± .028 | -.449 ± .041 | -.440 ± .095 |

Table 2. Results of two-way ANOVAs of seasonal soil water potential and light transmittance on the Throughfall Displacement Experiment in 1994 and 1995. Data are p values ($\leq$ ) of main effects and their interaction.

| | Topographic | Experimental | Interaction |
|---|---|---|---|
| Soil water 1994 | 0.001 | 0.001 | 0.001 |
| Soil water 1995 | 0.001 | 0.001 | 0.003 |
| Light | 0.002 | 0.09 | 0.63 |

Table 3. Topographic and experimental effects on seasonal soil water potential. Topographic levels are: T (top), M (middle), B (bottom). Experimental levels are: D (dry), C (control), W (wet). Data are p-values (≤ ) associated with the null hypothesis presented in the column heading.

Topographic effects

| | 1994 | | | 1995 | | |
|---|---|---|---|---|---|---|
| | T = M | T = B | M = B | T = M | T = B | M = B |
| wet | .99 | 1 | .99 | .38 | .95 | .10 |
| control | .99 | 1 | .99 | .89 | .53 | .96 |
| dry | <.0001 | <.0001 | .22 | .91 | <.0001 | 0.001 |

Experimental effects

| | 1994 | | | 1995 | | |
|---|---|---|---|---|---|---|
| | D = C | D = W | C = W | D = C | D = W | C = W |
| top | <.0001 | <.0001 | .99 | .018 | <.0001 | .01 |
| middle | .002 | .003 | .99 | .015 | .003 | .98 |
| bottom | .58 | .27 | .98 | .99 | .21 | .14 |

The 1995 season was much drier than the previous one (Table 1). In all the treatment combinations the average seasonal soil water potential dropped lower than -0.3 MPa, and reached -0.66 MPa in the upper slope of the dry plot (Table 1). But some spots were as dry as -1.5 MPa. Once again there was a significant interaction between the topographic and experimental factors (Table 2). In the dry plot, the upper and middle slope were not statistically different, but both were drier than the bottom slope (Table 3). In the control and wet experimental plots there were no differences between topographic positions

(Table 3). In general, the topographic gradient of soil water was stronger in the dry plot than in the other two experimental plots during both years, while the experimental gradient of soil water was stronger in the upper section of the slope (Table 1 and 3). Both seasons indicate that the upper slope of the dry plot is the driest area, followed by the intermediate position in the same plot and the top of the control area. Surprisingly, the wettest spots are located not only in the bottom section of the wet experimental treatment, but also on the upper slope of the wet plot.

Light transmittance was significantly lower on the upper portion of the slope (Table 4 and 5), and also tended to be lower in the dry experimental plot although the difference was not statistically significant (Table 4 and 5).

Table 4. Light transmittance (%) in the study site. Data are means and standard errors using the readings of all the planted seedlings growing in each experimental and topographic combination.

| | Wet | Control | Dry |
|---|---|---|---|
| Top | 20.4 ± 0.51 | 18.4 ± 0.73 | 16.9 ± 0.83 |
| Middle | 34.9 ± 1.92 | 31.4 ± 2.08 | 25.8 ± 2.59 |
| Bottom | 31.1 ± 2.61 | 32.2 ± 3.99 | 23.2 ± 2.58 |

Table 5. Topographic and experimental effects on light transmittance. Topographic levels are: T (top), M (middle), B (bottom). Experimental levels are: D (dry), C (control), W (wet). See Table 2 for main effects and interactions. Data are p-values (≤) associated with the null hypothesis indicated in the column heading.

| Topographic | | | Experimental | | |
|---|---|---|---|---|---|
| T = M | T = B | M = B | D = C | D = W | C = W |
| 0.006 | 0.01 | 0.93 | 0.16 | 0.15 | 0.99 |

In the TDE site, light and soil water availability tended to be positively correlated (Pearson r=0.24, p<0.001). This could be the result of two small natural gaps located in the intermediate section of the wet plot and in the bottom part of the control plot. Also the accumulation of dust, algae or leaves on the throughfall collectors might contribute to a reduction in light transmittance in the dry plot.

***Phenology of leaf area production***

Sugar maple produced its leaves earlier in spring than the other species (Fig 2). In April 1994, sugar maple had already produced 80% of the leaf area reached in July, while tulip poplar had only produced 16% of the July leaf area by that time, and white oak had expanded only 40% of the final leaf area in April.

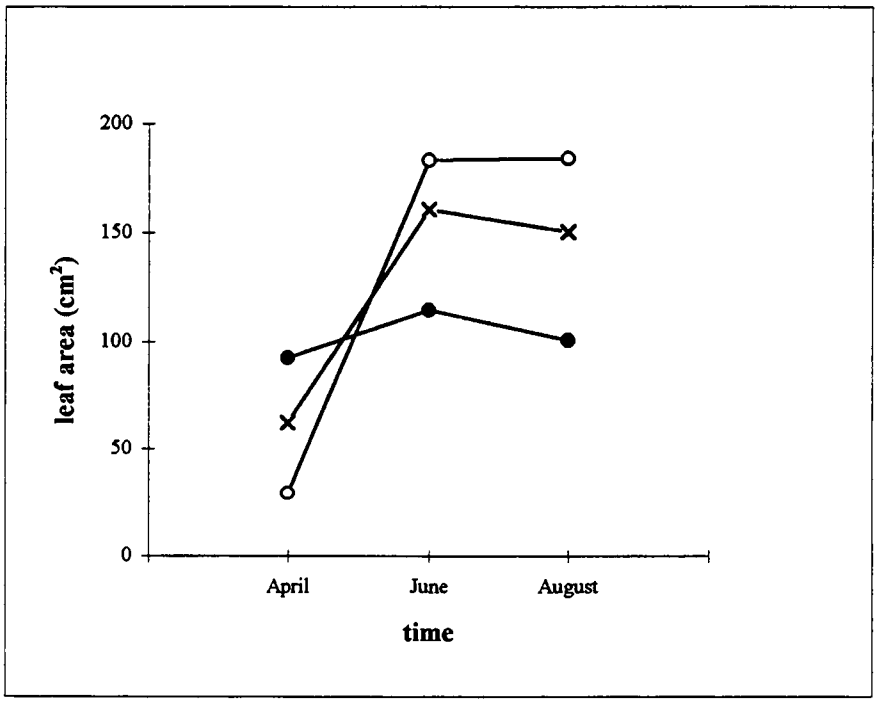


Figure 2. Phenology of leaf area production during the 1994 growing season (○ ) tulip poplar, (● ) sugar maple, (x) white oak. Standard errors are too small to be visible.

By early June, leaf area production had already reached the seasonal maximum for all species. On average, tulip poplar produced the largest leaf area, and sugar maple the smallest (Fig. 2). Roughly the same phenological pattern was observed in 1995.

### *Seedling growth and mortality*

#### *a) Tulip poplar*

Leaf area reached a maximum at intermediate light levels. In August 1994, leaf area peaked around 27% of light transmittance (Fig. 3).

