National Library of Canada
Acquisitions and Bibliographic Services Branch
395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale du Canada
Direction des acquisitions et des services bibliographiques
395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

Functional design and shade adaptation in Acer species

Thomas T. Lei

Department of Biology, McGill University,
1205 Avenue Docteur Penfield, Montréal,
Québec, H3A 1B1 Canada

June 1992

A Thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

National Library of Canada
Acquisitions and Bibliographic Services Branch
395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale du Canada
Direction des acquisitions et des services bibliographiques
395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

ISBN 0-315-80358-4

ABSTRACT

This is a broad, quantitative comparison of 12 maple species, representing both canopy and subcanopy growth forms, grown under two ecologically relevant light environments. The maple seedlings responded mainly to light intensity; light quality plays only a minor role in the induction of shade characteristics. While a light-mediated trade off between light and dark reactions of photosynthesis was evident at the chloroplast level, this did not lead to similar differences in assimilation rates. Gap-grown seedlings showed no apparent compromise in photosynthetic response to dim light and lightflecks. Seedlings of subcanopy trees trade off wood strength for increases in plant size while canopy seedlings sacrifice plant size for wood strength. The demand for greater wood strength in seedlings of canopy trees appears to pose a strong developmental constraint that delays maturation. Free of this constraint, subcanopy species can devote more resource to reach adult size quickly and at an earlier age.

RÉSUMÉ

Cette étude se veut une vaste comparaison de 12 espèces d'érables, incluant à la fois des espèces de la strate arbustive et arborescente, cultivée sous deux régimes de lumière typiques de sous-bois. Les semis d'érables ont répondu principalement à l'intensité de la lumière; la qualité de la lumière ne jouant qu'un rôle secondaire dans l'induction des caractéristiques liées à l'ombrage. Bien qu'un compromis, réglé par la luminosité, ait été observé au niveau des chloroplastes, entre les réactions photosynthétiques claires et sombres, cela n'a pas entrainé de différences au sein des taux d'assimilation. Les semis cultivés en trouée n'ont pas affichés de compromis apparent quant à leur réponse photosynthétique à une faible luminosité ou à une percée de lumière. Les semis d'espèces arbustives priment la taille à la solidité du bois, tandis qu'on observe l'inverse chez les semis d'espèces arborescentes. Le besoin d'une solidité de bois accrue chez ces derniers, semble poser une importante contrainte développementale qui retarde l'atteinte de la maturité. Libres de cette contrainte, les espèces arbustives peuvent allouer davantage de ressources afin d'atteindre la maturité rapidement, et en bas âge.

槭树结构及其对荫蔽条件的适应

摘要:

本文描述对了十二种槭树的三至四年生苗木进行遮荫实验研究的结果，揭示了三种光照条件对树苗生理生态特征和年生长率的影响. 这三种光照条件分别模拟了林隙，林荫和林荫加林隙的光质和光量. 据分析，不同光质对槭苗功能特征无显著影响. 与光质对比，光照强度对槭苗的生理和形态特征有一定的影响，并且特征反应格局与理论依据大约一致. 林隙树苗的净光合作用，单位叶面积干重和生长率都比林荫树苗较高，而且叶的叶绿素含量较低. 虽然荫苗具有某些荫蔽适应性特征，但这些特征与生长率无固定的联系. 例如荫生树苗具有较小的单位叶面积干重和较高的叶绿素含量，但上述二者并不能保证低的暗呼吸速率或高的净光合作. 因此个别的荫蔽特征不能被用来推断整棵树苗的生理和生长功能. 这十二种槭树包括乔木和小乔木各六种. 乔木必须伸至林冠，小乔木则可在林冠下成熟. 据分析，大小乔木具有悬殊的分枝类型. 乔木种以单轴主干为主，叶展多层，小乔木侧枝伸长数颇多，叶展呈单层. 此资料示意槭属分枝形态实属对其生长条件长期适应的结果. 径道分析 (path analysis) 结果显示槭苗种类的光合器官特性，叶结构和生物量的配置(于支长，细根生产和木质)对生长率有综合性的影响. 小乔木幼树偏重于高度和生物量的生长但木质强度较弱. 与此相反，大乔木幼树偏于木质强度而高度和生物量的生长则处于次要地位. 因此，大乔木致力于木质强度的生长而其个体发育则明显减缓. 小乔木幼树则更能有效地利用光合产物于个体发育从而更快且较早地趋近成熟. 本文从生理和功能生态学的角度对上述观点作出了解释.

ACKNOWLEDGEMENTS

The insightful motive force and trenchant guidance of Professor Martin Lechowicz propelled this study to greater relevance. Professor Rajinder Dhindsa and Professor Derek Roff provided counsel and encouragement in the formulation stage of the thesis. Professor Catherine Potvin kindly assisted by navigating me through statistical roadblocks I encountered.

The experiments could not have been possible without the help of the following people. Maria Murgante and Maria Fernandes invested much care and attention to the rearing of the maple seedlings. David Ghan, Lorraine Breton and Elizabeth Bush joined in the early part of sample collecting and processing; Christian Piché, Lucie Veillette and Stéphane Dumont contributed to the latter part of field and lab work. Special thanks go to Rebecca Ritchie who persisted with distinction through the major field season in 1990. Beyond the technical assistance these people contributed to a congenial work environment I thoroughly enjoyed and appreciated.

I gratefully acknowledge the Gault Estate Board of Directors for permission to work at the Mont St. Hilaire reserve. At the field site on Mont St. Hilaire, Michel Drew (Director, Gault Estate) and Professor Graham Bell (Research Director) were generous and prompt in their logistical assistance. Jean-Pierre Charbonneau constructed the experimental lath house and helped with the day-to-day operation and security of the site.

Robert Lamarche lent much needed help in the use of microscopes and computers. Clare Cooney and Mark Romer were ever so patient with my tinkering in the McGill University Phytotron trying to create the right environment for the maple seedlings. Ron Kara's multifaceted logistical support was indispensable. In their workshops, Tony Walsh and Tony Briza constructed the necessary components for the experiments. In the lab, Lee Jackson suggested the more efficient DMSO chlorophyll extraction method. Sara Griesbach and Professor Robert Peters provided the space and equipment required for chlorophyll analysis. Other instruments used in this study were also generously made available by Professor Catherine Potvin - Walz chlorophyll fluorimeter; Professor Pierre Bellefleur (Forestry Science, Laval), Professor John Lewis (Geography, McGill) and Professor Hardy Granberg (Sherbrooke)- Li-3100 spectroradiometer.

Several populations of maple seeds used in the experiments were collected by J. Brown, W. Crins, V. Feráková, P.A. Gregory, D. Larsen, M.J. Lechowicz, M. Murgante, J. Piezio-Biroli and N. Tanaka.

Partial funding in support of this study was provided by the Bourses Québec-République populaire de Chine and the Arthur Willey Memorial Fellowship (McGill University) to me, and by NSERC operating funds to MJL.

Dr. Andrée Nault kindly translated the thesis abstract into French; and Dr. Jianhua Zhang helped with the Chinese translation of the abstract.

Lastly, I thank my mother Kui Min Lei for creating an insouciant milieu during my study which not only aided in the progress and completion of the thesis but also allowed me the freedom to explore other tangential interests, and it is to her that I dedicate this work.

TABLE OF CONTENTS

LIST OF FIGURES

GENERAL INTRODUCTION

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

APPENDIX 3

LIST OF TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

APPENDIX 1

PREFACE

I am required by the Faculty of Graduate Studies to reproduce the following statements:

> "The candidate has the option, **subject to the approval of their Department**, of including as part of the thesis the text, or duplicated published text, of an original paper, or papers.
>
> -Manuscript-style theses must still conform to all other requirements explained in the Guidelines Concerning Thesis Preparation.
> -Additional material (procedural and design data as well as descriptions of equipment) must be provided in sufficient detail (eg. in appendices) to allow clear and precise judgement to be made of the importance and originality of the research reported.
> -The thesis should be more than a mere collection of manuscripts published or to be published. It must include a general abstract, a full introduction and literature review and a final overall conclusion. Connecting texts which provide logical bridges between different manuscripts are usually desirable in the interests of cohesion.
>
> It is acceptable for theses to include, as chapters, authentic copies of papers already published, provided these are duplicated clearly and bound as an integral part of the thesis. In such instances, connecting texts are mandatory and supplementary explanatory material is always necessary.
> -Photographs or other materials which do not duplicate well must be included in their original form.
>
> -While the inclusion of manuscripts co-authored by the candidate and others is acceptable, the candidate is required to make an explicit statement of who contributed to such work and to what extent, and supervisors must attest to the accuracy of the claims at the Ph.D. Oral Defense. Since the task of the Examiners is made more difficult in these cases, it is in the candidate's interest to make the responsibilities of authors perfectly clear."

The four chapters in this thesis are prepared for submission to scientific journals. A published paper (Lei and Lechowicz 1990) in Oecologia 84:224-228 was the result of data collected during my preliminary field season, but is not included in the thesis. The general introduction provides an overview of the various physical (i.e. the light environment) and plant characters considered in this study and parts of it, by necessity, are reiterated under each chapter's own introductions. The first person singular is used in the chapters although the publications of these chapters in scientific journals will be co-authored with my supervisor, Dr. Martin Lechowicz.

The preparation of the experimental setups (i.e. spectral filter for the lath house, artificial light chamber for gas exchange measurements), the design and execution of the experiments and the data analysis were my own effort in consultation with Dr. Lechowicz. In his supervisory capacity, Dr. Lechowicz also provided editorial advice and some interpretative input at various stages of the data analysis and manuscript preparation.

In accordance with the acceptable thesis format, a statement of my contributions to original knowledge has been incorporated into the General Conclusions. Since most of the key findings are "original" in nature, I chose this format in the interest of economy.

To reduce duplication of describing the experimental methods in the first two chapters, I have simply included the necessary additional methods in later chapters. Based on the same rationale, I avoided repetition of the same references cited in each chapters by having a single Literature Cited following the General Conclusions.

GENERAL INTRODUCTION

Part 1: Historical literature review and background to the study

While early agronomists were aware that the shade of the pine kills the grass but that of the fig permits the intercropping of vines (Pliny The Elder), the physical properties of canopy shade and the adaptive responses of plants have only recently been quantified.

The influence of irradiance on the growth of both natural and cultivated plants has been a long-standing concern to botanists and agronomists. Beginning about a century ago, experimental comparisons of light-mediated plant responses led to the general view that most plants can respond to shady environments by an accommodation of their phenotype that confers a growth advantage (Zon and Graves 1911, Haberlandt 1914, Evans, von Caemmerer and Adams 1988). While evidence for such acclimation of morphological and physiological traits to sun and shade abounds (references given in the following sections), the direct linkage between functional plant traits and whole plant performance (i.e., growth or reproductive success) has not been clearly demonstrated (Mooney 1991), particularly among woody plants. The overall goal of my thesis is to attempt to determine the phenotypic responses of maple species to growth under sun and shade, and to quantitatively link these responses to variations in seedling growth. As background to that effort, I will present a brief review of our current knowledge of sun/shade ecology focusing on three major topics: 1) the forest light regime, 2) plant functional response to light limitation and 3) persistence and survival of understory tree seedlings. I draw on references for all woody plants, but especially for maples and other shade tolerant hardwoods that grow in the forest understory, at least as juveniles.

I. Forest light regime

Forest light regimes are characterized by full insolation at the canopy crown (2000 μmol m^{-2} s^{-1} in summer) and a rapid attenuation of light energy through the foliage (Hutchison and Matt 1977, Runkle 1985, Lieberman et al 1989, Canham et al 1990); only 1-5% of full sun reaches the forest floor in most temperate and tropical forests (Pearcy 1983, Chazdon and Fetcher 1984). Concurrent with the reduction in the light intensity through the foliage layers, there is also a significant change in the spectral quality of shade light (Lee 1987). Through selective absorption of the chloroplast pigments, the red [660 nm]-to-far red [730 nm] ratio (R:FR) is reduced from 1.15 (canopy top) to 0.3 (forest floor) (Smith 1981). In the understory of a closed forest canopy, plants experience prolonged periods of such low intensity, diffuse shade light punctuated by brighter sunflecks (Wood and Turner 1971, Chazdon 1988, Canham et al 1990, Chazdon and Pearcy 1991). Sunflecks, 90% lasting less than 32 s (Chazdon 1988), are present only 5-12 min per day (Canham et al 1990), but they contribute 31-40% to the total daily light energy reaching the forest floor (Pearcy 1983, Canham et al 1990). While understory plants can generally maintain positive carbon uptake in the diffuse shade light (light compensation point of species), 40-60% of their daily carbon gain is derived from the intermittent sunflecks (Pearcy 1990) that have the most direct effect on seasonal growth (Pearcy 1983).

Natural disturbances such as windthrows or ice storms can create gaps within the intact forest cover (Whitney and Johnson 1984, Pickett and White 1985, Melancon and Lechowicz 1987, Canham et al 1990). Gaps typically occupy 3-25% of a forest area (Brokaw 1985) with 80% of the gaps less than 150 m^2 (Yamamoto 1989, Runkle 1990). Irradiance, air temperature, moisture and nutrient levels can vary dramatically in gaps compared to adjacent intact forest, but plant growth is found to associate most strongly with the higher light level in gaps (Minckler and Woerheide 1965, Collins et al 1985, Collins and Pickett 1987). The average light level in a gap with a diameter half the height of the crown is between 20-45% of full sun at the top of the canopy

(Minkler and Woerheide 1965, Chazdon and Fetcher 1984). With typical lateral growths of 6-14 cm yr^{-1} (Hibb 1982), a gap opening of 400 m^2 can effectively maintain accelerated growth in understory seedlings for 8-10 yrs before closure by lateral growth or an ascending sapling. For both canopy and subcanopy maple trees, the released growth in the gap plays a major role in reaching reproductive size (Hibbs et al 1980, Canham 1985). Given that the closed canopy shade and the forest gap are the two environments most relevant to the ecology of juvenile maples, I conducted the experiments described in this thesis under light regimes simulating a gap of about 120 m^2 and the shade of a closed canopy. The gap simulation provided 20% full sun and the shade simulation provided 2.5% full sun with additional sunflecks occurring at 13% of the daylight exposure and lowered R:FR ratio. In one experiment, I also simulated an "overcast" environment as might prevail in coastal or high elevation forests prone to cloudy or foggy weather; this provided 2% full sun but with no change in R:FR ratio from that of direct sunlight.

Chapter 1 reports the responses of Acer seedling to light quality and quantity in a simulated forest gap (both photosynthetically-active photon flux density [PPFD] and R:FR high), a closed canopy shade (both low) and an overcast environment (PPFD low and R:FR high, similar to the filtering effect of clouds). In recent years, there has been great emphasis placed on the importance of R:FR ratio as an environmental cue for plant responses to low light levels (e.g., Smith 1981, Smith and Morgan 1983, Casal and Smith 1989). Virtually all this work has been on herbaceous species including the demonstration that ruderal herbaceous species detect and respond to the onset of shading signalled by an increasing R:FR ratio even when PPFD remains high (Ballaré et al 1987, Casal and Smith 1989). In contrast, little is known about how tree seedlings respond to light quality shifts. In the forest understory, a response to increasing R:FR as cue to gap opening rather than shading actually could be advantageous. Turnbull (1991) found no difference in the photosynthetic response to R:FR among tropical tree seedlings of early and late successional stages. This experiment therefore examined whether maple seedlings responded differently to an increase in R:FR ratio alone (the overcast treatment) as opposed to the shade treatment where both PPFD and R:FR are low.

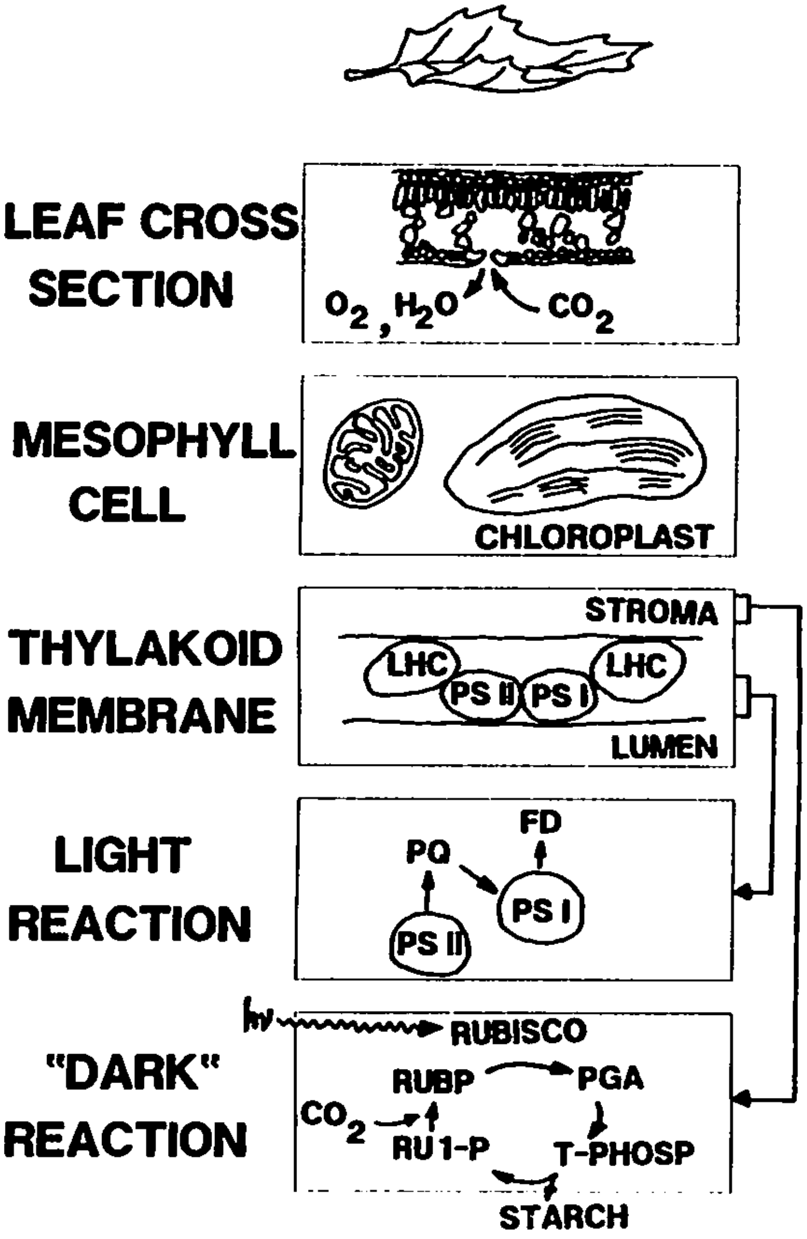
II. Plant functional response to light limitation

Early experimental evidence for light-mediated plant characters was provided by Stahl in 1880 and 1883 who showed that shading altered the laminal thickness and cellular arrangement in beech leaves (in a review by Zon and Graves 1911). In 1906, Lubimenko (in Zon and Graves 1911) established that in woody plants 1) leaf and chloroplast structures are light-dependent and together they affect photosynthesis, 2) chloroplast of shade tolerant species are more efficient at using light leading to a lower light compensation level (the irradiance level at which a net carbon uptake begins) than shade intolerant species, 3) maximum photosynthesis (A_{max}) differed among species and is likely caused by differences in chloroplast properties. Grafe (in Zon and Graves 1911) validated Lubimenko's assertion on photosynthesis by demonstrating the higher starch content in beech leaves (shade tolerant) than in birch leaves (intolerant) at 2% and 10% full sunlight. While later research did much to elucidate the biochemical and physiological basis of shade acclimation (see reviews by Boardman 1977, Björkman 1981, Givnish 1988), these early conclusions remain central to current discussions of light-mediated responses at the leaf level.

The current view on the plant response to varying irradiance can be broadly divided into leaf level biochemistry, anatomy and physiology, and whole plant structures such as branching pattern and carbon allocation to above- and belowground parts. The following is a summary of these topics.

Leaf biochemistry- The biochemical basis of light acclimation involves both the light-harvesting photosystems (PS) I and II in the light reaction component and the carbon reduction cycle (or Calvin cycle) of the dark reaction component (Figure 1; Anderson et al 1988). Variations in the amount of each component has a direct bearing on the

Figure 1. A schematic representation of selected functional traits in a leaf with increasing magnification from the top to the bottom panels. Given on the right is the expected direction of trait acclimation to high or low irradiance levels (based mainly on Boardman 1977, Bjorkman 1981 and Givnish 1988). The light harvesting complexes (LHC) of photosystem I (PSI) and photosystem II (PSII) are in close spatial proximity within the thylakoid membrane of the chloroplast. Within the thylakoid membrane (top arrow), the photosynthetic light reaction consists of the electron transport chain coupling PSII through Plastoquinone (PQ, an e^- transport carrier) to PSI and ferredoxin (FD, e^- carrier). Chemical energy produced by the light reaction is used to drive the "dark" reaction occurring in the chloroplast stroma (bottom arrow). The "dark" reaction also requires light activation on the catalytic enzyme ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco). CO_2 is assimilated via the Calvin cycle with the following intermediates: RUBP (ribulose-1,5-bisphosphate), PGA (3-phosphoglycerate), T-Phosp (triose phosphate) and RU-1-P (ribulose-1-phosphate). See accompanying text in the General Introduction for details on the functional traits given.



TRAIT	SUN	SHADE
SLM	HIGH	LOW
STOMATAL		
DENSITY	HIGH	LOW
CONDUCTANCE	HIGH	LOW
MAX. PHOTOSYNTHESIS	HIGH	LOW
NO. CHLOROPLAST	HIGH	LOW
CHLOROPLAST SIZE	SMALL	LARGE
GRANAL STACKING	LOW	HIGH
TOTAL CHLOROPHYLL	LOW	HIGH
CHLOROPHYLL a:b RATIO	HIGH	LOW
NITROGEN	HIGH	LOW
e^- TRANSPORT CARRIER POOL SIZE	LARGE	SMALL
QUANTUM YIELD EFFICIENCY	HIGH	LOW
CARBOXYLATION CAPACITY	HIGH	LOW
PHOTOCHEMICAL QUENCHING	HIGH	LOW

photosynthetic efficiency of the leaf (e.g., Evans et al 1988). In the light reaction component, shade acclimation is associated with greater PSII than PSI to maintain energy balance since there is a higher flux of 700 nm light than 680 nm in the shade (Björkman et al 1972a, Chow et al 1990a,b). This leads to a lower chlorophyll a to b ratio in shade plants (Willmot and Moore 1973, Wild 1979, Wallace and Dunn 1980, Sims and Pearcy 1989, Thayer and Björkman 1990, Dale and Causton 1992) as Chl b makes up 36% of PSII and only 10% of PSI (Nobel 1991). Light limitation can also increase the overall level of the light harvesting pigments per unit leaf weight and per unit leaf nitrogen (Loach 1967, Logan and Krotkov 1968, Young and Smith 1980, Björkman 1981, Langenheim et al 1984, Evans 1989a,b, Igbuanugo 1989, Masarovičová and Štefančík 1990, Strauss-Dibenedetti and Bazzaz 1991) but not per unit leaf area (McMillen and McClendon 1983, Pearcy 1987, Sims and Pearcy 1989, Adamson et al 1991). Electron transport carrier pool size and the number of coupling factor sites (CF) on the thylakoid (where ATP synthesis occurs) are both lower in shade-grown plants (Boardman 1979, Osmond 1987) consistent with the reduced influx of photon energy they receive. Changes in the chloroplast ultrastructure include more appressed versus nonappressed grana in shade plants and smaller but more tightly packed chloroplasts (Björkman et al 1972a, Wild 1979, Kasperbauer and Hamilton 1984, Igbuanugo 1989, Vidal et al 1990, Adamson et al 1991); these alterations should increase the photosynthetic surface per unit leaf area to improve the interception of both diffused light and sunflecks.

In the Calvin cycle, the amount of the major carboxylation enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is lower in shade acclimated plants (Wild 1979, Björkman 1981, Terashima and Evans 1988, Chow et al 1991). Since 15-30% of leaf N is invested in Rubisco (Chapin et al 1987, Sage et al 1987), there is a direct relationship between total leaf N and carboxylation enzyme activities (Sage et al 1987, Seemann et al 1987, Suzuki et al 1987, Evans and Terashima 1988, Evans 1989b). Several reports confirm the lower leaf N in shade-grown leaves (Wallace and Dunn 1980, Gulman and Chu 1981, Langenheim et al 1984, Pearcy 1987, Walters and Field 1987, Fredeen et al 1991, Ramos and Grace 1990, Strauss-Debenedetti and Bazzaz 1991). Since shade leaves are exposed to long periods of low diffuse light, high levels of Calvin cycle intermediate metabolites will likely be underutilized. This is consistent with Seemann et al's (1987) observation that plants grown in high irradiance have significantly greater Calvin cycle metabolite concentrations. The carboxylation process is initiated by light activation of Rubisco through the activities of CA1P (2-carboxyarabinitol-1-phosphate, a Rubisco inhibitor) and Rubisco activase (Kobza and Seemann 1988, Seemann et al 1988). We would expect this inductive process to be greater in shade-acclimated plants since quicker response to sunflecks plays an important role in the carbon balance of understory plants. While direct biochemical measures of the activation kinetics is lacking, shade plants appear to show greater photosynthetic induction response to sunflecks (Chazdon and Pearcy 1986a,b).

Leaf structures- Leaf anatomical changes in the shade, first described by Stahl in the 1880s, include smaller mesophyll cells and usually only a single layers of palisade cells (compared with 2-3 layers in the sun) leading to a thinner lamina (Penfound 1931, Wylie 1951, Jackson 1967, Willmot and Moore 1979, Chabot and Chabot 1977, Jurik et al 1979, Wild 1979, Young and Smith 1980, Carpenter and Smith 1981, McClendon and McMillen 1982, Corré 1983, Smith and Martin 1983, Oberbauer and Strain 1985, Goulet and Bellefleur 1986, Yun and Taylor 1986, Bonger and Pompa 1988, Lee 1988, Vidal et al 1990, Adamson et al 1991). Correlated with the thinner leaf, specific leaf mass (SLM) is also reduced in the shade (Chabot and Chabot 1977, Wooge and Barden 1987, Koike 1988) leading to a corresponding decrease in maximum photosynthetic capacity of the leaf per unit area (see Leaf Physiology for references). There is also a strong pattern of increasing stomatal density with higher SLM within and across species (Young and Smith 1980, Abrams 1986, Smith and Martin 1987, Bonger and Pompa 1988, Abrams and Kubiske 1990, Masarovičová and Štefančík 1990). As assimilation at high irradiance including sunflecks is partly limited by stomatal conductance (Woods and Turner 1971, Pearcy et al 1985, Pearcy 1987), higher stomatal density and larger stomatal pore size may be considered adaptive in high irradiance environments.

Leaf physiology- Shade acclimation in assimilation is thought to involve the scaling down of the photosynthetic apparatus (i.e. single palisade mesophyll layer, lower SLM, lower Rubisco activity) to lower the respiratory demand and the light compensation point (Ramos and Grace 1990). Leaf density and thickness are highly correlated with area-based photosynthesis (Pieters 1960, McClendon 1962, Chabot and Chabot 1977, Ledig and Korbobo 1983, Jurik 1986, Walters and Field 1987, Koike 1988, Pompa and Bonger 1988, Reich et al 1991, Sims and Pearcy 1991, Turnbull 1991). Within species, dark respiration is lower in shade-grown individuals having lower SLM (Loach 1967, Chabot and Chabot 1977, McMillen and McClendon 1983, Langenheim et al 1984, Walters and Field 1987, Fredeen and Field 1991). Plants acclimated to extremely shady conditions can have a light compensation point as low as 2.5 μmol m^{-2} s^{-1} or 0.13% of full sunlight (a fern Trichomanes elegans [Lee 1986] and a marine alga Ulva lactuca [Sand-Jensen 1988]). Along with an improved utilization of dim light, shade-grown plants have a lower photosynthesis at saturating PPFD. This tradeoff is considered adaptive since prolonged exposure to high light levels is rare in these environments except in the form of sunflecks.

Chapter 2 addresses the question: what chloroplast level traits show acclimation to simulated gap and shade regimes among forest maple seedlings? Chloroplast level traits such as nitrogen and chlorophyll content, Rubisco activity and the electron transport capacity are important leaf properties that are expressed in assimilation potential and quantum use efficiency. These are properties that can increase the marginal carbon budget in a light-limited environment or prevent photoinhibition in excessive light conditions, both critical to the survival of a plant. I assess whether these traits in Acer species change in ways consistent with adaptive expectations such as the tradeoff between light and dark reaction activities (Osmond 1987) and how are steady-state and transient (lightfleck response) rates of carbon assimilation influenced by chloroplast level activities.

Physiological responses to sunflecks have received considerable attention in recent years because of their importance in the total carbon budget for forest understory plants (Pearcy 1990, Chazdon and Pearcy 1991). A shade-acclimated plant ideally ought to possess features that maximize its capture and utilization of sunflecks. These features include a monolayer leaf canopy (discussed below), high stomatal conductance (g_s) in dim light to facilitate greater gas exchange and more rapid induction of the carboxylation process (i.e. the rate of reaching steady-state photosynthesis). There is evidence suggesting that shade-tolerant plants do maintain a higher g_s in dim light (Woods and Turner 1971) and attain a higher state of photosynthetic induction (Chazdon and Pearcy 1986a). By reaching a higher induction state when exposed to a sunfleck and minimizing the loss of induction during "darkflecks", an understory plant could maintain a greater seasonal carbon budget and can potentially attain a growth advantage over its less acclimated neighbours. However, at present, it remains unclear how leaf biochemical and structural characters might influence sunfleck utilization, particularly in woody species.

Chapter 3 examines the physiological response of maple seedlings grown under gap and shade irradiance levels. I will focus on the properties of seedling response to lightflecks. Although the energetic importance of sunflecks (Chazdon 1986b, 1988) and their link to understory seedling growth and survival (Pearcy 1983, 1990) is known, we are less certain about what functional traits (such as SLM, stomatal density and leaf nitrogen) confer superior photosynthetic induction to sunflecks or how variation in these traits among species and between light treatments influence the rate of induction. In this study, I ask the question do gap-light-acclimated traits associated with high steady-state photosynthesis compromise a seedling's ability to use lightflecks effectively?

Whole plant structure- Given the low margin of carbon balance, the aboveground architecture of a plant in the forest understory can have a significant influence on its growth and survival. A monolayer branching structure presents the most efficient light intercepting surface (Horn 1971) with minimum self-shading. This growth form is achieved through increased lateral branch extension (sympodial shoot) or a flexible main stem (Veres and Pickett 1982, Chabot-Jacquety et al 1986) and it sacrifices vertical height extension for a broader canopy. The selective advantage of sympodial growth form is demonstrated in Japanese maple species where 40% of subcanopy species were sympodial while it is only 20% in canopy species (Ogata 1965, Sakai 1990a). While there is an apparent architectural dichotomy among the adults of the maple species, it is not certain what developmental program juvenile maples follow growing in the same understory environment.

Consistent with the economics of biomass allocation (Bloom et al 1985), plants grown in dim light invest proportionally more to shoot than root in herbaceous (Cid-Benevento and Werner 1986) and woody species (Marks 1975) to improve the capture of photon energy. When irradiance levels are high, maintenance of photosynthetic activities impose a greater demand on water and nutrient supply by fine root growth. For light limited woody plants, however, the critical factor is how to effectively partition the aboveground biomass to maximize light interception. While the non-productive woody tissue function as carbon sink limiting resources available to the photosynthetic apparatus, it is necessary for the display of leaves and provide structural integrity to the plant. Higher efficiencies of leaf display (leaf area to stem mass) could improve the whole plant performance of understory plants (Chazdon 1985, 1986a, Canham 1988a, Lee 1988). To infer the presence of adaptive geometry, we need to clearly demonstrate the link between plant architecture and the relative whole plant performance in light limited environments.

III. Persistence and survival of understory tree seedlings

Forest tree seedlings experience high levels of mortality in their first years of growth ranging from 35% in Acer saccharum (Hett and Loucks 1971) to 88% in A. pensylvanicum (Hibbs 1979) and 100% in several shade intolerant tropical species (Augspurger 1984a,b). The major causes of mortality in the first year are often fungal and pathogen infections in the moist understory environment (Vaartaja 1962, Auspurger 1984a,b,c, Khan and Tripathi 1991). After surviving the first year, during which the seedling may be sustained by the nutrient reserve in the cotyledons (Grime and Jeffrey 1965, Augspurger 1984a), further growth and survival are critically dependent of autonomous energy capture and appropriate resource allocation. Significant loss of older seedlings under closed forest canopy is evidently due to a failure to maintain a positive carbon budget particularly when seedling density is high (Harper 1977), as in a patch of forest floor immediately following canopy gap closure. Both seedling survival rates and densities were higher in forest gaps relative to adjacent shaded sites (Augspurger 1984a,b, Oberbauer and Strain 1985). Since gaps are ephemeral, rapid response in growth before canopy closure could confer considerable competitive advantage to a seedling or sapling. Most canopy trees undergo several bouts of rapid growth during rare gap events to reach the forest crown (Canham 1985, Runkle and Yetter 1987, Runkle 1990). An Acer saccharum seedling may spend 90 years and three gap events in the understory before reaching the canopy crown (Runkle 1982, Canham 1985); adult fitness in this canopy species thus depends on both its ability to ascend to the forest crown during accelerated growth in forest gaps and its persistence through the deeply shaded interims. In contrast, a subcanopy species such as A. pensylvanicum may require only a single gap to attain mature size (Wilson and Fischer 1977, Hibbs et al 1980). While we know maple seedlings are capable of surviving under closed canopy for more than 15 years (Hett and Loucks 1971, Hibbs 1979), direct demonstrations of what functional traits confer such shade persistence is lacking. Given that seedling growth performance in height and biomass accumulation contribute substantially to increased juvenile survivorship and earlier age of reproduction, by measuring those plant traits that affect seedling growth, we can begin to make useful inferences on the contribution of traits to components of fitness in maples.

If we accept light as the main physical factor of selection in the understory shade and gap environments (Woodward 1990), then two tree seedling properties could carry significant adaptive value. First, under a closed canopy, the seedling must persist with marginal net carbon gain until the next gap opening (Björkman 1981, Teskey and Shrestha 1985). This may include efficient leaf display, low respiratory costs to roots and shoots, high assimilation rates in low diffuse irradiance and high rates of physiological induction to sunflecks. Second, with the creation of a gap, a seedling must respond rapidly with increases in size and height before crown closure. This requires the appropriate shift in leaf traits to utilize the increased irradiance and a priority to height extension. Clearly, these two properties involve the functional integration of processes ranging from the chloroplast to the pattern of biomass allocation. Recent studies have demonstrated the need to consider a suite of traits to effectively characterize the functional structure that influences reproductive fitness in herbaceous species (Maddox and Antonovics 1983, Lechowicz and Blais 1988, Farris and Lechowicz 1990); there have been no similar studies on how traits interact in woody species to affect whole plant performance.

Chapter 4 addressed the question: how do we best account for variations in seedling growth based on an integration of key functional traits in maple species? Since growth is largely determined by the interaction among traits that affect the production and utilization of carbon, in this study, I will consider the effect of both photosynthesis and wood and root activities on growth. In long-lived woody seedlings, gains in size and height are linked to survival and competitive ability (King 1990a,b, Kohyama 1987, Kohyama and Hotta 1991). Since subcanopy species mature in the understory, it is reasonable to expect even the seedlings to maintain a broad plant canopy that improves light interception. To attain reproductive size, canopy seedlings must place a growth priority on the vertical ascent to the forest crown but this could compromise their ability to persist under a closed canopy. I will verify these expectations by measuring the relative growth rates of height, total twig length and stem basal diameter between canopy and subcanopy seedlings.