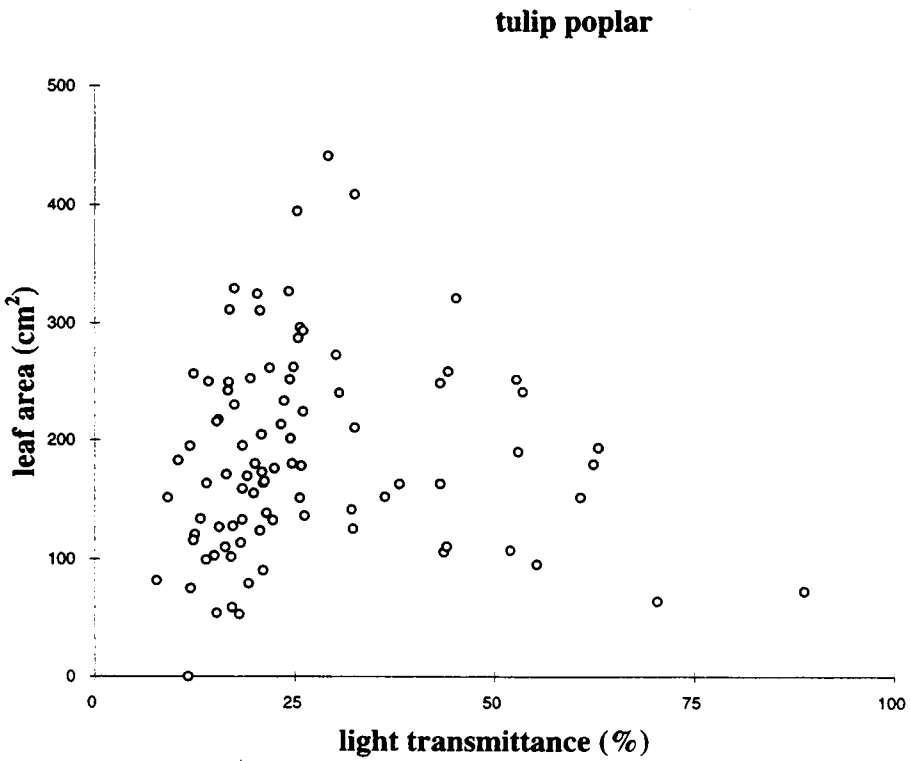


Figure 3. Leaf area ($cm^2$) of tulip poplar seedlings at increasing light transmittance (%) in August 1994.

Below 27% of light, leaf area increased with increasing light levels (Pearson r=0.45, p=0.0002). The positively-sloped envelope line delimiting the left part of the cloud of data points is also significant. In the original data set there are no data points beyond this line. In contrast, 998 of the 1000 random permutations of the values on both axes (leaf area and light) had one or more points above this line. Therefore, the pattern in which no values were observed above this line, as in the original data set, is very unlikely to be due to chance (p=0.002, Table 6). Also, the linear regression through the maximum growth values had a significant positive slope (p=0.01, Table 6). Interestingly, at light levels higher than 27%, leaf area tended to decrease with increasing light (Pearson r=-0.43, p=0.02). The probability of observing only one point outside the right curve, as in the original data set, is again very low (p=0.02, Table 6). In this case, the linear regression through the maximum points had a negative slope (p=0.003, Table 6) This optimum effect of light on leaf area production was already present in June 1994 (Table 6). In May 1995 leaf area also tended to increase with light availability in the more shady places (below 27% of light transmittance) and decrease at higher light (Table 6). Again, in July 1995, leaf area was positively correlated with light below 27% of light transmittance but the decrease at higher light levels was not significant (Table 6).

Stem diameter of tulip poplar also decreased at light transmittances higher than 27% during 1994 and 1995 (Table 6). Stem height was not clearly related to light. In both years stem growth (height and diameter) was positively correlated with leaf area production (Pearson, $p<0.001$).

Table 6. The optimum response of tulip poplar growth (y) to light transmittance (x). Data are results of three methods: permutations, linear regression through the maxima, and Pearson correlations. Below 27% of light transmittance growth increases with light (positive slopes and correlation), but above 27% growth decreases with light.

| | permutations | | linear regression | | | Pearson | |
|---|---|---|---|---|---|---|---|
| leaf area | boundary line | p≤ | y = ax + b | $r^2$ | p≤ | r | p≤ |
| June, 1994 | 54.46 x - 326.0 | .02 | 9.36 x + 113.54 | .58 | .01 | .41 | .0006 |
| | - 6.59 x + 599.0 | .01 | - 4.51 x + 422.81 | .66 | .0002 | -.55 | .02 |
| August, 1994 | 14.9 x + 73.85 | .002 | 10.6 x + 89.4 | .68 | .001 | .45 | .0002 |
| | - 7.19 x + 655.85 | .02 | - 4.79 x + 466.3 | .54 | .003 | -.43 | .02 |
| May, 1995 | 17.65 x + 22.84 | .004 | 15.32 x + 9.32 | .88 | .0002 | .30 | .03 |
| | - 5.43 x + 645.67 | .09 | - 3.89 x + 432.04 | .32 | 0.052 | -.21 | .28 |
| July, 1995 | not significant | | 15.6 x + 170.83 | .52 | .008 | .35 | .008 |
| | not significant | | - 5.09 x + 619.53 | .21 | .15 | -.20 | .30 |
| stem diameter | | | | | | | |
| August, 1994 | not significant | | 0.24 x + 1.08 | .5 | .18 | | |
| | - 0.04 x + 6.5 | .006 | - 0.02 x + 4.72 | .5 | .001 | -.33 | .08 |
| July, 1995 | 0 .11 x + 2.5 | .16 | 0.03 x - 0.19 | .44 | .03 | | |
| | - 0.05 x + 6.73 | .009 | - 0.01x + 1.05 | .3 | .06 | -.28 | .16 |

Soil water potential had no significant effect on any of the growth variables studied. In 1995, stem elongation and diameter tended to be negatively correlated with decreasing soil water potential but these relationships were not significant.

Mortality during 1994 was clearly related to the topographic and experimental positions (Table 7). Thirty percent of the tulip poplar seedlings planted in the dry plot died, especially the ones growing in the top row. In contrast, no seedlings died in the wet plot, and only 6% of the ones in the control plot died. Mortality was significantly correlated with lower soil water potentials (Table 8). During the dry summer of 1995, mortality was much higher. It reached 66% in the dry plot, 53% in the control area, and 41% in the wet plot (Table 7).

Table 7. Mortality of tulip poplar seedlings during the two growing seasons in the three experimental plots: wet (W), control (C), and dry (D), at three topographical positions. Data are the number of dead individuals at the end of a season / number of alive individuals at the beginning of that season.

| | initial n | | | 1994 | | | 1995 | | |
|---|---|---|---|---|---|---|---|---|---|
| | W | C | D | W | C | D | W | C | D |
| Top | 11 | 10 | 14 | 0 | 0.1 | 0.43 | 0.36 | 0.89 | 0.63 |
| Middle | 10 | 12 | 8 | 0 | 0 | 0.25 | 0.30 | 0.42 | 0.67 |
| Bottom | 8 | 10 | 8 | 0 | 0.1 | 0.1 | 0.63 | 0.33 | 0.71 |

In 1994, 45% of the dead seedlings had been reported with some herbivore damage (mainly by caterpillars). This fraction decreased to 24% during 1995. In both years, most of the affected plants (80%) had less than 10% of the total leaf area damaged. Herbivory among dead tulip poplars was scattered along topographic and experimental combinations.

Table 8. Seedling mortality as a function of light transmittance and soil water potential. Data are results of logistic regressions. The subscripts in the column of deviance difference identify the models that are being compared by using the first letter of the variables included in the model (a: intercept, l: light, w: water). Deviance differences were compared against $\chi^2$ distributions. Estimated coefficients can be found in Appendix 3.

| species/year | model | deviance | deviance difference | DF | tested | p≤ |
|---|---|---|---|---|---|---|
| tulip poplar 1994 | $m = a + b$ (light) | 64.24 | $d_{al}-d_{alw}$ =9.25 | 1 | water | 0.002 |
| | $m = a + c$ ($\psi_{soil}$) | 56.19 | $d_{aw}-d_{alw}$=1.2 | 1 | light | 0.273 |
| | $m = a + b$ (light) + c ($\psi_{soil}$) | 54.99 | | | | |
| sugar maple 1994 | $m = a + b$ (light) | 25.79 | $d_{al}-d_{alw}$ =1.76 | 1 | water | 0.18 |
| | $m = a + c$ ($\psi_{soil}$) | 29.10 | $d_{aw}-d_{alw}$=5.07 | 1 | light | 0.024 |
| | $m = a + b$ (light) + c ($\psi_{soil}$) | 24.03 | | | | |
| white oak 1995 | $m = a + b$ (light) | 92.42 | $d_{al}-d_{alw}$ =0.99 | 1 | water | 0.319 |
| | $m = a + c$ ($\psi_{soil}$) | 99.03 | $d_{aw}-d_{alw}$=7.6 | 1 | light | 0.005 |
| | $m = a + b$ (light) + c ($\psi_{soil}$) | 91.43 | | | | |

### *b) Sugar maple*

In 1994, growth of sugar maple was significantly reduced at lower soil water potentials. The leaf area produced by August, as well as stem elongation were significantly lower in drier areas (Pearson r= -0.21, p=0.06, and r= -0.25, p=0.02 respectively). Stem diameter also tended to be less at drier spots (Pearson r=-0.18, p=0.09). In 1995, stem elongation and diameter were both depressed at drier conditions (Pearson r=-0.28, p=0.01, and r=-

0.19 p=0.1 respectively). A stepwise regression was run for all above growth variables against light and soil water potential. Light was not significant in any of the analyses, while the coefficient for soil water potential was highly significant ($p<0.05$) for all mentioned growth variables except stem diameter in 1994. No significant relationship was found between leaf area and soil water in 1995.