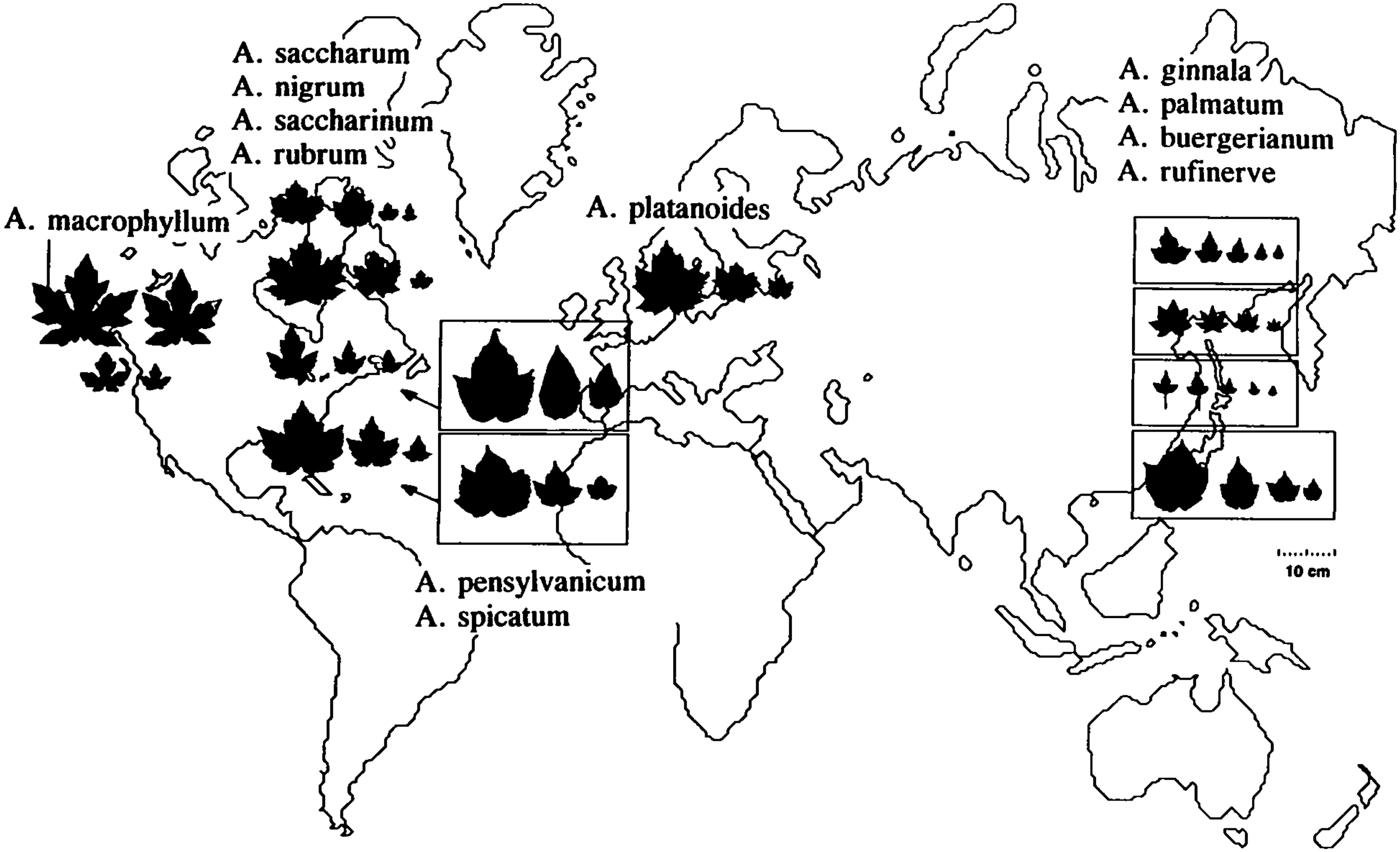
Part 2. General approach to the study

I. The Acer species

The choice of Acer species in this broad comparative study is based on the unambiguously defined taxonomy of this genus and the diverse species occurring in Asia, Europe and North America (Cronquist 1981, Röhrig and Ulrich 1991). By selecting a group of Acer with similar ecological association within the temperate forest but diverse in geographical origins (Figure 2, Appendix 1) and growth forms, a sound basis for quantitative comparison of variations in process and performance is established.

The genus Acer L. has about 140 species of evergreen and deciduous trees in the family Aceraceae (Order Sapindales). Acer shares the family with one other genus Dipteronia with two species in China. The most recent systematic treatments of Acer (Ogata 1967, De Jong (1976) both depend heavily on floral morphology and gender expression; Tanai (1978) classified the genus based on leaf vein architecture and Fang (1981) presents a more classical treatment of Chinese Acer (comprising 70% of all species). The earliest fossil record of Acer is from the early Tertiary in the Northern Hemisphere (Tanai 1978). While continental disjunction between the eastern Asia and eastern North American has existed since mid-Tertiary (White 1983), close phyletic affinity is still evident: for example, A. rufinerve (Asia) - A. pensylvanicum (eastern North America), A. ukurunduense (Asia) - A. spicatum (eastern North America) (Li 1952); A. japonicum (Japan) - A. circinatum (western North America) (Kruckeberg 1983). Relative to Asia, the lower species diversity of maples in North

Figure 2. The geographical origins of the Acer species used in the study. Each set of leaves shows the typical range of size and form for each species with the middle leaf or leaves representing the mean. Subcanopy species are framed and canopy species unframed. No canopy species from Asia were successfully established in sufficient quantity to use in these experiments. Acer platanoides has only a European distribution range.


A. saccharum
A. nigrum
A. saccharinum
A. rubrum
A. macrophyllum
A. platanoides
A. ginnala
A. palmatum
A. buergerianum
A. rufinerve
A. pensylvanicum
A. spicatum
10 cm

America and Europe is attributed to the effect of repeated widespread glaciation in the Quaternary (Davis 1983, White 1983). All Acer species are hypostomatous and have diffuse-porous wood anatomy (Ogata 1967, Powers 1967).

In this study, 12 Acer species representing two growth form classes (canopy and subcanopy) were raised from seed to provide the basis for the comparison among congeners. Figure 2 illustrates the geographical sources and the common leaf sizes and forms of each Acer. Growth form classes were determined based on published height and habitat data (Fang 1981, Fowells 1965, Hosie 1979, Ogata 1965,1967, personal observations). In general, the average reproductive size of subcanopy species are 5m, and >30 m for canopy species. To assess the within species variations, two populations from each species were used (Chapter 2-4). Seeds were acquired from various commercial, research institute and personally collected sources (Appendix 1). Germination procedure, dates of seedling establishment and greenhouse rearing conditions for the maple seedlings are also given in Appendix 1.

II. Functional design through trait integration

To make the link between process (i.e., the functional design) and performance (i.e., relative growth rate, RGR) that forms the basis for the adaptive argument, I monitored a suite of structural and physiological traits and determined the RGR in height, total twig length and basal diameter in the seedlings of 12 Acer species. The seedlings were 2-3 years old thus avoiding responses that might be confounded by cotyledon reserves if first-year seedlings were used. The seedlings were transferred to the experimental treatments from a common growth environment in the McGill Phytotron (about 50% full sun exposure). This in effect simulates the process of canopy closure for those seedlings placed in the shade treatment and continued gap exposure for gap treatment seedlings. Since maple leaf morphology is strongly determined by irradiance level during leaf expansion (Isanogle 1944, Critchfield 1971, Goulet and Bellefleur 1986) and less affected by early leaf primordia development in the previous summer (such as in *Fagus sylvatica*, Eschrich *et al* 1989), the overall effect of the previous growth environment on the experimental seedlings is considered minor in comparison to their responses to the experimental treatments.

A previous study of three co-occurring maple species in eastern North America showed that relative to the two subcanopy species *A. pensylvanicum* and *A. spicatum*, saplings of the canopy species *A. saccharum* had tougher leaves and greater wood density (Lei and Lechowicz 1990). For *A. saccharum*, these are traits beneficial to the adult canopy tree that are already expressed in the sapling stage. From these results, we suggest that juveniles of canopy and subcanopy maples may follow different developmental programs dictated by the constraints imposed on the adult tree. Using a larger set of species representing the two growth forms, this study is better able to quantitatively evaluate the variation among canopy and subcanopy seedlings across a broad range of functional traits.

This integrated approach to assessing the effect of a suite of interacting traits on the growth of tree seedlings addresses a past deficiency in the ecophysiological literature. Although evidence for the functional significance of differences in structure and physiology among hardwood trees abounds (e.g., Hicks and Chabot 1985, Givnish 1986), very few studies have attempted to relate functional traits with overall measures of plant performance, such as growth and competitive ability (e.g., Küppers 1984a,b,c, 1985). Although the link between single traits and fitness is not always apparent (e.g., Lechowicz 1984), changes in plant characters in different environments are often viewed as functionally adaptive without direct reference to the overall growth responses (e.g., Boardman 1977, Wallace and Dunn 1980). Recent studies have demonstrated the need to consider the interaction among somatic traits such as photosynthetic capacity and resource allocation patterns in determining whole-plant success (e.g., Chapin *et al* 1987, Lechowicz and Blais 1988, Evans 1989, Farris and Lechowicz 1990). This approach emphasizes a parsimonious depiction of functional complexity, while avoiding facile adaptive inferences. Such studies in woody perennials are virtually absent (but see Atipanumpai 1989, Ceulemans 1990) yet critical to our understanding of the fitness consequences of resource limitation in long-lived species.

I used path analysis for the integrated assessment of process and performance (Wright 1921, Li 1975). This is a multivariate analytical method that allows the investigator to construct a functional design model (the path diagram, Figure 1, Chapter 4) that depicts the relations among a parsimonious set of traits and their effect on whole plant performance (e.g., Kinsolver and Schemske 1990, Mitchell 1992). While earlier applications of path analysis dealt with intraspecific functional processes (e.g., Evans 1989, Farris and Lechowicz 1990), this study attempts to capture the effect of intrageneric variation in functional traits on maple growth. This "maple" model assumes that these closely related species share a common Bauplan. In comparing congeners, the interpretation of the contribution of particular functional processes to variations in performance will be less confounded by extraneous causes arising from phylogenetic differences. In effect, this approach increases the power of functional interpretation from a single species to a broader phenotypic range and still retains the necessary taxonomic resolution.

CHAPTER 1: The effects of light quality and quantity on seedlings of 11 canopy and subcanopy Acer species

Abstract

Two- and three-year-old seedlings of 5 canopy and 6 subcanopy Acer species were grown under three light treatments: "gap" (PPFD=400 μmol m^{-2} s^{-1}; R:FR=1.12), "shade" (PPFD=50 μmol m^{-2} s^{-1}; R:FR=0.6), and "overcast" (PPFD=30 μmol m^{-2} s^{-1}; R:FR=1.03). Gap seedlings had significantly greater height growth, greater specific leaf mass (SLM), higher root:shoot ratio and higher maximum photosynthetic rate compared with both the shade and overcast treatments. The R:FR ratio difference between shade and overcast had no significant affect on plant traits. These results suggest that, in maple seedlings, shade acclimation is mainly a response to light intensity and that R:FR plays only a minor role in induction of shade characteristics. This is consistent with other findings that only shade intolerant herbaceous and woody species exhibit a strong "shade avoidance" response to lowering R:FR ratio. The lack of R:FR response prevails regardless of differences in the adult size of canopy and subcanopy species and the associated contrasts in juvenile traits. Given that shade tolerance is critical to maple seedling survival in the forest understory, a shade avoidance response suited to species growing in open habitats may not have a selective advantage.

Introduction

Light quantity traditionally has been considered the most apparent factor affecting plant growth in the forest understory (e.g., Björkman 1981) while light quality has been considered to act only on more specific stages of understory life history such as seed germination (e.g., Smith 1981, Vasquez-Yanes and Smith 1983). Light quality, specifically red to far red ratio (R:FR), is frequently cited as an important factor for growth in more ruderal environments where shading has a more immediate impact on the fitness of sun-adapted plants (e.g., Smith and Morgan 1983, Ballaré et al 1987). Although there is a concurrent reduction of both PPFD and R:FR under increasing foliage shading (Lee 1987), in some situation such as coastal fog forest and montane cloud forest (e.g., Vogelmann 1973, Cavelier and Goldstein 1989), vegetation is often exposed to low PPFD but R:FR more similar to direct sunlight (Gates 1980). There are strong indications that plants are able to detect changes in light quality (R:FR) by phytochrome and light intensity (Blue light 400-500 nm) by cryptochrome; photomorphogenetic changes appear to occur under a yet unspecified interaction between the two photoreceptors (Morgan and Smith 1981; Mancinelli 1989). This suggests that the expression of shade-adapted or shade-avoidance characters may be the result of an integrated perception of both light intensity and R:FR ratio. Casal and Smith (1989) suggest that plants can evaluate the light environment by weighing changes in PPFD versus R:FR and respond adaptively.

Several recent experiments have shown that shade intolerant herbaceous and woody seedlings respond to reduced R:FR in ways consistent with an attempt to avoid shading by neighbours (e.g., Ballaré et al 1987; Casal and Smith 1989; Warrington et al 1989). Morgan et al (1983) found spruce seedlings responding to changing light quality by greater stem extension, a response similar to the ruderal herbaceous species (Morgan and Smith 1979). Low R:FR also promotes epicotyl growth of Pinus thunbergii (Morikawa et al 1976) and increase in stem extension in European oak (Quercus robur) (Axelsson et al 1979). Older seedlings of both Australian softwoods (Warrington et al 1989) and leguminous vines (Lee 1988) show increased shade-avoidance behaviour such as greater internodal length when low PPFD was combined with low R:FR compared with high R:FR. It appears then that seedlings of light-demanding woody species show shade-avoidance growth similar to ruderal herbs but more shade-tolerant tropical and coniferous species are less responsive to changes in light quality (Kwesiga and Grace 1986; Warrington et al 1989).

The present study of eleven Acer species is the first to test the effects of both light intensity and R:FR on temperate hardwood trees. Acer seedlings growing in the forest understory experience persistently low diffuse light of low R:FR ratio punctuated periodically by sunflecks of high PPFD and R:FR. Some Acer species reach maturity only after reaching the forest canopy (e.g., A. saccharum) while others complete their life cycle entirely in the subcanopy (e.g., A. pensylvanicum). Studies by Lei and Lechowicz (1990) and Sakai (1990a,b) agree that there is a difference in structure between the two life history classes of forest species of Acer. Canopy species even in the seedling stage, express traits such as stronger wood and tougher leaves that are more adapted to demands of the seedlings' canopy position at maturity. Seedlings of canopy species that must reach the forest crown to reproduce should respond more strongly to an increase in R:RF ratio as a cue to the occurrence of a canopy gap, while subcanopy species may be more shade-tolerant and less responsive to changing light quality. Early growth response to a gap opening might be considered adaptive, but is it sufficient to increase R:FR alone to effect such changes in plant traits that represent a "gap" response or must PPFD also increase? Given the critical importance of canopy gaps in maple ecology (Wilson and Fischer 1977, Hibbs et al 1980, Canham 1985, 1988a), that is the question addressed experimentally in this chapter.

Methods and Materials

To address the question of light quantity and quality responses in juvenile Acer, seedlings of 5 canopy and 6 subcanopy species were grown under three light regimes that simulate a forest gap (intensity and R:FR both high), a closed canopy (intensity and R:FR both low), and an "overcast" environment (intensity low and R:FR high). Structural and physiological traits and growth among the light regimes were compared to partition the effect of light quality and R:FR ratio in species and in life history classes.

The two- or three-year-old seedlings of eleven Acer species used in the experiment (Figure 1) were raised from seed in a common environment in the McGill Phytotron. In April 1990, the seedlings were transferred to a lath house at the university's Mont St. Hilaire Research Centre (45°33'N, 73°09'W) where leafing out took place in the light treatments described below. Seedlings were grown in cylindrical Plexiglas "rhizotrons" (7.7cm in diameter and 61cm in height) filled with commercial top soil (Fafard et Fréres Ltée, St. Guillaume, Quebec) and covered with an opaque plastic wrapping that could be removed to assay root characters. During the experiment, seedlings were fertilized with Hoagland's solution (Dunn and Arditti 1968, Version 2) once a week, and watered regularly.

Experimental plants were arranged in four blocks in each treatment, one seedling per species-population per block. There was minimum shading from neighbouring plants. Analysis of variance showed no significant block effect in traits measured and block effects will not be considered in subsequent analyses. Plants were taken temporarily indoors (by random treatment and block) and placed under standard lighting conditions for dynamic and steady-state gas exchange measurements.

Experimental light treatments

Acer seedlings were grown under three light treatments in the lath house: gap, shade and overcast. The gap treatment with lath covering the compartment's roof and sides simulated a relatively small forest gap. The lath with 37% open area reduced irradiance to an average of 400 μmol m^{-2} s^{-1} with a red to far red ratio (R:FR) of 1.1 (Figure 2). R:FR ratio (photon fluence rate (655-665 nm)/photon fluence rate (725-735 nm; Smith 1981) was measured with a Li-Cor 1800 Spectroradiometer. To simulate a closed forest canopy, the shade compartment was covered with a spectral filter covering the lathed roof and sides to 1 m from the ground. The lower portion of the compartment was shielded with 32% transmittance shade cloth (Les Industries Harnois Inc., St-Thomas-de-Joliette, Quebec). The spectral filter consisted of

Figure 1. Experimental design showing the three treatment light regimes and the Acer species and populations used within each growth form class. Total number of seedlings used in the experiment was 168 (4 replicates per species-population per treatment). For seed source information, see Appendix 1.

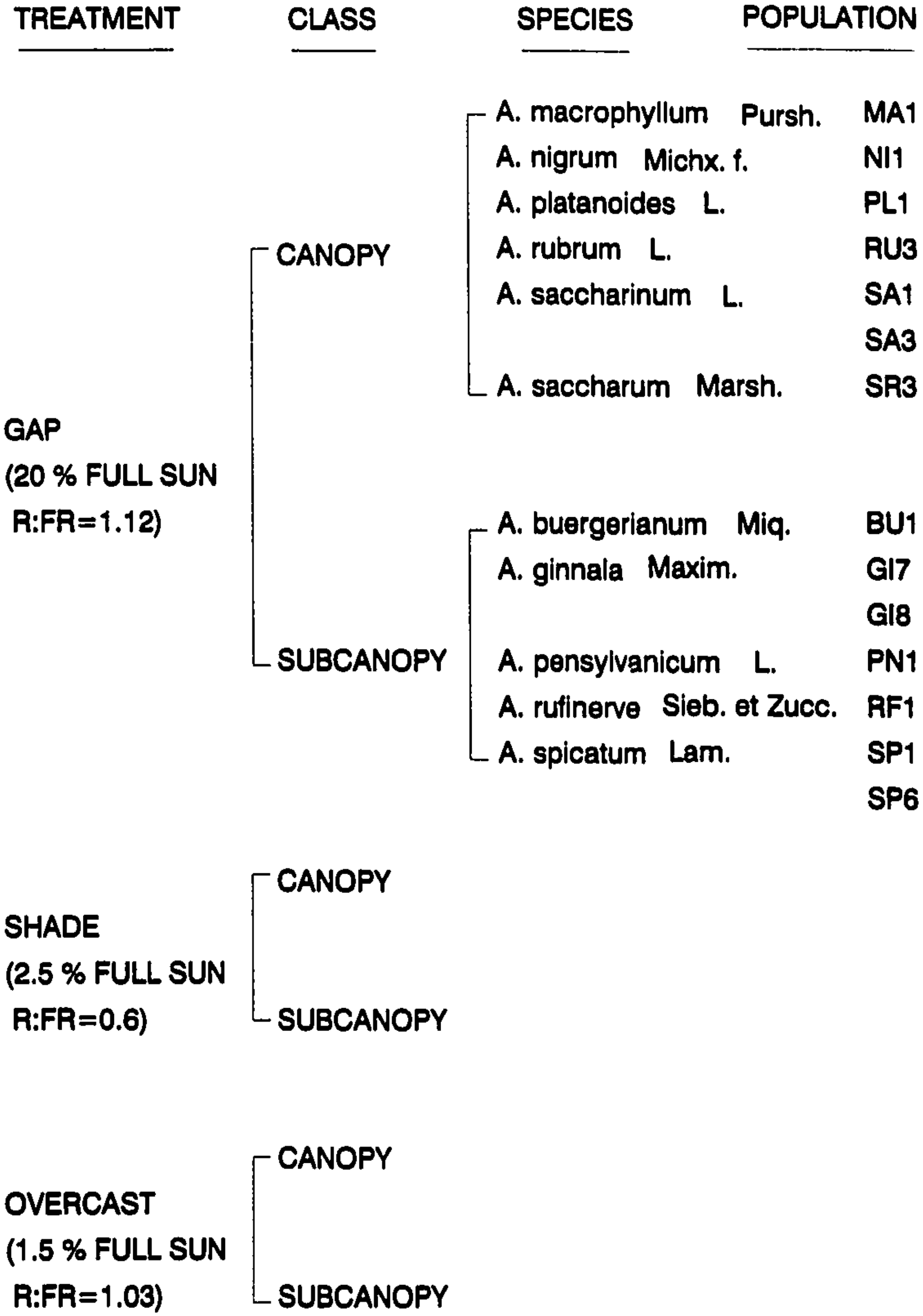
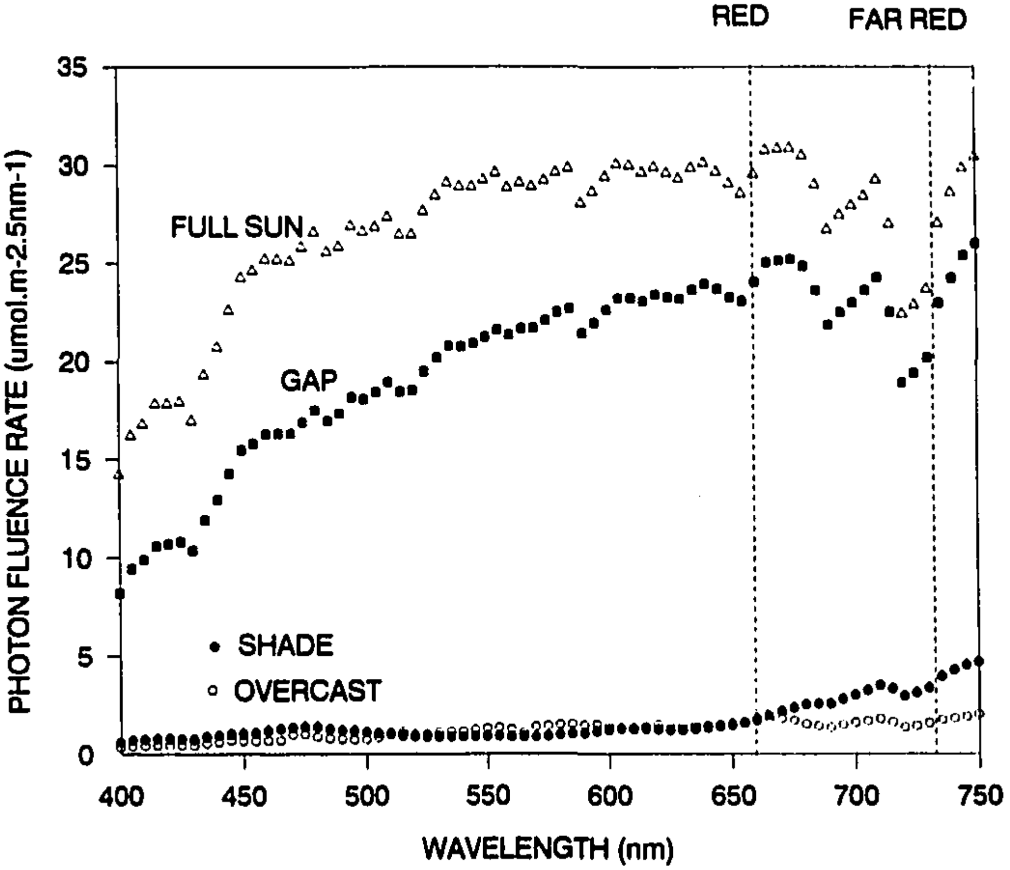

TREATMENT
CLASS
SPECIES
POPULATION
A. macrophyllum Pursh. MA1
A. nigrum Michx. f. NI1
A. platanoides L. PL1
A. rubrum L. RU3
A. saccharinum L. SA1
SA3
A. saccharum Marsh. SR3
CANOPY
GAP
(20 % FULL SUN
R:FR=1.12)
A. buergerianum Miq. BU1
A. ginnala Maxim. GI7
GI8
SUBCANOPY
A. pensylvanicum L. PN1
A. rufinerve Sieb. et Zucc. RF1
A. spicatum Lam. SP1
SP6
CANOPY
SHADE
(2.5 % FULL SUN
R:FR=0.6)
SUBCANOPY
CANOPY
OVERCAST
(1.5 % FULL SUN
R:FR=1.03)
SUBCANOPY

Figure 2. Spectral distribution of the three treatments and of full sun for comparison. Measurements taken at solar noon, August 18, 1990 under clear skies. Red and far red regions are indicated.


RED
FAR RED
PHOTON FLUENCE RATE (umol.m-2.5nm-1)
35
30
25
20
15
10
5
0
FULL SUN
GAP
● SHADE
○ OVERCAST
400
450
500
550
600
650
700
750
WAVELENGTH (nm)

alternating strips of filter pigments (17 cm) and clear (2.5 cm) bands on polyurethane sheet (Durafilm 1, CIL, from Les Industries Harnois Inc.). The banding pattern, perpendicular to the solar track, created alternating sunflecks and shade lasting 2 min and 13 min respectively at the plant level 1.5 m below the lath house roof. The mixture of filter pigments used was 1 g 14-4006 Hostaperm Violet RL SP to 0.25 g HS-100 Solvaperm Yellow G (both from American Hoechst Co., Somerville NJ, USA) dissolved in 30 ml of 3:2 varnish-paint thinner base. The pigment mixture used follows Lee (1985) but without the carbon black. In the shade treatment, mean PPFD was 50 μmol m^{-2} s^{-1} and R:FR was 0.6, but both variables were substantially higher in sunflecks (Figure 2 in Chapter 2). These two treatments represent distinct combinations of light quality and quantity that approximate natural conditions found in forest gap and under closed forest canopy (Minckler and Woerheide 1965, Lee 1987, Messier and Bellefleur 1988). The overcast treatment was designed to simulate the natural light properties of low PPFD and high R:FR prevailing during heavy cloud cover. The treatment consisted of 10% transmittance shade cloth on the roof (without lathe) and 17% transmittance shade cloth on all four sides. Irradiance under this treatment was 30 μmol m^{-2} s^{-1} and R:FR was comparable to gap (Figure 1,2). This treatment provides a combination of light quality and quantity allowing the evaluation of their independent effects on Acer seedling growth by comparison to the shade and gap regimes.

Light chamber design for gas exchange determination

Two complete sets of photosynthetic measurements were taken on June 26-July 2 and July 23-30, 1990. Photosynthesis, leaf internal CO_2 and stomatal conductance were determined with a LiCor 6200 Portable Photosynthetic System (Lincoln, Nebraska, USA). Photosynthetic responses of seedlings were measured under standard artificial light conditions in the Mont St. Hilaire Research Centre a few meters from the lath house. Plants were acclimated under dim light for at least one hour. Lighting was supplied by a mixed array of fluorescent tubes and incandescent bulbs, mean PPFD was 29 μmol m^{-2} s^{-1} at 124 cm from source and R:FR was 0.95. Photosynthesis was measured under dim light on one randomly selected leaf per plant after the acclimation period. Seedlings were then moved under a GE Cool Beam Flood Lamp (300W PAR 56/2MFL) suspended over a 5 cm thick thermal barrier. Mean PPFD was 1260 μmol m^{-2} s^{-1} and R:FR was 1.9. Estimates of photosynthesis after 0.5 min, 4.5 min and 24.5 min of exposure to this bright light were taken on the same leaf measured under dim light. This procedure simulates the photosynthetic inductive response of a dim-light-acclimated leaf to a saturating sunfleck of the three durations. Photosynthesis at 24.5 min is referred to as A_{max} based on preliminary determinations that the seedling response curves began to plateau at approximately 10 min in all the Acer species. Repeated handling of the same leaf at these time intervals had no affect on the photosynthetic activities.

Plant characters

In June 1990, fine root ($\leq$ 2 mm dia.) density was estimated by counting the number of intercepted fine roots along six circumferences (24.2cm each) of the "rhizotron" at 5, 8, 26, 29, 47 and 50 cm depths. A record of the root positions along the transects was kept on acetate sheet. One month later, a second census was taken at the same positions and by overlapping the two tracings. I estimated fine root production as the number of new roots intercepting the six transect lines on the second census. Production rate is expressed as number of fine roots per cm per day between the censuses. Acer root growth is maintained at a steady rate from June to senescence (Millard and Proe 1991) and root production rates determined in this study are representative of the summer belowground growth activities.

On September 22-23, 1990, abaxial leaf (Acer is a hypostomatous genus; Powers 1967) impressions were made with clear nail polish for stomatal density and pore diameter measurements (Lei and Lechowicz 1990). Impressions were taken from three randomly chosen leaves per plant. We made three stomatal density counts and four stomatal pore diameter measurements per impression.

After leaf impressions were collected, all leaves from each plant were harvested. A random subsample of 10 discs (19.8 mm^2) from 5 leaves was used to determine specific leaf mass (SLM); the remaining tissue was kept in a freezer (-18°C) for subsequent chlorophyll determination. A LiCor Area Meter (Li-3100) was used to measure total leaf area. Lengths and number of shoots on each plant were recorded, leaf, twig and roots were separated and oven-dried for biomass determination. Plant height and basal diameter were measured in May and in September.

Chlorophyll a and b levels were determined on freshly frozen leaves (one pooled sample per tree) using a DMSO extraction method (described in Appendix 2) modified from Hisox and Israelstam (1979). No chlorophyll degradation products were evident as a result of this procedure (Figure 1 in Appendix 2). Leaf N was determined by a standard Kjeldahl digestion method (Lechowicz and Blais 1990 unpublished) using a pooled sample of oven-dried (70°C) leaves for each plant. Ground leaf samples (0.100g each) were digested using 6 selenium catalyst granules, 0.5 g of K_2SO_4, and 5 ml of concentrated H_2SO_4. Average time of digestion was about 90 min. Nitrogen levels obtained were comparable to those reported for mature A. rubrum trees at 1.98% (upper crown) and 1.93% (lower crown) (Erdman and Crow 1988).

Statistical methods

Differences between light treatments, growth form classes and species were analysed using Procedure GLM in SAS (1988) for a three-factor mixed model using the appropriate MS error terms (Table 1). To properly partition the sources of variance, traits without significant interaction terms (at $P=0.05$) were re-analysed using an additive model (by removing the interaction terms); the outcome remained essentially

Table 1. Partitioning of variances in the three-factor mixed model experimental design. Treatments= gap, shade and overcast; class= canopy and subcanopy species. Species and populations used are given in Figure 1. Expected MS were derived from Winer (1971). The appropriate error terms are used in the GLM procedure of SAS.

SOURCE OF VARIATION	TREATMENT EFFECT	DF	EXPECTED MS
TREATMENT	FIXED	2	$E(MS_A)=\delta^2_e+4\delta^2_{AC}+56\delta^2\Sigma(\alpha)$
CLASS	FIXED	1	$E(MS_B)=\delta^2_e+12\delta^2_C+84\delta^2\Sigma(\beta)$
TREAT*CLASS	FIXED	2	$E(MS_{AB})=\delta^2_e+4\delta^2_{AC}+28\delta^2_{AB}$
SPECIES(CLASS)	RANDOM	12	$E(MS_C)=\delta^2_e+12\delta^2_C$
TREAT*SPECIES(CLASS)	RANDOM	24	$E(MS_{AC})=\delta^2_e+4\delta^2_{AC}$

unchanged. Imbalance in the model (in the analysis, the number of species-population was 6 for subcanopy and 7 for canopy class) was a source of concern in the proper estimation of variance terms in the full model. To test the magnitude of this possible effect, data were reanalysed by removing a replicate population from A. ginnala, A. saccharinum (subcanopy), and A. nigrum (canopy, closely related to A. saccharum) subcanopy class; no differences with the original model were found.

Results

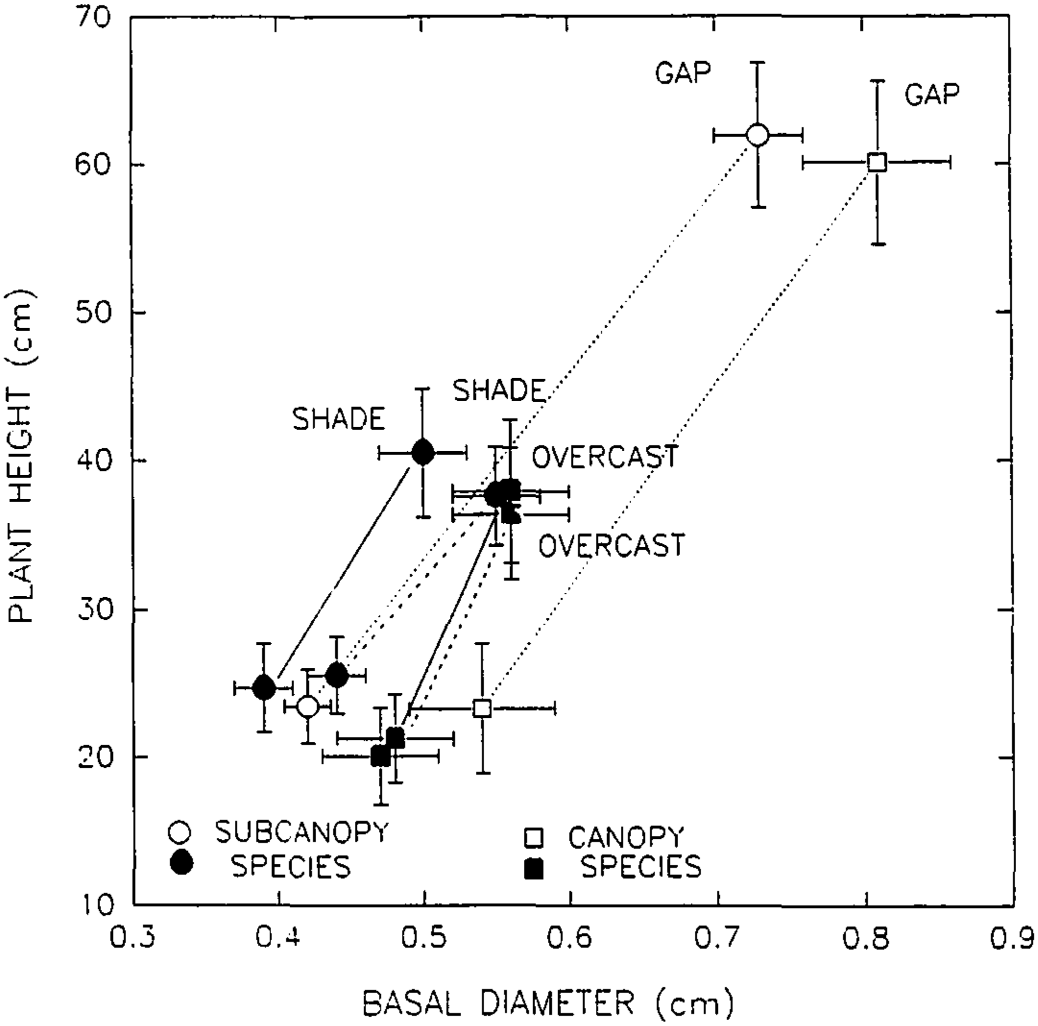
Plant size and shoot growth

At the start of the experiment, the plants randomly assigned to the three light treatments and those in the two growth form classes were all of similar size (Figure 3). At the outset, canopy plants tended to have a larger stem for a given height than subcanopy ones, a reflection of the inherent architectural difference between the two growth form classes. By the end of the experimental season, all seedlings showed significant increase in size. Increases in gap plants were three times greater than in the two low PPFD treatments both of which had seedlings similar in size. In addition, there were no differences between shade and "overcast" seedlings in apical shoot length and the sum of all current year twig lengths (not shown). Difference in R:FR in the two low PPFD treatments did not have an effect on stem growth of maple seedlings.