The scatter plots of light against leaf area in 1994 indicated a possible optimum around 20% light transmittance (Fig. 4).

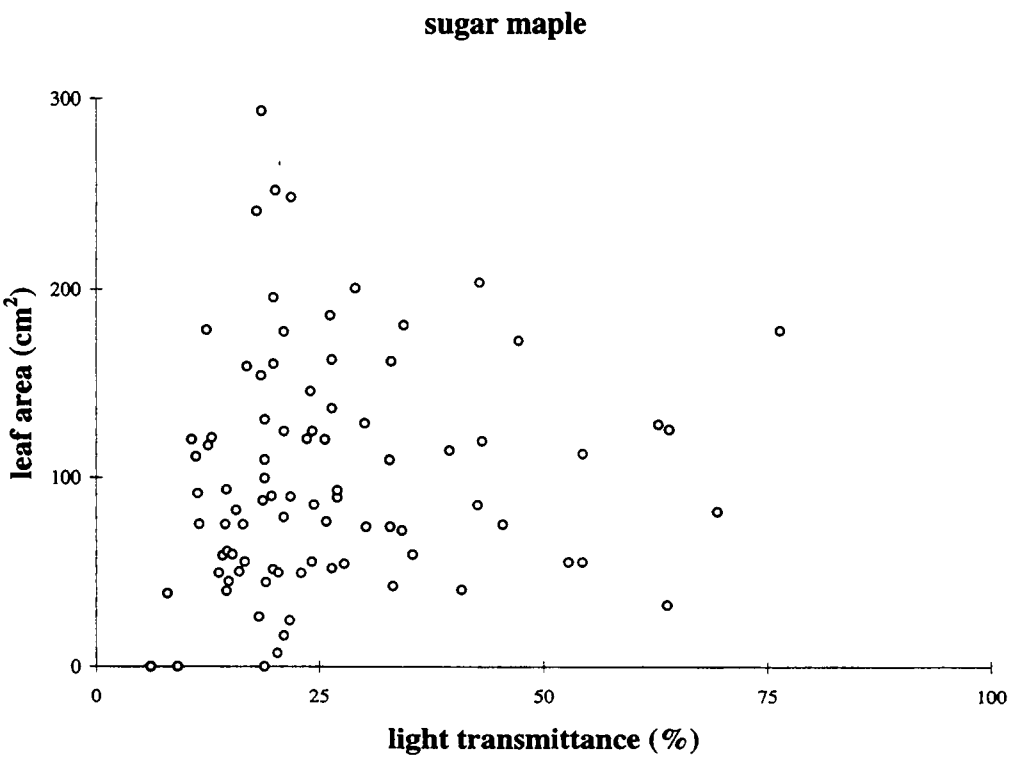


Figure 4. Leaf area ($cm^2$) of sugar maple seedlings at increasing light transmittance (%) in August 1994.

Below this point leaf area tends to increase with light (Pearson r=0.29, p=0.09). The permutation analysis indicated that the probability of observing zero values outside the left hand side of the depicted envelope, as in the original data, is very low (p=0.05, Table 9), and the linear regression through the maxima points had also a significant positive slope (p=0.007, Table 9). The right hand side of the scatter-plot suggests that leaf area tends to decrease with light. The significance of the right hand side of the delimiting envelope was not very high with the permutation approach (p=0.09), but was more clearly defined with the linear regression through the maxima (p=0.04, Table 9). Stem growth in height and diameter tended to increase below 20% of light transmittance, but only stem height seems to decrease at higher light levels (Table 9). During 1995 no clear patterns were found in relation to light availability. In both years, stem growth in diameter as well as height were highly correlated with leaf area production (Pearson, $p < 0.001$).

Sugar maple mortality during 1994 was only 3.4% and was concentrated in the upper and intermediate slope positions of the dry plot (14% and 12% respectively) (Table 10). The logistic regressions indicated a significantly negative effect of light (p=0.02, Table 8; coef. $b = -0.20 \pm 0.1$ Appendix 3), but this result should be taken cautiously because of the small sample size. Mortality slightly increased to 4.7% during the 1995 growing season (Table 10). By the end of the second growing season, 17% of the seedlings in the dry plot had died compared to only 3% in both the wet and control plots. Mortality was also related with the topographic position. At the end of the second year 14% of the seedlings originally planted in the upper part of the slope had died, compared to only 3% and 4% in the intermediate and bottom slope locations. Herbivore damage

had been observed in 2 of the 7 individuals that died, and it had always affected more than 50% of the total plant leaf area. Both seedlings were located in the top row of the dry treatment.

Table 9. The optimum response of sugar maple growth (y) to light transmittance (x) in August 1994. Data are results of three methods: permutations, linear regression through the maxima, and Pearson correlations. Below 20% of light transmittance growth tends to increase with light (positive slopes and correlation), but above 20% growth decreases with light.

| | permutations | | linear regression | | | Pearson | |
|---|---|---|---|---|---|---|---|
| | boundary lines | p≤ | y = ax + b | $r^2$ | p≤ | r | p≤ |
| leaf area | 22.58 x + 106.45 | .05 | 15.81 x - 82.07 | .79 | .007 | .29 | .09 |
| | - 3.74 x + 367.35 | .09 | - 1.69 x + 219.23 | .22 | .04 | | |
| stem height | not significant | | 1.60 x + 2.64 | .78 | .008 | .28 | .1 |
| | - 0.32 x + 42.5 | .08 | - 0.19 x + 29.65 | .22 | .03 | | |
| stem diameter | not significant | | 0.21 x - 0.34 | .76 | .002 | .26 | .13 |
| | not significant | | - 0.02 x + 3.85 | .22 | .04 | | |

Table 10. Mortality of sugar maple seedlings during the two growing seasons. Data are the number of dead individuals at the end of a season / number of alive individuals at the beginning of that season.

| | initial n | | | 1994 | | | 1995 | | |
|---|---|---|---|---|---|---|---|---|---|
| | W | C | D | W | C | D | W | C | D |
| Top | 12 | 9 | 14 | 0 | 0 | 0.14 | 0.08 | 0.11 | 0.08 |
| Middle | 9 | 12 | 8 | 0 | 0 | 0.12 | 0 | 0 | 0 |
| Bottom | 7 | 9 | 8 | 0 | 0 | 0 | 0 | 0 | 0.12 |

*c) White oak*

White oak has a 'fixed growth' pattern in which the primordia of all the leaves that will expand during a growing season are already present as overwintering buds. Therefore, growth is affected in part by the environmental conditions during the previous growing season. Because of this, only the growth during 1995 was analyzed. There was no clear unimodal response to light as observed for tulip poplar and sugar maple (Fig. 5).