Leaf and root structural traits

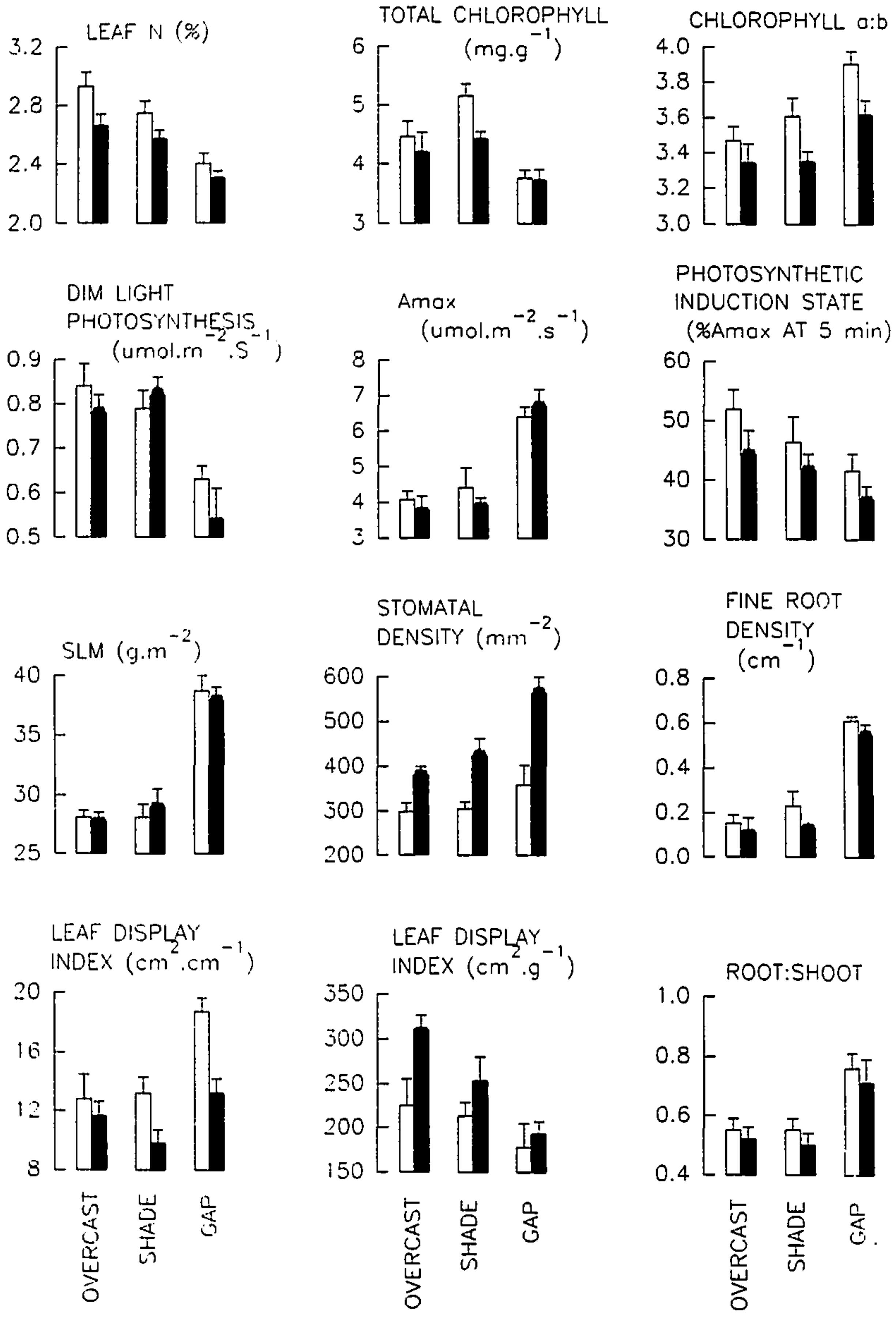
Leaf characters were significantly different between gap and the two low light (shade and overcast) treatments but showed no difference between the two low irradiance treatments. SLM, leaf display index (total leaf area/total twig length), root:shoot ratio and fine root density were lower in shade and "overcast" and significantly higher in gap (Figure 4). Higher SLM was associated with thicker leaves and greater

Figure 3. _Acer_ seedling size (mean ± 1SE) before (lower point of each pair) and after (upper point of each pair) the experiment. Each point represents the mean of 28 plants (seven species-populations, 4 replicates each; see Figure 1).



GAP
GAP
SHADE
SHADE
OVERCAST
OVERCAST
○ SUBCANOPY
● SPECIES
□ CANOPY
■ SPECIES
PLANT HEIGHT (cm)
BASAL DIAMETER (cm)
10
20
30
40
50
60
70
0.3
0.4
0.5
0.6
0.7
0.8
0.9

Figure 4. Summary histograms of traits in Acer seedlings representing the canopy (open bar) and subcanopy (solid bar) growth forms when grown under the three light treatments. Each bar represents the mean (+1SE) of 28 plants (seven species-populations, 4 replicates each; see Figure 1).


LEAF N (%)
3.2
2.8
2.4
2.0
TOTAL CHLOROPHYLL (mg.g⁻¹)
6
5
4
3
CHLOROPHYLL a:b
4.0
3.8
3.6
3.4
3.2
3.0
DIM LIGHT PHOTOSYNTHESIS (umol.m⁻².S⁻¹)
0.9
0.8
0.7
0.6
0.5
Amax (umol.m⁻².s⁻¹)
8
7
6
5
4
3
PHOTOSYNTHETIC INDUCTION STATE (%Amax AT 5 min)
60
50
40
30
SLM (g.m⁻²)
40
35
30
25
STOMATAL DENSITY (mm⁻²)
600
500
400
300
200
FINE ROOT DENSITY (cm⁻¹)
0.8
0.6
0.4
0.2
0.0
LEAF DISPLAY INDEX (cm².cm⁻¹)
20
16
12
8
LEAF DISPLAY INDEX (cm².g⁻¹)
350
300
250
200
150
ROOT:SHOOT
1.0
0.8
0.6
0.4
OVERCAST
SHADE
GAP
OVERCAST
SHADE
GAP
OVERCAST
SHADE
GAP

photosynthetic capacity (A_{max} in Figure 4). Leaf display index refers to the amount of photosynthetic surface area to woody support structure; the greater the ratio, the more efficient the display of assimilation surface. Canopy seedlings had more efficient display relative to subcanopy in all three treatments. Gap plants allocated more assimilates to the roots resulting in 70% of total biomass belowground versus 50% in the low PPFD treatments. This pattern is reflected in the fine root density in which gap plants were three times denser than the other treatments. As expected, fine root production rates (FRP) was also much higher in gap plants but when FRP rates were estimated per unit total root density, there were no difference between treatments: the daily fine root replacement was approximately 3% per plant in July. Root architecture appears similar among species except in A. spicatum which produced more numerous slender roots. Stomatal density was lower in low PPFD treatments; there was greater variation in stomatal density in subcanopy species compared with canopy species.

Leaf biochemical traits

Leaf N and chlorophyll content followed expected trends between high and low PPFD treatments: leaf N was significantly higher in shade and "overcast" plants and subcanopy plants tended to show lower leaf N than canopy plants at each treatment. Chlorophyll a:b was significantly higher in gap plants of each class (Figure 4) but gap plants had lower level of total chlorophyll (3.7 mg g^{-1}) than shade (4.8 mg g^{-1}) and "overcast" (4.3 mg g^{-1}). The trend of lower chlorophyll a:b in subcanopy plants in each treatment is the result of 10% lower chlorophyll a content relative to canopy plants. Between the two low PPFD growth environments, the level of total chlorophyll was higher in the shade (low R:FR) than in the "overcast" (high R:FR) treatment; Chl a:b showed only a marginal corresponding increase in these two treatments.

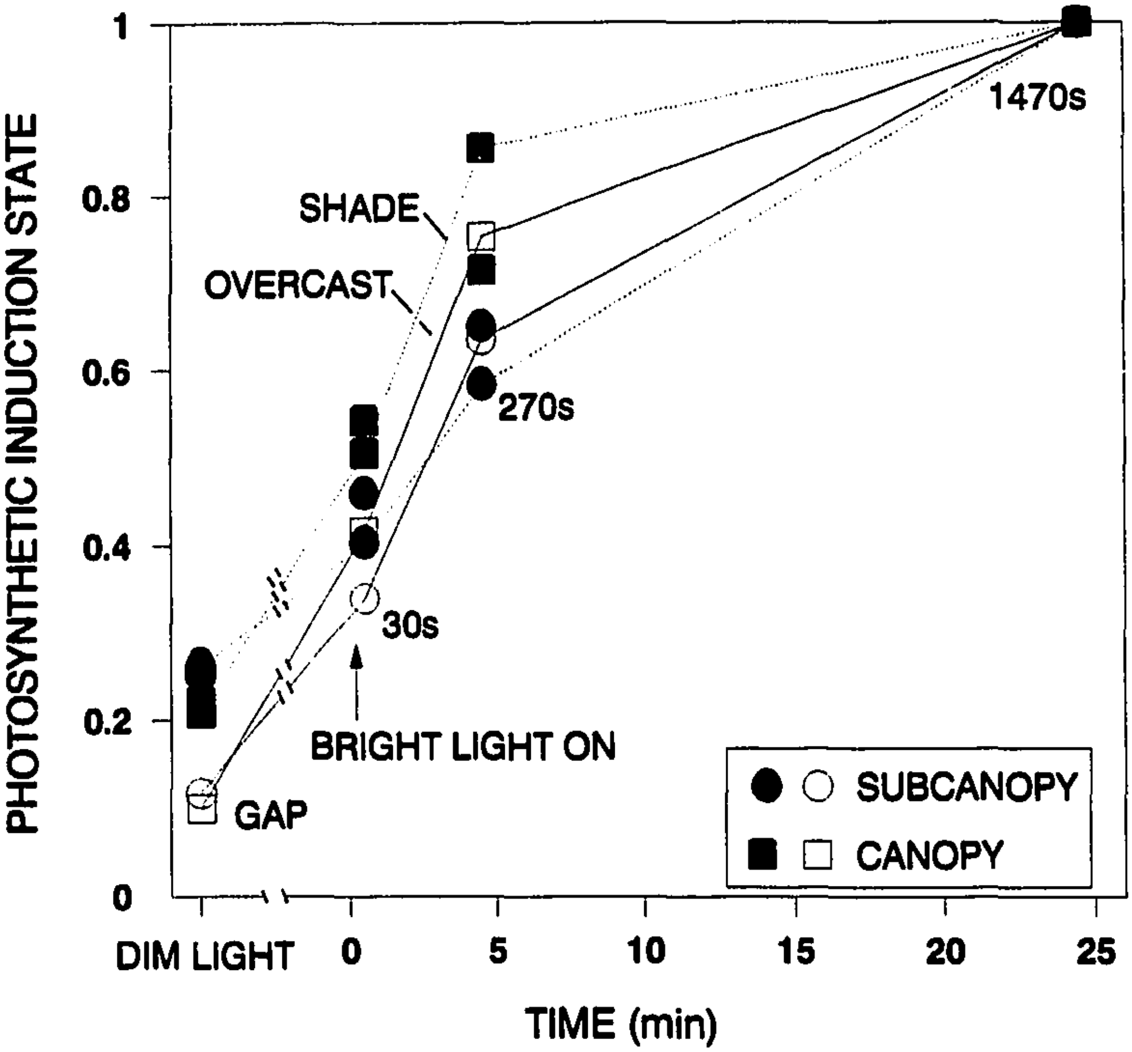
Physiological traits

Gap-grown plants attained higher maximum photosynthetic rates (A_{max}) when they were monitored under saturating artificial light (Figure 4). This is consistent with their higher SLM which is correlated with assimilation potential. Plants in the low PPFD treatments did not reach the same level of A_{max} but were able to maintain significantly higher assimilation rates under low artificial light. These results indicate that there is a trade off in photosynthetic performance under saturating and dim lights for all Acer seedlings affected by the light regime during growth. Again, R:FR appears to have no effect on photosynthesis between the two low PPFD treatments. Low PPFD seedlings were initially able to attain a higher state of induction than gap plants (Figure 5). They maintained a higher induction state when acclimated to dim light (30 μmol m^{-2} s^{-1}) and at 0.5 min after exposure to bright light (1260 μmol m^{-2} s^{-1}), but the difference was lost after 4.5 min. These results suggest that based on photosynthetic induction rate, low PPFD plants were able to utilize short pulses (<1 min) of sunflecks more effectively, however, if we consider the actual photosynthetic rates at 0.5 min, this is not the case. At 0.5 min, photosynthesis was 2.6 μmol m^{-2} s^{-1} in the gap-grown plants, 60% higher than the low PPFD-grown plants.

DISCUSSION

These forest Acer species did not respond to high and low R:FR ratio alone (between shade and overcast treatments) in any of the structural and physiological traits examined. This agrees with the expectation that shade-tolerant plants (including all Acer species) are less sensitive to light quality serving as a cue of changing light environment. Shade-avoidance through stem extension is selectively advantageous for a plant only if such behaviour succeeds in moving its productive surface area (i.e. leaves) into a location of higher PPFD. Previous reports on light responses of tree seedlings indicate shade-intolerant species such as P. radiata show greater stem extension when grown under high R:FR (Morgan et al 1983, Warrington et al 1989).

Figure 5. Transient photosynthetic performance of Acer seedlings in dim light (acclimated for >1 hr) and in bright light. Each point represents the mean of 28 plants (seven species-populations, 4 replicates each; see Figure 1) of a given treatment and growth form combination. Photosynthetic induction state is the fraction of steady-state photosynthesis (at 1470 s, A_{max} as given in Figure 4) attained at the two intermediate exposure times under saturating light (1260 μmol m^{-2} s^{-1}). PPFD in the dim light was 30 μmol m^{-2} s^{-1}.


PHOTOSYNTHETIC INDUCTION STATE
1
0.8
0.6
0.4
0.2
0
SHADE
OVERCAST
GAP
1470s
270s
30s
BRIGHT LIGHT ON
● ○ SUBCANOPY
■ □ CANOPY
DIM LIGHT
0
5
10
15
20
25
TIME (min)

Such a growth response may be adaptive for P. radiata seedling dispersed to open sites but under an herbaceous canopy. Seedlings of two African trees: Terminalia ivorensis (shade intolerant) and Khaya senegalensis (shade tolerant) showed similar height growth responses to high and low R:FR at 18 $\mu mol\ m^{-2}\ s^{-1}$ PPFD (Kwesiga and Grace 1986). It may be that, for P. radiata colonizing an open, disturbed site, the shade-avoidance strategy is selectively favoured over establishing in the more ephemeral forest gap site for T. ivorensis. Based on this argument, we would expect greater light quality response in growth in the more ruderal species such as A. negundo (Maeglin and Ohmann 1973) and A. campestre (Küppers 1984a) than the shade tolerant species examined here. For woody seedlings growing in the shade, the margin of seasonal carbon gain will tend to be small and the cost of support structure high, and inappropriate allocation of biomass may result in higher mortality (Augspurger 1984a,b; Bloom et al 1985). Avoidance mechanism confers no survival value under a closed forest canopy but appropriate acclimation response to light quality in photosynthetic apparatus can confer a survival advantage to the seedling.

Chlorophyll levels

Among the maple seedlings, the observed increase in total chlorophyll level in response to PPFD agrees with other reports and with the function expectation of improving light harvesting capacity in the shade (Björkman et al 1972a, Chow et al 1990a,b). However, there is no apparent functional relationship between light quality and chlorophyll level. Low R:FR alone decreased total chlorophyll level in some: Phaseolus vulgaris (shade intolerant; Hoddinott and Hall 1982), Rumex (McLaren and Smith 1978), Petunia axilaris (shade tolerant; Casal et al 1987), corn (Eskins et al 1985), and among ruderal and woodland herbs (Morgan and Smith 1979); but increased in another: Veronica (Fitter and Ashmore 1974). Among woody species, the decrease in chlorophyll level in high R:FR reported in this study is not supported by those found in tropical tree seedlings of different successional status (Turnbull 1991) and in tropical vines (Lee 1988). At the biochemical level, the complex effect of phytochrome and other photoreceptors on chlorophyll synthesis has not been resolved (e.g., Eskins et al 1985, Senger and Bauer 1987); and the functional basis of light quality response of chlorophyll remains unclear. But from this and other reports, it is clear that PPFD (and the cryptochrome receptor) has a greater influence on chlorophyll level than R:FR alone, and that light quality response is not associated with levels of shade tolerance or successional status among woody and herbaceous species.

Photosynthesis

Turnbull (1991) reported lowered A_{max} and stomatal conductance in Australian tree seedlings when grown in low R:FR compared to neutrally shaded plants at 15% full sunlight but this difference was not obvious at 1% and 5% full sunlight. He also failed to find a clear distinction in photosynthetic response to light quality between tree species of different successional status. Another study reported a decrease in net assimilation rate under low R:FR in the seedlings of shade intolerant Terminalia ivorensis trees but there was no change in the shade-tolerant Khaya senegalensis (Kwesiga and Grace 1986). These results suggest that at natural levels of shadelight, tree seedlings do not show strongly phytochrome-mediated photosynthetic response, particularly in late-successional and shade tolerant species. Consistent with this argument, I did not observe photosynthetic and conductance changes due to R:FR alone among the shade tolerant forest Acer. Since seedlings show similar SLM, levels of leaf N and chlorophyll between shade and overcast treatments, comparable photosynthetic capacity at steady-state and in response to lightflecks is expected (Figure 4,5). The absence of photosynthetic response to R:FR between canopy and subcanopy species also reflect the similarity in successional status of both groups of forest Acer. Sunfleck response, as represented by the photosynthetic induction rate (Figure 5), was quicker for seedlings grown in the two low PPFD treatments relative to gap-grown seedlings. This physiological acclimation of shaded maple seedlings agrees with that found in tropical species (Chazdon and Pearcy 1986a,b). A more detailed discussion of lightfleck responses to gap and shade treatments is given in Chapter 3.

Light response between canopy and subcanopy growth forms

In this study, similarity in R:FR response by canopy and subcanopy species indicate that although the two classes differ in growth priorities, canopy species were not more sensitive to R:FR as postulated. It is reported elsewhere (Chapter 4) that canopy species tends to show greater apical dominance, compatible with the requirement in their life history of reaching the forest crown to reproduce (Sakai 1990a). Since the branching architecture is largely developmentally constrained (Sakai 1990b), the influence of variations in light quality alone appears to be minor. Although their maturation is strongly dependent of release growth during gap periods (Canham 1985, 1988), canopy maple species do not have greater sensitivity to the increase in R:FR alone as a cue for a gap opening. Instead, they respond more to the increased quantity of light in a gap.

Conclusions

By partitioning the effects of R:FR and PPFD on Acer traits of functional importance, I found that PPFD is the predominant stimulus for phenotypic variations. Differences in growth and functional traits between gap- and the two low PPFD treatments clearly indicate the importance of light intensity for these seedlings. Functionally linked traits such as SLM, photosynthesis and root:shoot ratio were significantly higher in gap-grown plants similar to other reports of hardwood trees (Logan and Krotkov 1968, Marks 1975, McClendon and McMillen 1982, Jurik 1986, Koike 1988). Stem extension and growth were not affected by R:FR levels alone. In the forest understory, selection for "shade avoidance" behaviour (Grime 1966, Smith 1986) mediated by phytochromes appears weak. Rather, it is the response of plant traits to PPFD that permit persistence in the shade and rapid growth in the gap that is favoured in the growth and survival of these seedlings. Gap light is perceived through PPFD and an increase in R:FR alone is an insufficient cue to elicit the rapid growth response characteristic of seedling release in newly formed gaps.

CHAPTER 2: Functional responses to simulated gap and shade environments in seedlings of eight Acer species: chloroplast-level properties and photosynthesis

Abstract

Seedlings of 4 canopy and 4 subcanopy Acer species were grown under two light treatments in summer 1990: "shade" (photosynthetic photon flux density (PPFD)=30 μmol m^{-2} s^{-1}; R:FR=0.6) and "gap" (PPFD=400 μmol m^{-2} s^{-1}; R:FR=1.12). Although leaf nitrogen (N) concentration did not differ between the light treatments (2.4% leaf DW), shade-grown plants invested significantly more nitrogen into total chlorophyll (4.5 mg g^{-1}) than gap-grown plants (3.5 mg g^{-1}). There was also a significantly lower chlorophyll a:b ratio in shade-grown plants (3.9 vs. 3.3). In terms of photosynthesis, A_{max} in gap-grown plants was 60% higher than in shade-grown plants. These results are consistent with the functional expectation that shade-acclimated plants will increase their light harvesting capacity due to limited photon input while gap-acclimated plants will operate more efficiently under bright light by increasing their carboxylation capacity. This inverse relationship between the capacity of light and dark reactions is supported by chlorophyll fluorescence measurements of intact leaves. Total fluorescence quenching (Q_T) was significantly greater in gap-grown compared to shade-grown plants, indicating a more efficient photochemical process. The positive relationship between Q_T and A_{max} corroborates the expected light-mediated biochemical adjustments among Acer seedlings. Higher chlorophyll levels in shade-grown plants did not result in enhanced low light photosynthesis or lightfleck utilization. Since the trade off between light and dark reaction components evident in the chloroplast-level traits was not fully borne out by assimilation performance, adaptive inferences should not be made without considering the functional relationships of associated traits within the larger plant design.

Introduction

Many plant characters respond to changing irradiance in the growth environment in ways that are considered adaptive (Björkman 1981). Among the chloroplast-level traits, leaves exposed to sun and shade differ in the number and size of chloroplasts, thylakoid configuration, chlorophyll a and b contents, photosystem e^- transport capacity and photosynthetic carbon reduction (PCR) cycle capacity (Boardman 1977, Wild 1979, Björkman 1981, Terashima and Evans 1988; Figure 1 in General Introduction). An increase in total chlorophyll per unit weight and a lowering of chlorophyll a:b ratio in shade-grown plants are considered adaptive in that these characteristics improve the efficiency of capturing photons in the forest understory (Björkman 1981). In addition, the influence of light on leaf N can also affect the activity of chloroplast components (e.g., Rubisco) (Anderson and Osmond 1987) and photosynthesis (Evans 1989a,b). In a moderately shade-tolerant tropical tree, Flindersia brayleyana, low-irradiance-grown seedlings had higher total chlorophyll levels and assimilation rates per unit leaf N (Thompson et al 1988). For a shade leaf, it is more advantageous to divert available nitrogen from Rubisco synthesis to light harvesting components of the chloroplast (Evans 1989b). Corroborating chlorophyll fluorescence results indicate that shade plants contain greater amounts of light harvesting complex (LHC) molecules in Photosystem II (PSII) and showed low PCR cycle activities (Schreiber et al 1977, Fork and Govinjee 1980, Lichtenthaler 1985).

In general, a sun leaf is expected to have a greater photosynthetic capacity resulting from higher area-based leaf N and the correlated increase in allocation to carboxylation processes. On the light harvesting side of photosynthesis, e^- transport activity is also expected to be higher in a sun leaf, to accommodate the increased flux of chemical energy under high irradiance (Boardman 1977, Evans 1989b, Harrington et al 1989). In this mode, the chloroplast is not expected to function well under low light conditions. The inference of a trade off between light harvesting and carboxylation components of the chloroplast is supported in several herbaceous species (Osmond 1987) but this relationship and its functional link to photosynthesis has not been investigated in temperate forest trees seedlings.

Another important component of energy capture in shade plants is the photosynthetic response to sunflecks (Chazdon 1988). These short pulses of high PPFD commonly make up more than 50% of the light energy received by an understory plant. Shade plants have been shown to respond more efficiently to lightflecks (Chazdon and Pearcy 1986a,b) but it is not clear how chloroplast-level properties such as level of chlorophylls and N contribute to this process. For a group of temperate forest Acer species, I will test the expected adaptive acclimation in chloroplast properties to lightfleck utilization in seedlings grown under simulated shade and gap light regimes. I examine the properties of light and dark reaction components in seedlings of 8 Acer species grown under the two simulated light environments similar to those commonly experienced by these seedlings in nature. Chlorophyll and nitrogen levels, chlorophyll fluorescence and photosynthetic activities will be determined to answer the questions: 1) are Acer seedlings capable of acclimating in chloroplast-level traits to the two contrasting light regimes? and 2), are light-mediated biochemical changes associated with adaptive physiological performance in shade- and gap-grown maple seedlings?

Methods and Materials

Experimental design

Eight species of Acer (two populations each) were used in this study (Figure 1). Seedlings were 3-4 years old and raised from seed under a common greenhouse environment in the McGill Phytotron. In April 1990, the seedlings were placed under two experimental light treatments beginning in the budbreak period (Figure 2). The construction of the simulated shade (PPFD= 30 μmol m^{-2} s^{-1}; R:FR=0.55) with 13% sunfleck occurrence and simulated gap (400 μmol m^{-2} s^{-1}; R:FR=1.1) environments is described in detail elsewhere (Methods and Materials, Chapter 1). Experimental plants

Figure 1. Experimental design showing the two treatment light regimes and the Acer species and populations used within each growth form class. Total number of seedlings used in the experiment was 160 (5 replicates per species-population per treatment). For seed source information, see Appendix 1.

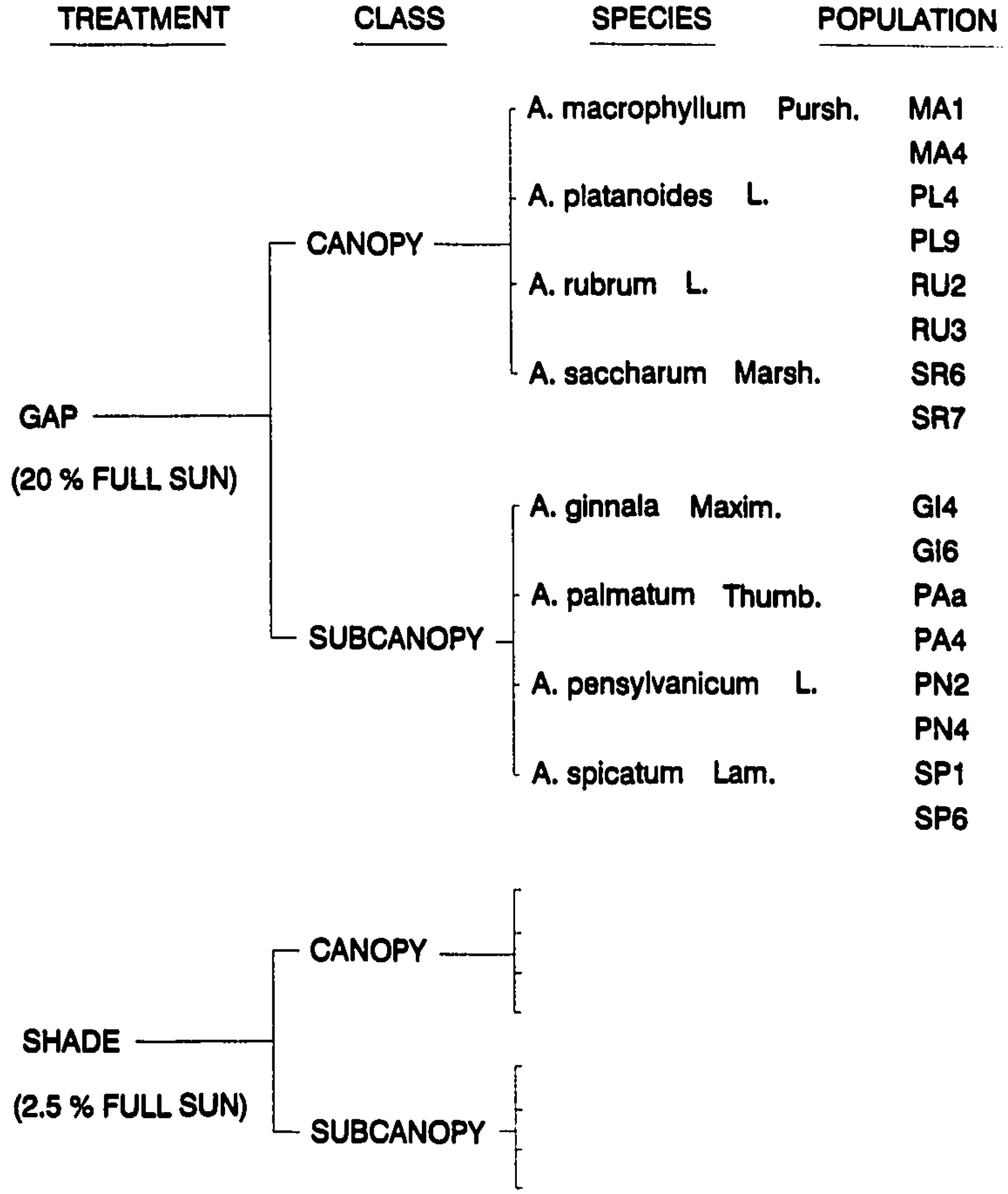
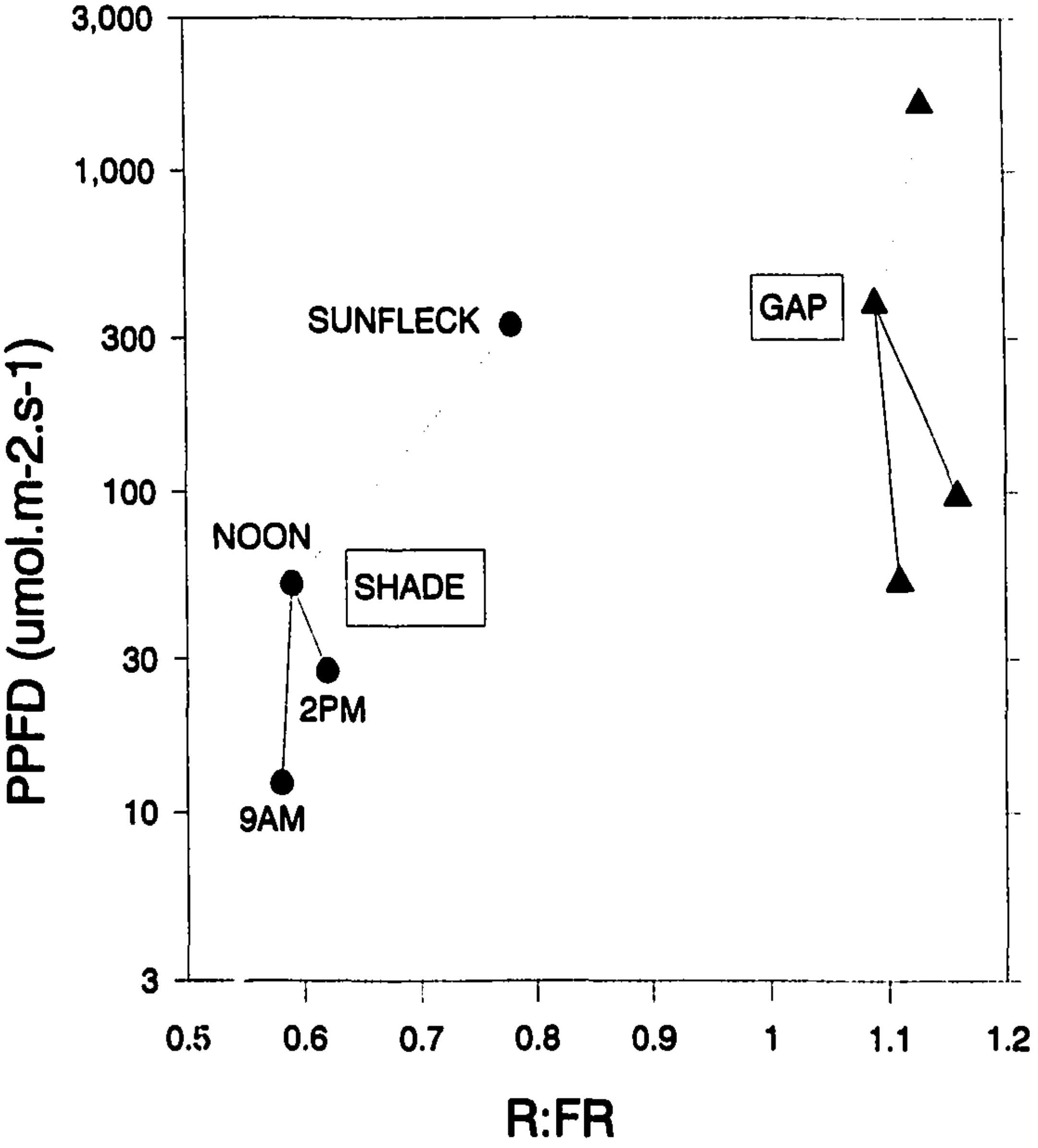

TREATMENT
CLASS
SPECIES
POPULATION
GAP
(20 % FULL SUN)
CANOPY
A. macrophyllum Pursh.
MA1
MA4
A. platanoides L.
PL4
PL9
A. rubrum L.
RU2
RU3
A. saccharum Marsh.
SR6
SR7
SUBCANOPY
A. ginnala Maxim.
GI4
GI6
A. palmatum Thumb.
PAa
PA4
A. pensylvanicum L.
PN2
PN4
A. spicatum Lam.
SP1
SP6
SHADE
(2.5 % FULL SUN)
CANOPY
SUBCANOPY

Figure 2. Light quantity and quality regimes in the simulated gap and shade treatments on a typical day during the experiment. Measurements were taken on August 10, 1990, under clear skies. Dotted lines represent the ambient and peak (i.e., direct beam through the spectral filter in the shade treatment and through the lathe opening in the gap treatment) conditions at solar noon.

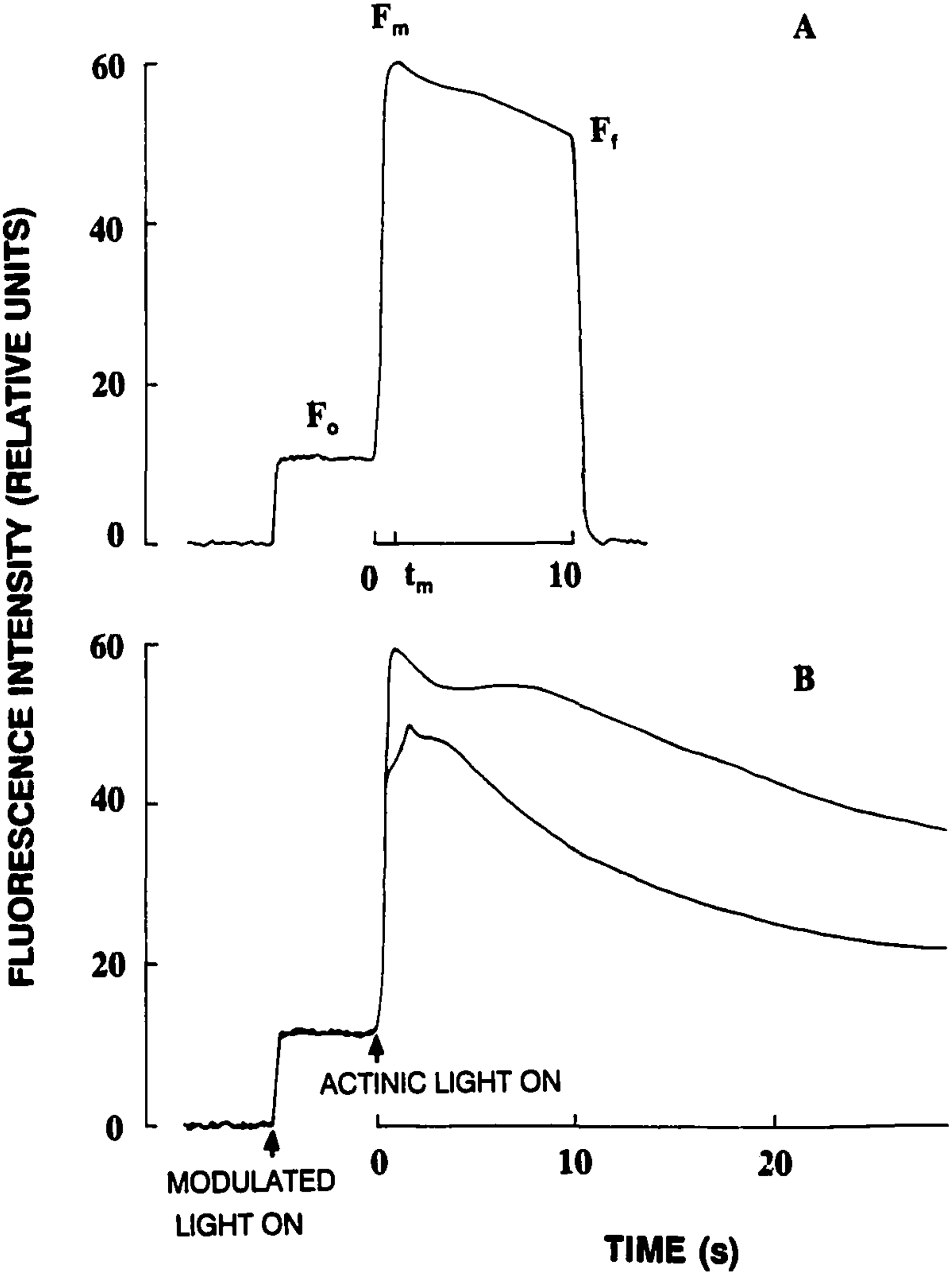

3,000
1,000
300
100
30
10
3
PPFD (umol.m-2.s-1)
SUNFLECK
GAP
NOON
SHADE
2PM
9AM
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
R:FR

were arranged in five blocks in each treatment, one seedling per species-population per block. There was minimum shading from neighbouring plants. Analysis of variance showed no significant block effect in traits measured and block effects will not be considered in subsequent analyses. Seedling maintenance during the experimental period follows Chapter 1. The total number of seedlings used in this experiment was 160. Methods used in the determination of chlorophyll content and leaf N and photosynthesis are given in Chapter 1.