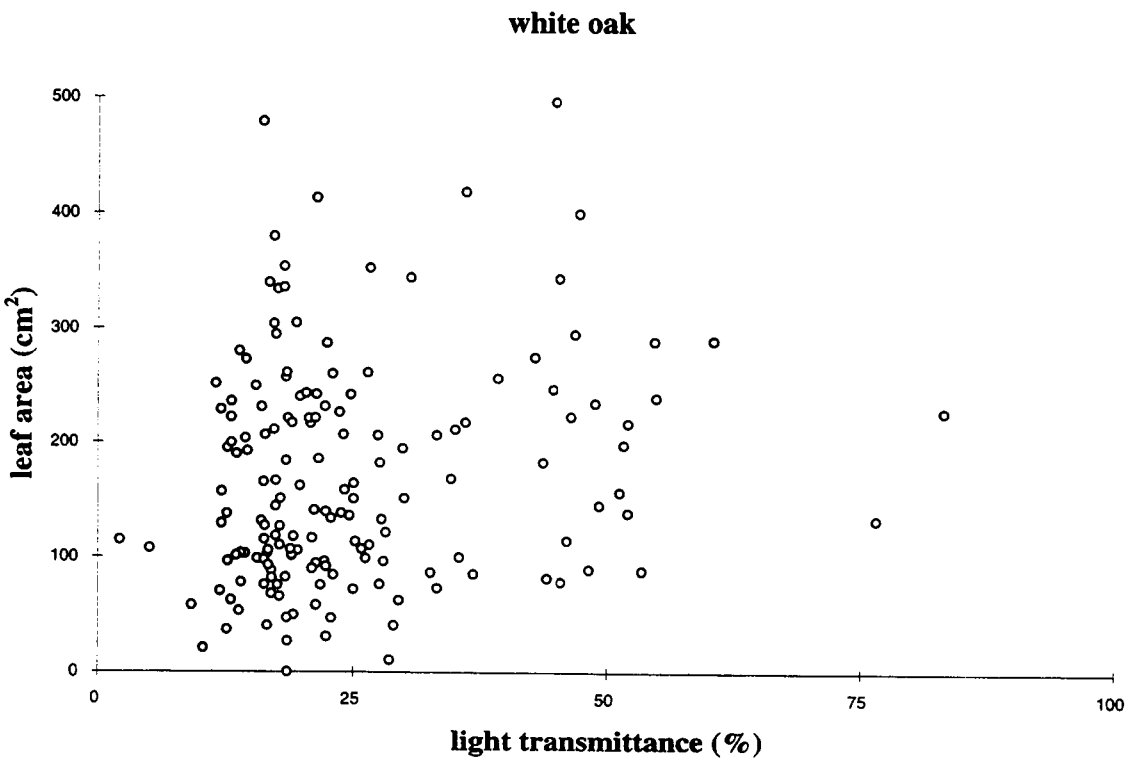


Figure 5. Leaf area ($cm^2$) of white oak seedlings at increasing light transmittance (%) in July 1995.

Leaf area in July was positively correlated with light transmittance (stepwise regression, p=0.006) and with the combined mean soil water potential of both years (stepwise

regression, p=0.0017). Stem height was also positively correlated with light (stepwise regression, p=0.04) and the seasonal soil water potential of 1995 (stepwise regression, p=0.01). Once again, stem and leaf area growth were positively correlated (Pearson, p<0.001).

During 1994 only 1% of the seedlings died. Because of this, it was not possible to statistically relate mortality to soil water potential. However, the spatial pattern suggests that mortality was related to drier conditions. All the dead seedlings in 1994 were in the top slope of the control and dry plots (Table 11). Mortality increased to 9% in 1995. It reached 11% in the dry plot, 13% in the control plot and 2% in the wet plot (Table 11). Once again mortality was concentrated in the top row (15% versus 4% in the bottom row). The logistic regression analysis indicated a significant light effect (Table 8 and Appendix 3).

Table 11. Mortality of white oak seedlings during the two growing seasons. Data are number of dead individuals at the end of a season / number of alive individuals at the beginning of that season.

| | initial n | | | 1994 | | | 1995 | | |
|---|---|---|---|---|---|---|---|---|---|
| | W | C | D | W | C | D | W | C | D |
| Top | 22 | 20 | 26 | 0 | 0.05 | 0.04 | 0 | 0.26 | 0.20 |
| Middle | 19 | 23 | 13 | 0 | 0 | 0 | 0.05 | 0.04 | 0.08 |
| Bottom | 15 | 18 | 16 | 0 | 0 | 0 | 0 | 0.11 | 0 |

At the end of the second year, 65% of the individuals that died had been affected by leaf eaters, mainly caterpillars. The damage tended to be severe: only 9% of the affected plants had less than 10% of the leaf area damaged, while 45% had more than 50% of the leaf area eaten. Herbivore effects were concentrated in the top row of the control and dry treatments.

***Natural patterns***

The 1993 growing season, prior to the initiation of the experiment, was very dry especially during June and July. Seasonal soil water potential dropped l MPa everywhere in the study site. Table 12 shows the natural topograph water, and the patterns of seedling abundance found in spring and sumn

Table 12. Seasonal soil water potential (MPa) and number of seedlings (< 15 cm tall) found in May (M) and August (A) of 1993, before the Throughfall Displacement Experiment was installed. Data for soil water are means and SD.

| | Soil water | Tulip poplar | | Sugar maple | | White oak | |
|---|---|---|---|---|---|---|---|
| | | M | A | M | A | M | A |
| Top | -0.80± 0.02 | 4 | 1 | 1 | 1 | 8 | 5 |
| Middle | -0.71± 0.13 | 16 | 4 | 0 | 0 | 7 | 7 |
| Bottom | -0.52± 0.18 | 90 | 18 | 8 | 4 | 7 | 5 |

Most tulip poplar and sugar maple seedlings were found down the slope while white oaks were more evenly distributed in the study site. Species differed also in the mortality patterns. Mortality reached 79% among tulip poplars, 44% among sugar maples and 23%

among white oaks. Tulip poplars died everywhere in the study site, while dead sugar maples were concentrated down the slope.

## Discussion

### *Growth patterns*

Effects of soil water potential on growth were not very pronounced in this study. In both years, leaf area production and stem growth of tulip poplar were reduced at lower soil water potentials, but the relationships were only significant in sugar maple. Probably this is related to the phenology of these species. Most of the leaf area growth, for example, occurs before early June, when usually water stress is not severe. Lack of soil water effects on growth were also found by Pacala et al. (1994) in their description of light and soil water effects on northern hardwood saplings.

The growth responses to light were more pronounced. During both growing seasons, tulip poplar growth showed a unimodal response to light transmittance. Leaf area production reached an optimum around 27% of light transmittance and declined at higher light levels. It is well known that the leaf area ratio (i.e. leaf area/total biomass) increases as a response to shading and tends to decrease at increasing levels of photosynthetically active radiation (e.g. Kozlowski et al., 1991). Interestingly though, stem diameter also showed the same pattern, which is an indication that plant growth, in general, was favored at intermediate light levels. The negative effect of high light is also consistent with the results of the shade-house experiment (Part three of this thesis). There I found that

biomass accumulation tended to decrease at light levels over 12% of ambient. Although less significantly, the growth of sugar maple seedlings also decreased at high light in the field. In 1994, the maximum leaf area and stem elongation were reached around 20% of light transmittance, and decreased at higher light levels.

The observed decrease of growth of tulip poplar and sugar maple at high light occurred despite relatively high seasonal soil water conditions in 1994. However, this decrease is likely to be related to an increase in water stress. Higher irradiance, as found in forest gaps, is associated with higher air temperatures (Sipe and Bazzaz, 1994), and can be expressed also as a reduction in soil water in the top soil layers (Kozlowski et al., 1991). As a consequence of this, vapor pressure deficit increases, and therefore so do the transpiration demands. Thus, water stress will tend to increase with light availability. Probably, thermal and water stresses tend to be stronger and concentrated during sunflecks when the understory is illuminated by direct radiation penetrating the canopy. Despite their tremendous spatial and temporal variability (Chazdon, 1988), sunflecks represent a large portion of the incoming radiation. In a forest near the TDE site it has been estimated that sunflecks contribute approximately 50% of the total solar radiation during the summer (Hutchinson and Matt, 1977). Carbon fixation during sunfleck periods is also significant. Estimates for sugar maple seedlings in a northern deciduous forest indicate that approximately 35% of the daily carbon gain, during the summer, occurred during sunflecks (Weber et al., 1985). The inherent variability associated with sunflecks imposes difficult sampling problems, especially for large number of plants, because permanent sensors must automatically record light conditions throughout a whole

growing season. In the Throughfall Displacement Experiment I intended to characterize relative differences in light levels among plants using the transmittance of diffuse radiation, which is highly correlated to the transmittance of direct radiation (Ross, 1976; Canham, et al., 1990). Penetration of both forms of radiation depends on stand architecture (height and leaf area), but variations in diffuse light penetration are smaller than direct light transmittance because the former integrates light incident from different angles (Ross, 1976).