Chlorophyll fluorescence

Plants were allowed to acclimate to total darkness for >2 hr before fluorescence measurement. For healthy leaves, a dark adaptation period of 15-30 min is normally considered to be sufficient (Bolhàr-Nordenkampf et al 1989). Fluorescence was determined on the same leaf as earlier photosynthetic measurements were made. The leaf was held in a plexiglas holder, 0.8 cm from the fibre optic light source/detector of the chlorophyll fluorometer (PAM 101, 103; H. Walz, Effeltrich, Germany; Schreiber 1986). The saturating actinic light pulses were provided by a Schott KL1500 lamp (Schott, Stafford, UK) with a PPFD of 220 W m^{-2} at the leaf surface. Constant fluorescence (F_o) level was determined using modulated light at 0.08 W m^{-2}. Fluorescence kinetics were recorded on an Omega RD2030/60 Function Recorder at 2.5 mm s^{-1} (Omega Engineering, Inc. Stamford, Conn. USA). Air temperatures during all measurements were 18-23°C. The leaf was exposed to the actinic light for 10 s. The rate of fluorescence quenching was expressed as percent decrease in fluorescence from F_m after a 10 s exposure to actinic light (Figure 3). Chlorophyll fluorescence parameters were determined in the manner indicated in Figure 3a. The relatively high actinic light used in this study insured the full saturation of chlorophyll a molecules with the drawback of losing some resolving power in estimating $t_{1/2}$ (the limit of resolution for the chart recorder is estimated at 0.08 s). Values of Fo, F_m, F_v and $t_{1/2}$ are dependent of actinic light intensity (Öquist and Wass 1988) where the first three parameters increase while $t_{1/2}$ decreases with light intensity. The protocol

Figure 3a. Sample chlorophyll fluorescence kinetics determined for Acer seedlings. F_o=constant fluorescence, F_m=maximum fluorescence, F_f=photochemical fluorescence quenching after a 10s exposure to actinic light (220 Wm-2). t_m=time to F_m. The following parameters referred to in the results are derived as: $t_{1/2}$= $t_m/2$; total fluorescence quenching (Q_T) is expressed as % decrease in fluorescence from F_m to F_f (i.e. $Q_T=(F_m-F_f)*100/F_m$); F_v/F_m (referred to in Chapter 4) is the quantum yield efficiency where F_v is F_m-F_o. Plants were acclimated to total darkness for >2hr before fluorescence measurement was taken. Figure 3b demonstrates the pattern of fluorescence quenching with prolonged actinic light exposure (conditions same as in 3a) where, for the two quenching kinetic curves, the truncation of fluorescence at 10 s is a reasonable representation of the steady-state fluorescence.


A
F_m
F_f
F_o
60
40
20
0
0
t_m
10
B
60
40
20
0
0
10
20
ACTINIC LIGHT ON
MODULATED LIGHT ON
FLUORESCENCE INTENSITY (RELATIVE UNITS)
TIME (s)

used here also truncated the quenching kinetics at 10 s before steady-state was attained. This time interval was adopted after preliminary tests showing fluorescence quenching after 10 s was representative of the steady-state level reached after exposure of >30 s (Figure 3b). This protocol was adopted to permit the rapid processing of a large number of samples with minimum loss of resolution in Q_T.

Statistical methods

Differences between light treatments, growth form classes and species were analyzed using Procedure GLM in SAS (1988) for a three-factorial mixed model (Table 1). The appropriate MS error terms were derived following Winer (1971). To properly partition the sources of variance, traits without significant interaction terms (at P=0.05) were re-analyzed using an additive model (by removing the interaction terms); the outcome remained virtually unchanged.

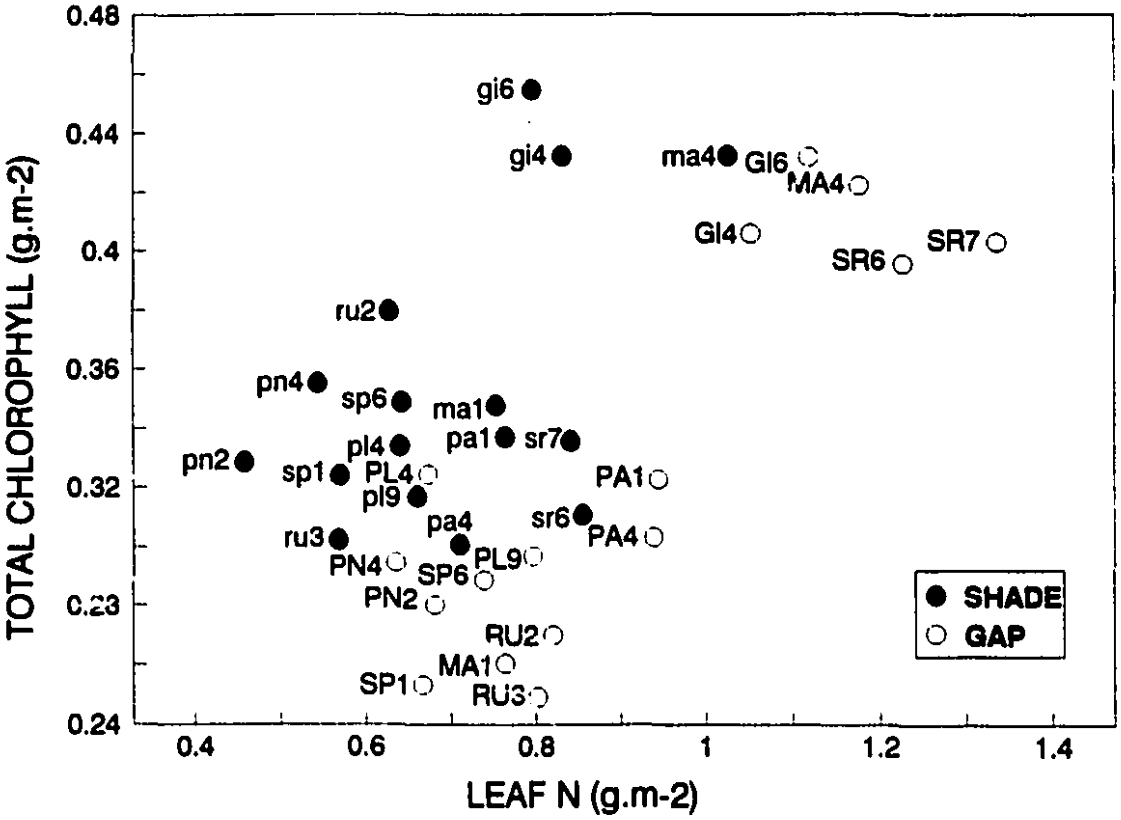
Results

There is a an overall positive relationship between leaf N and total chlorophyll (Figure 4); the higher slope in the shade-grown plants indicates that they invested proportionally more leaf N to chlorophyll than gap-grown plants. Relative levels of chlorophyll and leaf N vary among species; both are higher in A. saccharum, A. ginnala and A. macrophyllum. While high leaf N led to a higher A_{max} in the latter two species, this was not the case for A. saccharum (Figure 5). In most species, both chlorophyll and leaf N increased from shade to gap treatment, partly mediated by the higher SLM (specific leaf mass) of the gap-grown leaves (Table 1 in Chapter 4); A. ginnala and one population of A. macrophyllum maintained high chlorophyll levels regardless of the irradiance treatment leading to a significant treatment by species interaction (Table 2).

Table 1. Partitioning of variances in the three-factor mixed model experimental design. Treatments= gap and shade; class= canopy and subcanopy species. Species and populations used are given in Figure 1. Expected MS were derived from Winer (1971). The appropriate error terms are used in the GLM procedure of SAS.

SOURCE OF VARIATION	TREATMENT EFFECT	DF	EXPECTED MS
TREATMENT	FIXED	1	$E(MS_A)=\delta^2_\epsilon+5\delta^2_{AD}+10\delta^2_{AC}+80\delta^2\Sigma(\alpha)$
CLASS	FIXED	1	$E(MS_B)=\delta^2_\epsilon+10\delta^2_D+20\delta^2_C+80\delta^2\Sigma(\beta)$
TREAT*CLASS	FIXED	1	$E(MS_{AB})=\delta^2_\epsilon+5\delta^2_{AD}+10\delta^2_{AC}+40\delta^2_{AB}$
SPECIES(CLASS)	RANDOM	6	$E(MS_C)=\delta^2_\epsilon+10\delta^2_D+20\delta^2_C$
POPULATION (CLASS*SP)	RANDOM	8	$E(MS_D)=\delta^2_\epsilon+10\delta^2_D$
TREAT*SP(CLASS)	RANDOM	6	$E(MS_{AC})=\delta^2_\epsilon+5\delta^2_{AD}+10\delta^2_{AC}$
TREAT*POP(CLASS*SP)	RANDOM	8	$E(MS_{AD})=\delta^2_\epsilon+5\delta^2_{AD}$

Figure 4. Mean chlorophyll and leaf N levels (both area-based) in the 8 maple species (number following species is the population code) grown under gap and shade treatments. Each point is the mean of 5 plants. Average SE for chlorophyll and leaf N were both 7% of the respective means. Species codes are canopy growth form: MA=*A. macrophyllum*, PL=*A. platanoides*, RU=*A. rubrum* and SR=*A. saccharum*; subcanopy growth form: GI=*A. ginnala*, PA=*A. palmatum*, PN=*A. pensylvanicum* and SP=*A. spicatum*.



0.48
0.44
0.4
0.36
0.32
0.28
0.24
TOTAL CHLOROPHYLL (g.m-2)
0.4
0.6
0.8
1
1.2
1.4
LEAF N (g.m-2)
gi6
gi4
ma4
GI6
MA4
GI4
SR7
SR6
ru2
pn4
sp6
ma1
pl4
pa1
sr7
pn2
sp1
PL4
PA1
pl9
pa4
sr6
PA4
ru3
PN4
PL9
SP6
PN2
RU2
MA1
SP1
RU3
● SHADE
○ GAP

Figure 5. Relationship between Q_T and steady-state photosynthesis at saturating PPFD in the 8 maple species (number following species is the population code) grown under gap and shade treatments. Both traits were measured in August 1990. Each point is the mean of 5 plants. Average SE for Q_T and A_{max} were 19% and 15% of the respective means. Species codes same as Figure 4.

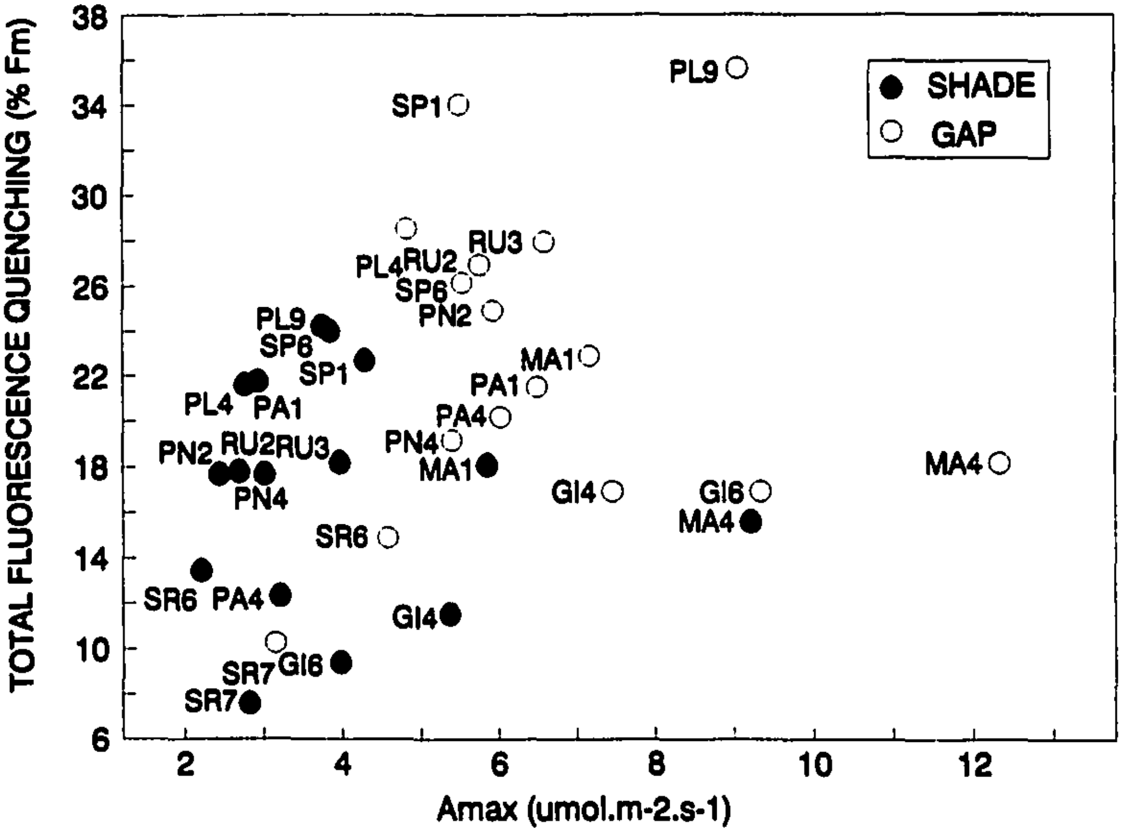

TOTAL FLUORESCENCE QUENCHING (% Fm)
38
34
30
26
22
18
14
10
6
2
4
6
8
10
12
Amax (umol.m-2.s-1)
● SHADE
○ GAP
PL9
SP1
RU3
PL4
RU2
SP6
PN2
PL9
SP6
SP1
MA1
PA1
PL4
PA1
PA4
PN4
PN2
RU2
RU3
MA1
GI4
GI6
MA4
MA4
PN4
SR6
SR6
PA4
GI4
SR7
GI6
SR7

Table 2. Significance of variances of leaf-level traits partitioned among treatments (gap, shade), classes (canopy, subcanopy), species (SP) and populations (P). Appropriate MS error terms derived from Winer (1971) are in Table 1 (Chapter2). Species and populations of <u>Acer</u> used are given in Figure 1 (Chapter2). NS P>.05; * P=0.05; ** P=0.01; *** P=0.001.

TRAIT	SOURCE OF VARIATION						
	TREAT	CLASS	T*C	SP(C)	P(SP,C)	T*SP(C)	T*P(SP,C)
NITROGEN (WEIGHT-BASED)	NS	NS	NS	NS	NS	*	NS
NITROGEN (AREA-BASED)	***	***	NS	***	***	***	NS
CHLOROPHYLL a	**	NS	NS	**	NS	NS	NS
CHLOROPHYLL b	***	NS	NS	NS	NS	NS	NS
TOTAL CHLOROPHYLL	**	NS	NS	**	NS	NS	NS
CHLOROPHYLL a:b	***	NS	NS	***	NS	NS	NS
CHLOROPHYLL FLUORESCENCE							
$T_{1/2}$ (AUG)	**	NS	NS	**	NS	NS	NS
$T_{1/2}$ (SEPT)	NS	NS	NS	*	NS	NS	NS
Q_T (AUG)	**	NS	NS	**	NS	NS	NS
Q_T (SEPT)	**	NS	NS	*	NS	*	NS
PHOTOSYNTHESIS (AUGUST 1990)							
DIM LIGHT	NS	NS	NS	*	NS	NS	NS
A_{max}	***	NS	*	***	NS	NS	NS
DARK RESPIRATION	*	NS	NS	NS	NS	NS	NS

The correlation between chlorophyll a and b levels in each treatment was strong ($R^2=0.69$ and 0.84 for shade and gap respectively). Levels of both light-harvesting pigments increased from gap to shade for all species producing two distinct treatment clusters (Figure 6). While the ratio of the Chl a to b remain unchanged in the two treatments (both with a slope=0.19), shade plants invested proportionally more to Chl b at a given level of Chl a (Figure 6; Chl a:b in Table 3). In general, chlorophyll a and b tended to be highest in A. platanoides and A. saccharum and lowest in A. rubrum and A. spicatum in both treatments. There was considerable variation in pigment levels between species and populations but the maples did not separate into canopy versus subcanopy classes (Table 3).

Chlorophyll fluorescence results indicate that the treatment effect on total fluorescence quenching (Q_T) was strong but more modest for both fluorescence at F_o and the e^- transport carrier pool size of PSII ($t_{1/2}$) (Table 2,3). Since most of the total fluorescence at steady state is attributable to photochemical quenching in non-stressed plants (Bolhàr-Nordenkempf 1989) and that a linear relationship between photochemical quenching and assimilation rate is expected (Schreiber and Bilger 1987), higher Q_T (i.e., electron transport efficiency) in gap-grown plants corresponded tightly with greater carboxylation potential. While Q_T was higher in gap-grown plant for both census periods, values decreased from August to September (Table 2), possibly associated with initiation of leaf senescence. While there was some uncertainty associated with the precision of obtaining $t_{1/2}$, the central tendency between treatments indicates that $t_{1/2}$ was higher in shade-grown plants. (Table 2, Figure 7). This implies that shade-grown plants have larger e^- transport carrier pool sizes. Fluorescence traits were similar between canopy and subcanopy classes but significantly different between species for $t_{1/2}$ and Q_T (Table 3).