Interestingly, the unimodal response to light transmittance was found in tulip poplar and sugar maple, which were the most sensitive species to dry conditions (either in terms of survival, or growth). In contrast, the growth of white oak, the most drought tolerant of the three species, did not show a statistically significant unimodal response to light availability. According to the trade-off hypothesis between shade and drought tolerance (Smith and Huston, 1989), plant growth under dry conditions should increase with light availability. However, the experimental results indicate that this is not the case for tulip poplar and sugar maple seedlings. This is in agreement with the results of several other studies. In early successional communities of deciduous forest in eastern USA, Berkowitz, et al (1995) experimentally showed that surrounding vegetation could strongly inhibit tree seedling growth in productive sites, but had little effect, or even improved it on harsh sites, especially during drought periods. Also, Sipe and Bazzaz (1995) found that tree seedling survival was substantially reduced in large gaps, suggesting a negative effect of high irradiance.

Clearly, the negative response to light at drier conditions will depend on the actual soil water conditions, and on the drought tolerance of the species. In deserts, even very drought tolerant species are known to perform better in the shade of other plants than in the open (Part 2 of this thesis). The range of soil water conditions examined were sufficiently severe to cause effects for the two less drought tolerant species. Under even drier conditions, it may be possible that also white oak growth would decrease at high light conditions.

***Survival patterns***

In this experiment, the effects of low water availability on seedling survival were more dramatic than on growth. Among the three species, tulip poplar was the most sensitive to drought. In 1994, 12% of the tulip poplar seedlings died, compared to only 1% of white oaks, and 3% of sugar maple. The 1994 season was very wet. Seasonal soil water potentials dropped lower than -0.2 MPa only in the upper slope of the dry experimental plot. It was here that mortality was more severe. In the dry experimental plot, 43% of the tulip poplar seedlings growing on the highest part of the slope, and 25% of the seedlings in the intermediate slope position died. These patterns are consistent with the results of the shade-house experiment where a seasonal average predawn leaf water potential less than -0.2 MPa was the threshold to find significant differences in growth and mortality for tulip poplar seedlings (Part three of this thesis). The 1995 growing season was much drier than the previous one. Seasonal soil water potentials dropped lower than -0.30 MPa

everywhere in the experimental site. Mortality increased for the three species, but once again tulip poplar was the most susceptible (52%).

An interesting mortality pattern occurred during the drier 1995 growing season in the two species that had not been strongly affected the first year. While the rate of mortality remained practically constant for sugar maples, it increased from 1 to 9% in white oaks. White oaks are frequently more successful under dry conditions, which has been related to several morphological and physiological responses to drought (Abrams, 1990). White oak has a lower leaf water potential threshold for stomatal closure than sugar maple (Bahari et al., 1985). In addition, the root system of white oak reaches deeper, and is more extensive, than that of sugar maple which increases white oak's access to deeper soil water sources (Hinckley et al., 1979). As a result, the critical leaf water potentials for stomatal closure are reached later than in sugar maple. Therefore, under dry conditions, stomatal closure occurs for shorter periods in white oak than in sugar maple (Hinckley et al., 1979). Often, white oak exhibits higher photosynthetic rates than sugar maple, and although this difference is maintained as water stress increases (Dougherty and Hinckley, 1981; Bahari et al., 1985), it becomes narrower during severe drought (Ni and Pallardy, 1991). These ecophysiological studies indicate that white oak is more drought tolerant than sugar maple. However, in this study, white oak mortality increased more than sugar maple's during the drier 1995 season. The reason for this might be related to the interaction with herbivore effects. While herbivore damage was observed in only 24% of the dead tulip poplars and 25% of the dead sugar maples, it had

affected 60% of the white oaks that died in 1995, and in most of them the damage had been very severe.

Herbivorous insect outbreaks under drought conditions have been frequently reported but the relationship seems to be nonlinear and insect feeding-guild dependent (Mattson and Haack, 1987; Larsson, 1989). The effect of variations in a resource availability, such as water, on plant-herbivorous interaction is usually explained based on changes in the growth/differentiation balance. The hypothesis suggests that when plant growth is slowed down more than photosynthesis, the increased pool of carbohydrates will be preferentially allocated to the production of secondary compounds that might have a defensive effect (i.e. Chapin et al., 1987; Herms and Mattson, 1992). For example, under mild to moderate water stress, leaf nutrients and carbohydrates concentrations usually tend to increase because photosynthesis slows down slower than cell enlargement, and also because of osmotic adjustment (i.e. Hsiao, 1973). At this point, plant quality as insect food is supposed to increase and herbivore damage is expected to be higher. However, under water stress plant palatability should eventually decrease due to the conversion of some accumulated carbohydrates into phenolic compounds, and also to an increase in leaf thickness. At increasingly severe water stress, nutrient uptake, and photosynthesis will decrease. As a consequence, plant quality and quantity will eventually diminish which has a negative impact on the herbivore population. Therefore, production of phenolic compounds and herbivore effects are expected to have a nonlinear response along a water availability gradient (Horner, 1990). Since these physiological and

biochemical effects depend on how plants are perceiving water stress, the herbivore effects should also depend on plant drought tolerance.

A preliminary comparison between seedlings of tulip poplar and white oak that did not survive either the wet 1994 or the dry 1995 growing seasons suggests some interesting patterns. Herbivore effects on tulip poplar seedlings seem to be less important than the direct effects of water and thermal stress to explain mortality patterns. In both years leaf eaters affected less than 10% of the total plant leaf area, and affected plants showed no clear spatial distribution. However, in the much drier 1995 season a smaller fraction of dead seedlings was reported with some herbivore damage (24% versus 45% in 1994). In contrast, there was an apparent herbivore outbreak among white oaks during the 1995 that is related with an increase in mortality from 1 to 9%. In 1995, 60% of the dead seedlings had been reported with damage, often affecting more than 50% of the total plant leaf area. Most herbivore effects were concentrated in the upper part of the control and dry plots. These results suggest that the mechanisms through which drought affects the survival of species with different drought tolerance could be different. Very drought intolerant species, like tulip poplar, respond rapidly to the direct effects of water stress on plant physiology (Part 3 of this thesis ), and survival (Part 4). But drought might affect more tolerant species, like white oak, in a more indirect way. Further analysis of herbivory patterns in relation to light, soil water and growth using all the experimental seedlings might contribute to a more complete understanding.

The distribution patterns of naturally established seedlings are consistent with the experimental results. In the late summer of 1993, after a very dry season, most tulip

poplar and sugar maple seedlings were found at relatively moister sites down the slope, while white oaks were more evenly distributed. These patterns probably reflect both the availability of seeds and the differential survival of the seedlings. In 1993, mortality was particularly high among tulip poplar seedlings, but was also very high for sugar maples. The long term consequences of this spatial pattern of survival among seedlings are reflected in the distribution of older individuals. Indeed, most tulip poplar saplings and trees in the study site are found at the lowest topographic positions, while white oaks are more abundant towards the upper slope positions (personal observation, and P. Hanson personal communication).

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# Part 5

## General Summary

# Objectives

Smith and Huston (1989) hypothesized that the response of plants to the combined effects of light and water is characterized by a trade-off between drought tolerance and shade tolerance. The authors used the hypothetical trade-off model to predict the growth and survival of different plant functional types along gradients of light and water availability, and showed that several natural patterns of plant distribution and succession could, in principle, be explained from this hypothesized response-model.

The trade-off hypothesis assumes that under drier conditions plants allocate relatively more biomass to roots than to aboveground structures. As a consequence, the ratio of respiring biomass to photosynthetic material would increase, and therefore the amount of light necessary to keep a positive carbon balance should be higher (i.e. whole plant light compensation point). Also, since at low water conditions plants avoid water loss by closing their stomata, it was assumed that higher light levels could compensate for reductions in photosynthetic activity by enhancing the photosynthetic rate. Based on these assumptions, Smith and Huston (1989) predicted that under drier conditions the whole plant light compensation point (i.e., amount of light at which photosynthesis equals respiration) would shift to higher values. Since, under drier conditions plants would become less shade tolerant, it was predicted that they would grow and survive better under higher light conditions. Similarly, plants would become more sensitive to dry conditions when exposed to low light levels. The trade-off model focuses on plant responses during acclimation to shade and low water availability. The predictions are

expected to hold within a population (for individuals growing in different conditions of light and water), as well as between populations (for populations growing in different conditions of light and water). Also, it is expected that different species should show the same basic pattern, although shade tolerant species are predicted to be more susceptible to dry conditions.

The physiological evidence for the hypothesized trade-off between shade tolerance and drought tolerance has been equivocal (i.e., Gauhl, 1979, Björkman and Powles, 1984; Ludlow and Björkman, 1984; Ogren and Oquist, 1985; Gamon and Pearcy, 1990; Kolb et al., 1990; Abrams, et al., 1992). However, the interpretation of some of the results should be considered with caution, because the trade-off model is based on whole plant responses and not responses at the leaf level.

The third part of this dissertation describes a shade-house experiment designed to test the physiological and morphological responses predicted by the trade-off model within any particular species along gradients of light and water availability. Two-year-old seedlings of tulip poplar (*Liriodendron tulipifera*, L.) were grown under five levels of light (1%, 5%, 12%, 17%, and 27% of ambient) and three ranges of soil water content (5-9%, 11-15%, >20%) during the growing season of 1994. Whole aboveground gas exchange (net photosynthesis and dark respiration) as well as transpiration rates were measured, and used to estimate carbon gain in plants grown under different treatment combinations. Growth measurements included leaf area, stem height and diameter, as well as final dry weight of leaves, petioles, stem, and three categories of root diameter (<1mm, 1-2 mm, >2mm).

The field evidence for the trade-off model is also controversial. If plants become shade intolerant under dry conditions, one would not expect plant establishment to be higher in the shade. However, in ecosystems where plants are exposed to severe stress, for instance as a result of heat and desiccating conditions, the establishment of new individuals is often restricted to the shady places under the canopy of other plants, called nurse plants.

In the second part of this dissertation, I review an array of examples of this facilitative interaction in which amelioration of water stress is an important mechanism, and present a graphical model to discuss the interplay of facilitative and competitive effects in view of the combined response of plants to light and moisture conditions.

On the other hand, there are some patterns consistent with the predictions of Smith and Huston's model. Vance and Zaerr (1991) found that shaded seedlings of Pinus ponderosa were less tolerant to drought and died at higher soil moisture than unshaded plants. Jarvis (1989) also found patterns consistent with the trade-off model.

In part four of this thesis, I describe an experiment designed to test the predictions of the trade-off model under field conditions, and compare the responses between species with different shade tolerance. In the forest area covered by the Throughfall Displacement Experiment (TDE) in Oak Ridge, TN, USA, soil water availability is being manipulated by intercepting about 30% of the throughfall precipitation in a (80x80 m) dry-treatment plot, transporting it through a control area, and using it to irrigate a wet- treatment plot. The light conditions vary from closed understory to small gaps. In late winter 1993, I planted seedlings of three tree species with different shade tolerance: *Liriodendron*

*tulipifera* (intolerant), *Quercus alba* (intermediate) and *Acer saccharum* (tolerant) (Baker, 1949; Fowells, 1965). The seedlings were planted at three topographical positions (upper slope, middle slope and lower slope) in each of the water treatments of the TDE (dry, control, wet), and their growth and survival followed during the next two growing seasons. The experimental results were compared with the patterns of abundance and survival found for naturally established seedlings sampled in 1993, prior to the complete installation of the experimental treatments.

## Summary of Results

***Shade-house experiment***

The results show that mesic conditions do not increase the growth of tulip poplar seedlings under low light levels, and also that higher light levels only slightly increase plant growth under low soil water conditions. These results are not in agreement with the trade-off model of Smith and Huston (1989).

The growth rate of a plant depends on the whole carbon balance, which is mainly the result of photosynthetic inputs and respiratory losses. A main assumption of the trade-off model is that an increase in light availability under dry conditions can increase the daily net photosynthetic input, which is a positive function of the leaf area ratio (LAR: leaf area/plant biomass) and the whole plant net photosynthetic rate ($\mu$mol C $m^{-2}d^{-1}$).

The results show that under high light conditions, the leaf area ratio tends to decrease with light. When high light is combined with low soil water conditions, the

shoot net photosynthetic rate also decreases with light. Estimates for the whole shoot indicate that plants under dry conditions have lower daily photosynthetic rates under high light than under low light conditions. This seems to be mainly the result of prolonged stomatal closure under combined dry and high light conditions. Thus, in this experiment, higher light levels did not compensate for the shorter period the stomata were opened. The measurements of whole shoot dark respiration rates were consistently lower for plants under dry conditions. This indicates that the reduction of the gains (daily net photosynthetic rate) under dry conditions is at least partly compensated by a reduction of the losses (dark respiration rate). Contrary to what was predicted by the trade-off hypothesis, I found that the light compensation point also tends to decrease under drier conditions. There was no evidence of an increase in the root-to-shoot ratio under drier conditions as predicted from the model.

***Field experiment***

During the relatively wet 1994 growing season, mortality differed with experimental treatment, slope position, and species. Mortality was highest in tulip poplar, highest in the dry treatment and highest at the upper part of the slope. There was no mortality of any species in the wet treatment.

During the much drier 1995 season, mortality was higher than in the previous year for all species. Once again tulip poplar had the highest mortality, but it was more evenly distributed across treatments and slope positions than in 1994. Indeed, soil water had dropped to very low levels everywhere in the experimental site. Mortality of sugar maple

and white oak showed strong treatment and topographic effects. White oaks are frequently more successful under dry conditions, which has been related to several morphological and physiological responses to drought (Hinckley et al., 1979; Dougherty and Hinckley, 1981; Bahari et al., 1985; Abrams, 1990; (Ni and Pallardy, 1991). However, in the TDE site, white oak mortality increased more than sugar maple's during the drier 1995 growing season. My results indicate that this is related to herbivore effects, mainly caterpillars. While herbivore damage was observed in only 26% of the dead tulip poplars and 29% of the dead sugar maples, it had affected 65% of the dead white oaks, and in most of them the damage had been very severe.

The distribution patterns of naturally established seedlings are consistent with the experimental results. In the late summer of 1993, prior to the experimental treatments, but after a very dry season, most of the tulip poplar and sugar maple were found at the relatively moist sites down the slope, while white oaks were more evenly distributed across the experimental site.

The growth of tulip poplar and sugar maple seedlings showed a unimodal response to light. At light transmittance over 27% for tulip poplar, and 20% for sugar maple, growth decreased with increasing light. In contrast, the growth of white oak, the most drought tolerant of the three species, was not significantly reduced with light. The observed decrease of growth of tulip poplar and sugar maple under high light is likely to be related to an increase in water stress. Higher irradiance, as found in forest gaps, is associated with increasing water stress conditions ( Kozlowski et al., 1991; Sipe and Bazzaz, 1994; Berkowitz, et al., 1995; Sipe and Bazzaz, 1995). According to the trade-off

hypothesis between shade and drought tolerance (Smith and Huston, 1989), plant growth under dry conditions should increase with light availability. My results indicate that this is not the case for tulip poplar and sugar maple.

### *Field patterns*

According to the trade-off model, under dry conditions, plants should be expected to be less tolerant to shading by competitors. An observation that is, at first sight, incompatible with this idea, is the fact that in dry areas the establishment of new plants is often restricted to the shady places under the canopy of other plants, called nurse plants. Such facilitative interactions have been found over a wide array of different plant communities such as deserts, Mediterranean shrublands, tropical savannas, temperate forests and grasslands, salt marshes, dunes and tundras.

Although several explanations for facilitative patterns are found, enhanced moisture conditions for establishing seedlings under the canopy of nurse plants is one of the most reported. Whether facilitation occurs depends on the way in which the various environmental factors change over a gradient from the canopy to the open. I present a graphical model to point out that facilitation occurs only if the increase in microsite moisture under the canopy exceeds the increase in moisture demand when plants acclimate to shade by investing less in roots and more in leaves. If there is no such trade-off between shade and drought tolerance, we should expect facilitation to occur whenever the improvement of water conditions under the canopy exceeds the costs of reduced light levels. Note that for this to occur there is no need to call for an increased

demand for water due to shading. The model focuses on the interaction between light and water but the results can be generalized to other environmental factors such as nutrients, or herbivory.

The net effect of nurse canopies on the understory may shift from facilitative to competitive or vice versa when conditions change. Many studies show, for instance, that facilitative effects are stronger on the drier sites and in drier years (Parker and Muller, 1982; Fuentes et al., 1984; Frost and McDougald, 1989; Hillier, 1990; Belsky et al., 1993, Berkowitz et al., 1995), and experimental addition of water has been shown to enhance seedling survival and growth much more in open areas than under the canopy (De Jong and Klinkhamer, 1988; Shumway and Bertness, 1992). Also experimental manipulations in salt marshes have shown that alleviation of the stress can switch the effects of the interaction from facilitative to competitive (Bertness and Shumway, 1993; Bertness and Hacker, 1994; Bertness and Yeh, 1994; Shumway and Bertness, 1994). In addition, the net effect of plants on other plants can change dramatically over time as a result of growth. Newly established plants can eventually shade out the former nurse, and their extending root systems allow uptake from limited sources that were previously available only to the nurse plant (Conard and Radosevich, 1982; McAuliffe, 1984a; Valiente et al., 1991a,b). Moreover, competition with other small plants in the shade can increase because of the common exploitation of limited resources in the top soil layers (Aguiar and Sala, 1994).

Competition and facilitation are often discussed almost as if they were completely exclusive processes. The presented model stresses the view that these terms are just

qualitative labels for the net effect of a complex of changes in the environment of a plant caused by the presence of other plants. In practice, this net effect of one plant on another plant can easily shift from negative to positive and vice versa.

## Concluding Remarks

My results indicate a problem with applying the trade-off model for shade and drought tolerance to actual field conditions, namely the implicit assumption that light and water conditions experienced by a plant vary independently. In reality, an increase in light will usually lead to an increase in temperature and therefore in the vapor pressure deficit, which increases the transpiration demands. Therefore, water-stress will tend to increase with light, and vice-versa, shading can enhance the plant water relations under dry conditions. Clearly, the negative response to light at drier conditions will depend on the actual soil water conditions, and on the drought tolerance of the species. The shadehouse and field experiments showed this very clearly. The field patterns reviewed extend this result to other plant communities. Indeed in arid ecosystems, the distribution of small, shallowly rooted plants is frequently confined to the shade of taller plants, and there is strong evidence that in a wide range of plant communities, shade of these so-called nurse plants enhances the growth and survival of smaller plants indeed by improvement of their plant-water relations.

# Future directions

Although the main results of this dissertation indicate problems in both the assumptions and predictions of the trade-off model, the theoretical approach used for Smith and Huston (1989) is very valuable for the development of links between individual responses and natural patterns in plant ecology. Much can be gained if theoretical, experimental and field efforts are combined. Hopefully, this dissertation also helps to clarify the physiological mechanisms and abiotic factors that make facilitation a common interaction under dry conditions. There are some particular aspects of this dissertation that should be expanded.

The conceptual model presented in **Part II** can probably be improved to make it more predictive for particular plant communities. Facilitative effects should be more common among nurse plants with deep root systems because partitioning of soil water between the nurse plant and the small seedlings should reduce the effects of competition. For example, Belsky (1994) found that in low-rainfall savannas nurse effects were in part possible due to a lower concentration of the nurse roots under its own canopy than in high-rainfall sites. Since root architecture depends on both genetic and environmental components, it might be possible to identify plant communities or environmental conditions where certain root growth patterns are more common than others, and use them to predict the relative frequency of facilitative interactions.

This dissertation has stressed the importance of resource correlations and plant physiological responses to them. It would be particularly interesting to study the

interaction of shade and drought tolerance under a gradient of natural conditions and to link this with the relative importance of facilitation and competition for certain plant communities. The best way of doing this is through field experiments. For example, seedlings could be planted under and outside shade (i.e. nurse-tree and/or artificial shade) along a natural gradient of water availability. Gradients like this could be studied in both xeric and humid areas because, as discussed in **Part II** of this dissertation, the slope describing the microclimatic changes in irradiance and water availability between the nurse shade and the open area is expected to be very different depending on the general climatic conditions. Careful microclimatic description and physiological measurements are necessary, and the combination of both with patterns of biomass allocation and survival. Field ecophysiological studies would have to pay particular attention to the effect of sunflecks and air humidity. Even different types of tree nurses, with distinctive architecture, could be chosen to compare the effects of microclimatic conditions and root competition. Under natural conditions gradients in nutrient availability might be unavoidably correlated with water availability. As mentioned in **Part I** of this dissertation our knowledge of the combined effect of nutrients, light and water stress is still very limited, and the potential outcomes can not be easily predicted. Few factorial experiments have been executed, especially with woody plants.

In the shadehouse experiment described in **Part III** light compensation point decreased under drier conditions. The explanation I offered was a decrease in dark respiration rates. It would be very interesting to understand how the two components of respiration (maintenance and growth) are affected by a reduction in soil water potential.

Changes in light compensation point could also be linked to plant architecture, such as changes in stem allocation. The data recorded can probably also be used to predict the effect of a change in light compensation point on carbon gain rates under different soil water conditions. Making a link between my estimates daily carbon gain and observed growth is not an easy task because the carbon gain estimations were made on a subset of conditions for a relatively short time. A mechanistic growth model with parameters adjusted on the basis of observed physiological responses could probably help. Although the shadehouse experiment was performed with two species, *Liriodendron tulipifera* and *Acer saccharum,* **Part III** presented only the results with the first one. The results with sugar maple will be presented in a separate paper.

The field experiment described in **Part IV** is still under way. Particular attention will be given to herbivore effects. Herbivore effects were discussed only in relation to seedlings that did not survive either the 1994 or 1995 growing seasons. Because herbivore observations were performed for all seedlings, it will be possible to link the degree of herbivore damage with specific conditions of light and soil water during both years, as well as with growth parameters.

The ecophysiological and demographic results of field experiments could be probably expanded using individual-based models. An interesting preliminary exercise would be to return to the Smith and Huston (1989) trade-off model assuming a decrease in light compensation point under drier conditions.

This dissertation has challenged some interesting hypotheses and, in addition, has identified some areas where further research can improve our understanding of the dynamics of plant growth and survival along environmental gradients.

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# Appendices

Appendix 1. Seasonal soil water content (TDR: %), and estimates of seasonal predawn leaf water potential ($\Psi_{leaf}$ : MPa) for the shadehouse experiment (Part III). Data are means ± standard deviations (n=4) for different combinations of shade (L: % of ambient light) and soil water content (LW: low water, IW: intermediate water, HW: high water).

| | TDR | $\Psi_{leaf}$ |
|---|---|---|
| L 5% | | |
| LW | 15.01 ± 1.42 | - 0.40 ± 0.11 |
| IW | 16.85 ± 1.80 | - 0.25 ± 0.04 |
| HW | 24.94 ± 0.41 | - 0.10 ± 0.00 |
| L12% | | |
| LW | 13.67 ± 1.73 | - 0.51 ± 0.10 |
| IW | 16.39 ± 1.06 | - 0.27 ± 0.03 |
| HW | 22.56 ± 2.03 | - 0.13 ± 0.02 |
| L17% | | |
| LW | 13.20 ± 3.17 | - 0.53 ± 0.16 |
| IW | 14.72 ± 1.27 | - 0.32 ± 0.04 |
| HW | 22.78 ± 1.84 | - 0.13 ± 0.02 |
| L 27% | | |
| LW | 15.02 ± 1.30 | - 0.42 ± 0.11 |
| IW | 14.32 ± 0.36 | - 0.35 ± 0.02 |
| HW | 23.10 ± 0.84 | - 0.12 ± 0.00 |

Appendix 2. Final biomass (g of dry weight) of tulip poplar seedlings grown under different combinations of shade (L: % of ambient light) and soil water content (LW: low water, IW: intermediate water, HW: high water). Data are mean ± standard errors (n=4).

| | Leaves | Petioles | Stem | Shoot | Roots | Total |
|---|---|---|---|---|---|---|
| L 5% | | | | | | |
| LW | 2.44±0.66 | 0.31±0.06 | 2.64±0.57 | 5.4±1.3 | 2.5±0.3 | 7.9±0.5 |
| IW | 1.76±0.04 | 0.22±0.01 | 2.3±0.27 | 4.2±0.2 | 1.8 ±0.5 | 6.1±0.4 |
| HW | 3.04±0.79 | 0.44±0.12 | 3.05±0.51 | 6.5±1.4 | 2.3±0.4 | 8.9±1.6 |
| L12% | | | | | | |
| LW | 2.76±0.19 | 0.40±0.02 | 3.09±0.43 | 6.2± 0.6 | 3.1±0.5 | 9.3±1.1 |
| IW | 3.00±0.57 | 0.42±0.15 | 3.20±0.59 | 6.6±1.3 | 4.8±1.1 | 11.4±2.1 |
| HW | 12.36±1.3 | 1.92±0.34 | 11.7±1.55 | 26±2.6 | 13.6±1.5 | 39.6±3.4 |
| L17% | | | | | | |
| LW | 2.80±0.46 | 0.42 ±0.06 | 2.58±0.16 | 5.8± 0.7 | 2.5±0.1 | 8.3±0.7 |
| IW | 5.47±1.63 | 0.44±0.14 | 4.38±1.13 | 10.3±2.9 | 5.8±0.8 | 16.1±3.6 |
| HW | 9.76±2.32 | 1.17±0.39 | 9.53±2.37 | 20.4±4.8 | 12.7±5.8 | 33.2±9.7 |
| L 27% | | | | | | |
| LW | 2.38±0.76 | 0.29±0.09 | 2.92±0.57 | 5.6±1.4 | 3.0±0.6 | 8.6±1.9 |
| IW | 4.98±0.50 | 0.50±0.05 | 5.71±0.68 | 11.2±1.0 | 12.0±1.7 | 23.3± 2.8 |
| HW | 12.2±1.98 | 1.17±0.18 | 8.78± 1.58 | 22.1±3.5 | 15.1±3.5 | 37.3±6.3 |

Appendix 2. Continuation. The responses codes are: LA (leaf area), LAR (leaf area ratio), SLA (specific leaf area), LWR (leaf weight ratio), S/R (shoot/root ratio), R1/TR (fine roots < 1mm /total root weight). Data are mean and standard errors (n = 4).

| | LA ($cm^2$) | LAR ($cm^2/g$) | SLA ($cm^2/g$) | LWR | S/R | R1/TR |
|---|---|---|---|---|---|---|
| L 5% | | | | | | |
| LW | 484±90.1 | 64.5±11.8 | 222.8± 42.5 | 0.29±0.02 | 2.07±0.30 | 0.25±0.04 |
| IW | 765±188.1 | 126.7±34.1 | 433.2±103.0 | 0.28±0.01 | 3.14±1.25 | 0.34±0.07 |
| HW | 1052±258 | 115.1±12.1 | 349.7±28.3 | 0.33±0.03 | 2.90±0.54 | 0.31±0.03 |
| L 12% | | | | | | |
| LW | 329±97.2 | 40.1±15.3 | 132.1±50.2 | 0.30±0.02 | 2.15±0.27 | 0.35±0.02 |
| IW | 604±103.1 | 54.6±4.1 | 204.9±13.9 | 0.26±0.02 | 1.49±0.23 | 0.39±0.01 |
| HW | 2701±203 | 68.4±2.0 | 222.0±17.5 | 0.31±0.03 | 1.95±0.23 | 0.31±0.04 |
| L 17% | | | | | | |
| LW | 473±84.5 | 59.0±13.9 | 201.3±66.2 | 0.32±0.03 | 2.29±0.24 | 0.36±0.02 |
| IW | 1156±350 | 67.1±6.8 | 209.9±3.6 | 0.31±0.03 | 1.67±0.32 | 0.37±0.02 |
| HW | 2526±615 | 80.3±9.1 | 253.5±16.1 | 0.32±0.04 | 2.21±0.53 | 0.32±0.03 |
| L 27% | | | | | | |
| LW | 416±124 | 44.4±5.8 | 179.9±19.3 | 0.25±0.04 | 1.76±0.21 | 0.39±0.04 |
| IW | 1108±121 | 52.9±14.8 | 235.6±48.4 | 0.21±0.04 | 0.96±0.08 | 0.45±0.03 |
| HW | 2376±247 | 71.8±19.5 | 205.4±29.0 | 0.34±0.05 | 1.73±0.45 | 0.31±0.02 |

Appendix 3. Estimated coefficients of logistic regressions for seedling mortality in relation to light transmittance and soil water potential in the Throughfall Displacement Experiment (Part IV).

| species | year | model | estimate ± SE | p ≤ |
|---|---|---|---|---|
| tulip poplar | 94 | $m = a + b\,(light) + c\,(\psi_{soil})$ | a = -1.93 ± 0.98 | 0.05 |
| | | | b = -0.04 ± 0.04 | 0.34 |
| | | | c = -4.74 ± 0.04 | 0.01 |
| | | $m = a + c\,(\psi_{soil})$ | a = -2.84 ± 0.49 | 0.01 |
| | | | c = -5.07 ±1.57 | 0.01 |
| | | $m = a + b\,(light)$ | a = - 0.87 ± 0.77 | 0.25 |
| | | | b = -0.04 ± 0.03 | 0.15 |
| sugar maple | 94 | $m = a + b\,(light) + c\,(\psi_{soil})$ | a = -0.08 ± 1.77 | 0.96 |
| | | | b = -0.20 ± 0.10 | 0.06 |
| | | | c = -3.29 ± 2.40 | 0.17 |
| | | $m = a + c\,(\psi_{soil})$ | a = -3.80 ± 0.77 | 0.01 |
| | | | c = -4.07 ±2.05 | 0.04 |
| | | $m = a + b\,(light)$ | a = 0.84 ±1.62 | 0.6 |
| | | | b = -.21 ± 0.10 | 0.04 |
| white oak | 95 | $m = a + b\,(light) + c\,(\psi_{soil})$ | a = -1.47 ± 1.46 | 0.31 |
| | | | b = -0.09 ± 0.04 | 0.02 |
| | | | c = -2.12 ± 2.17 | 0.32 |
| | | $m = a + c\,(\psi_{soil})$ | a = -3.98 ± 1.16 | 0.01 |
| | | | c = -3.22 ± 2.12 | 0.13 |
| | | $m = a + b\,(light)$ | a = -0.28 ± 0.78 | 0.72 |
| | | | b = -0.10 ± 0.04 | 0.01 |

# Vita

Milena Holmgren studied Biology in Mexico City where she graduated from Universidad Autónoma Metropolitana, Unidad Xochimilco, in 1985. In Mexico, she was trained in plant community dynamics of rainforest and semiarid ecosystems. Her social service consisted of a description of the bird community in the Fuerte River, Sinaloa, and the development of a manual on basic ecological concepts for the primary-grades public school of the area. A year later, she started a specialization in Applied Statistics at the Instituto de Investigación en Matemáticas Aplicadas y Sistemas, of the Universidad Nacional Autónoma de México where she graduated in 1988 (with the Gabino Barreda distinction). Her thesis analyzed circadian rhythms of yawning in the rat. After her studies, she spent two years at the Universidad Católica de Chile, in Santiago, where she worked as a research assistant and instructor. Her research in Chile focused on successional dynamics of Mediterranean shrublands after human-induced disturbances (especially fire). In January 1992, she started a Ph.D. in Ecology at the University of Tennessee. Simultaneously, she worked as a research assistant in the Environmental Sciences Division at Oak Ridge National Laboratory. She received the Science Alliance award in 1994 from the UT Ecology Program. Her research focused on the interactive effects of shade and drought on seedling physiology, growth and survival (especially tree seedlings of the eastern North American deciduous forests ). The doctoral degree was received in August, 1996. She is presently in The Netherlands.