The positive relationship between chlorophyll a and $t_{1/2}$ (Figure 8) indicates that light harvesting pigment and e^- transport carriers covary within the chloroplast ($R^2=0.4$, $P<0.001$, $n=32$). Photochemical quenching, in contrast, decreases with increasing

Figure 6. Relationship between chlorophyll a and b in the 8 maple species (number following species is the population code) grown under gap and shade treatments. The slope of the two regression lines are the same: gap treatment- Chl b=0.18+0.19*Chl a ($R^2=0.84$, N=16), shade treatment- Chl b=0.39+0.19*Chl a ($R^2=0.69$, N=16). Each point is the mean of 5 plants. Average SE for chlorophyll a and b were 6% and 8% of the respective means. A pooled sample of each plant was used in the chlorophyll determination. Species codes same as Figure 4.

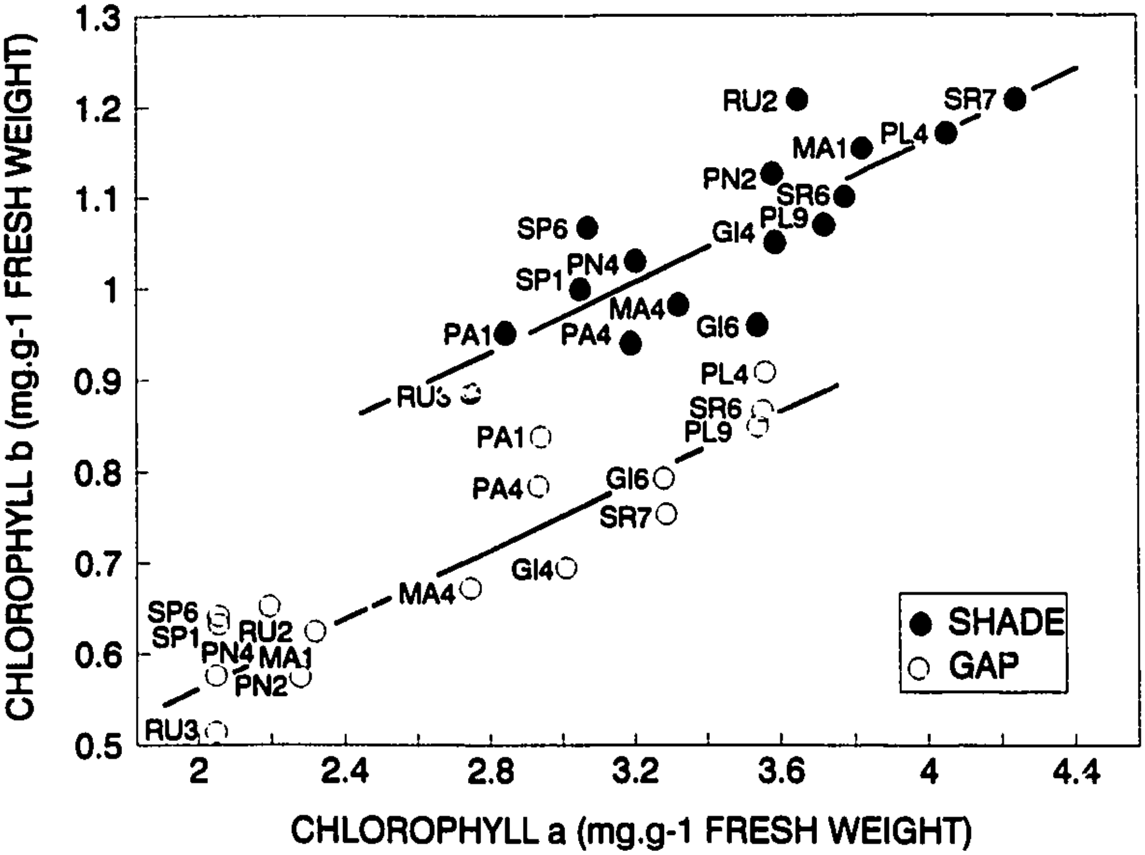

CHLOROPHYLL b (mg.g-1 FRESH WEIGHT)
CHLOROPHYLL a (mg.g-1 FRESH WEIGHT)
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
2
2.4
2.8
3.2
3.6
4
4.4
● SHADE
○ GAP
RU2
SR7
MA1
PL4
PN2
SR6
PL9
SP6
GI4
PN4
SP1
MA4
GI6
PA1
PA4
PL4
RU3
SR6
PL9
PA1
PA4
GI6
SR7
GI4
MA4
SP6
SP1
RU2
PN4
MA1
PN2
RU3

Table 3. Leaf N, chlorophyll levels, chlorophyll fluorescence and maximum photosynthetic rate (mean±1SE) in the two light treatments. Each value is the mean of 80 plants, representing the 8 Acer species of A. macrophyllum, A. platanoides, A. rubrum and A. saccharum (canopy species); A. ginnala, A. palmatum, A. pensylvanicum and A. spicatum (subcanopy species).

TRAIT	TREATMENT	
	SHADE	GAP
LEAF BIOCHEMISTRY		
Leaf N (% DW)	2.49±0.05	2.39±0.06
Leaf N (g.m^{-2})	0.71±0.02	0.90±0.03
CHLOROPHYLL a (mg.g^{-1})	3.45±0.07	2.76±0.08
CHLOROPHYLL b (mg.g^{-1})	1.06±0.02	0.71±0.02
TOTAL CHLOROPHYLL (mg.g^{-1})	4.51±0.09	3.46±0.10
CHLOROPHYLL a:b	3.28±0.04	3.88±0.04
CHLOROPHYLL FLUORESCENCE		
Fo (AUG)	12.0±0.2	10.9±0.1
Fo (SEPT)	11.5±0.2	10.6±0.2
$t_{1/2}$ (s) (AUG)	0.52±0.01	0.48±0.01
$t_{1/2}$ (s) (SEPT)	0.54±0.01	0.52±0.01
Q_T (%F_m) (AUG)	1.90±0.11	2.49±0.13
Q_T (%F_m) (SEPT)	1.02±0.05	1.65±0.07
PHOTOSYNTHESIS (AUGUST 1990)		
DIM LIGHT (umol.m^{-2}.s^{-1})	0.93±0.05	0.85±0.05
Amax (umol.m^{-2}.s^{-1})	4.03±0.23	6.55±0.30

Figure 7. Relationship between fluorescence parameters $t_{1/2}$ and total fluorescence quenching (Q_T) in the 8 maple species (number following species is the population code) grown under gap and shade treatments. Q_T is expressed as % F_m (see Figure 1). The regression equation is $t_{1/2}=0.608+0.049*Q_T$ ($R^2=0.58$, N=32). Each point is the mean of 5 plants. Average SE for $t_{1/2}$ and Q_T were 6% and 19% of the respective means. Fluorescence measurements were taken in August 1990. Species codes same as Figure 4.

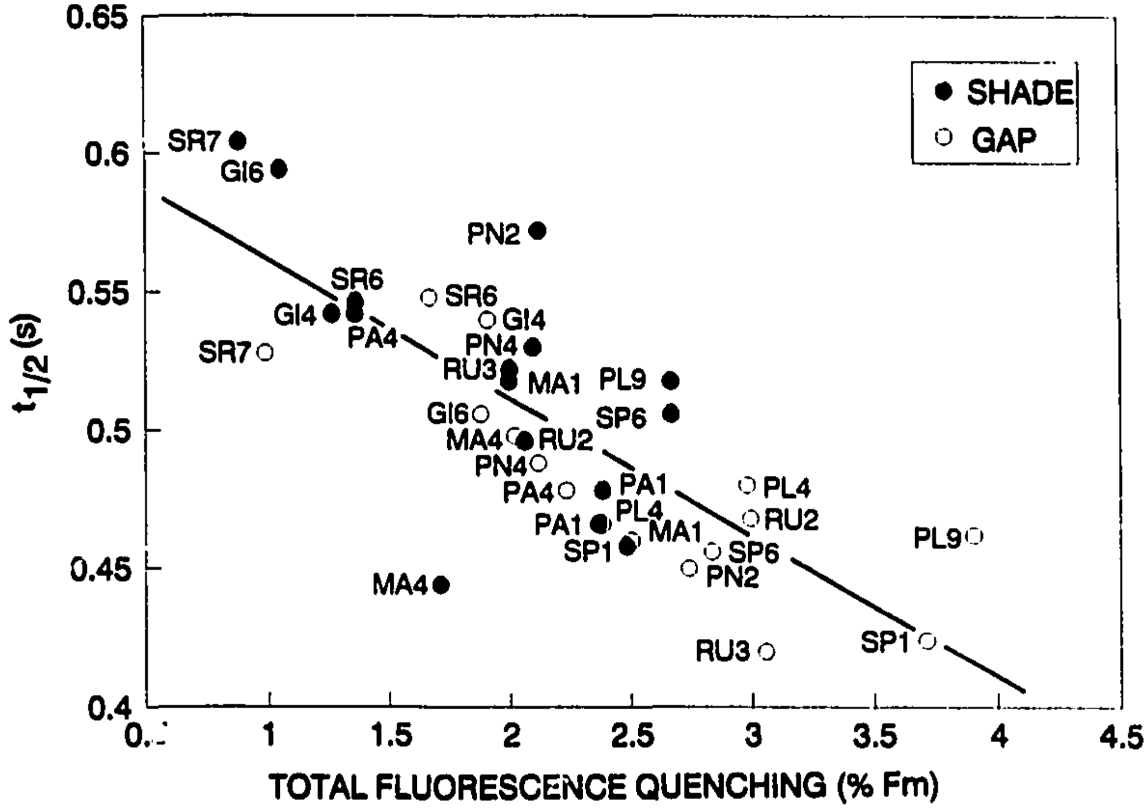
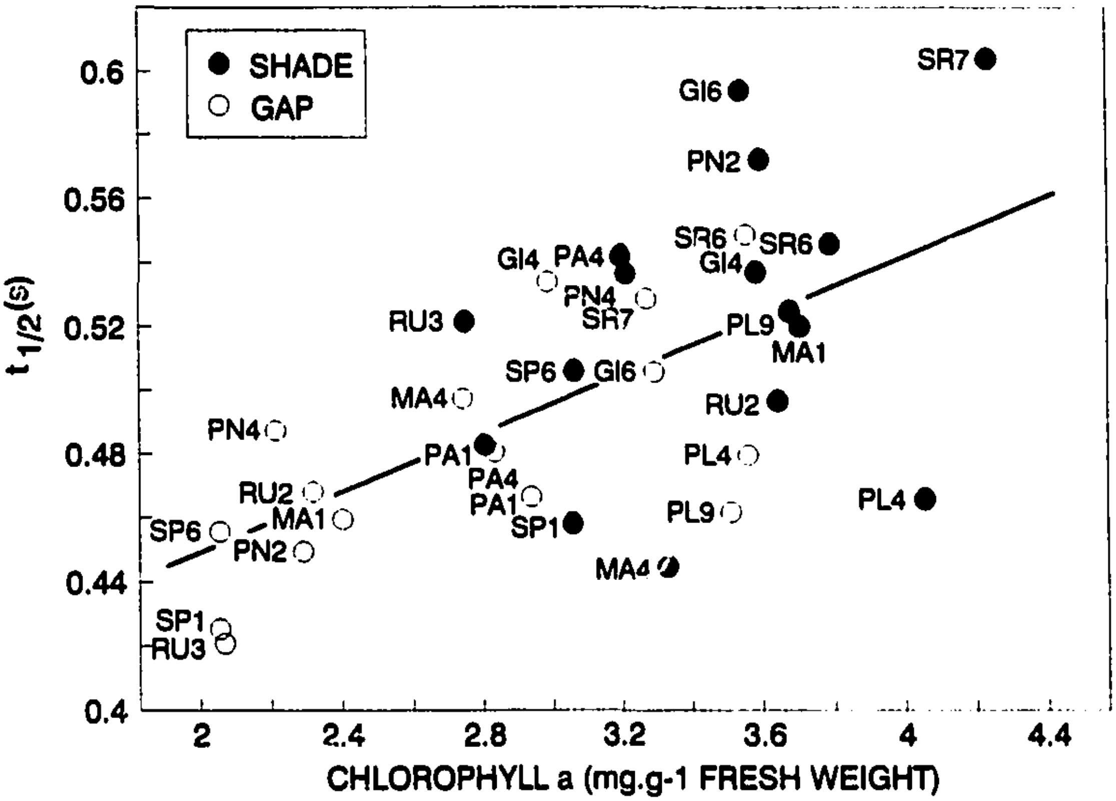

● SHADE
○ GAP
$t_{1/2}$ (s)
0.65
0.6
0.55
0.5
0.45
0.4
0.5
1
1.5
2
2.5
3
3.5
4
4.5
TOTAL FLUORESCENCE QUENCHING (% Fm)
SR7
GI6
PN2
SR6
GI4
PA4
SR7
SR6
GI4
PN4
RU3
MA1
PL9
SP6
GI6
MA4
RU2
PN4
PA4
PA1
PL4
RU2
PA1
PL4
MA1
SP1
SP6
PN2
PL9
MA4
RU3
SP1

Figure 8. Relationship between $t_{1/2}$ (for definition see Figure 1) and chlorophyll a in the 8 maple species (number following species is the population code) grown under gap and shade treatments. The regression equation is $t_{1/2}=0.357+0.046*Chl\ a$ ($R^2=0.37$, $N=32$). Each point is the mean of 5 plants. Average SE for $t_{1/2}$ and chlorophyll a were 6% and 8% of the respective means. $t_{1/2}$ measurements were taken in August 1990. Species codes same as Figure 4.


● SHADE
○ GAP
t 1/2(s)
0.6
0.56
0.52
0.48
0.44
0.4
2
2.4
2.8
3.2
3.6
4
4.4
CHLOROPHYLL a (mg.g-1 FRESH WEIGHT)
SR7
GI6
PN2
SR6
SR6
GI4
PA4
GI4
PN4
SR7
RU3
PL9
MA1
SP6
GI6
MA4
RU2
PN4
PA1
PL4
PA4
PA1
RU2
MA1
SP6
SP1
PL9
PL4
PN2
MA4
SP1
RU3

$t_{1/2}$ ($R^2=0.59$, $P<0.001$, $n=32$, Figure 7). Since Q_T depends on the rate of chemical energy transfer from the photosystems to the carboxylation process, it is an estimate of basal PCR reaction capacity in these dark-acclimated plants. The negative relationship between $t_{1/2}$ and Q_T indicates a trade off of light and dark reaction capacities within plants and the pattern of trade off is significantly affected by the light treatments. Q_T is also positively associated with photosynthetic capacity represented by A_{max} (Figure 5). Similar to Q_T, maximum photosynthesis was strongly influenced by treatment where rates in gap-grown plants were 60% greater than shade-grown plants; but rates in dim light photosynthesis was only marginally different indicating minor differences in respiratory cost (Table 2). The pattern of high A_{max} and Q_T and low chlorophyll and $t_{1/2}$ in gap-grown plants, and the opposite pattern in shade-grown plants, strongly suggest a trade off between light harvesting and carbon assimilation components of the chloroplast.

Discussion

These results show clear evidence for differential partitioning of nitrogen between the light and dark reaction components that suggests the functional basis for acclimation of chloroplasts to high versus low light regimes. Leaf N per unit dry weight was only marginally higher in shade-grown plants but they showed significantly higher chlorophyll content. Similar to these findings, Terashima and Evans (1988) reported a decreasing ratio of chlorophyll to total leaf N in spinach with increasing PPFD. The adjustment of leaf N to irradiance is a dynamic process. Evans (1989a) reported the acclimation of mature Cucumis leaves to a different light regime within 2 weeks after the transfer. Nitrogen was translocated out of leaves that experienced a decrease in PPFD and into those exposed to high PPFD. The acclimation resulted in more favourable distribution of chlorophyll, electron transport carriers and carboxylation enzymes (i.e., Rubisco) that increased the photosynthetic potential for a given level of leaf N. The proportional N in thylakoid versus soluble proteins increases with lower PPFD growth environment signalling a trade off between the light and dark reaction components. In this study, all Acer seedlings grown in the shade invested a greater proportion of their leaf N resource in the maintenance of the light-harvesting systems than conspecific gap-grown plants.

The close correspondence between chlorophyll a and b levels suggests a strong overall developmental control in the synthesis of the two pigments. Lower chlorophyll a:b ratio in shade-grown Acer seedlings agrees with those found in other species where chl a:b was 2-2.2 in shade plants and 2.6-3.6 in sun plants (Anderson et al 1988). The smaller difference in chlorophyll a:b of 3.2 and 3.9 (in shade and gap treatments respectively) in Acer species seems to suggest a more limited acclimation potential. But in a group of 14 herbaceous species, Wild (1979) found an average 17% increase in chl a:b between low- and high-light treatments, similar to the findings in Acer. Increasing chlorophyll content improves the absorption of the green and far-red region and "confers a significant advantage" to shade plants surviving in low irradiance environments (Björkman 1981; Anderson et al 1988). The relatively greater investment in chlorophyll b to chlorophyll a is thought to shift the energy distribution from PSI (where the peak of light absorption at 700 nm) more to PSII (where most of Chl b resides and has an absorption peak at 680 nm), concurrent with a richer far-red excitation energy in the forest understory (Björkman 1981). For forest-grown Acer seedlings, such an acclimation is expected and confirmed in this study.

The functional interpretation of fluorescence signals is still somewhat "problematic" (Krause and Weis 1991). Krause and Weis (1984) have suggested that the chlorophyll fluorescence parameter F_o is indicative of antenna chlorophyll a content so that the two should vary in the same direction. This is borne out by this study (Table 1). F_o , therefore, could be used to estimate the levels of chlorophyll a and total chlorophyll (given the close relationship between chlorophyll a and b (Figure 6) in a leaf. The $t_{1/2}$ parameter is generally recognized as an index of the "photochemical reaction and the pool size of electron acceptors on the reducing side of photosystem II" (Öquist and Wass 1988, Bolhàr-Nordenkempf 1989); $t_{1/2}=0$ (i.e. fluorescence rises virtually instantaneously to F_m) when e^- transport carriers are inhibited by the herbicide DCMU (Krause and Weis 1984).

In the Acer seedlings, the significant regression between $t_{1/2}$ and chlorophyll a indicates a concurrent increase between e^- transport carrier pool size and light-harvesting pigments; both were higher in shade-grown plants (Figure 8). These findings, however, are contrary to other reports where forest herbs (Fork and Govindjee 1980) and shaded leaves of deciduous trees (Lichtenthaler 1985) showed compared to plants or leaves exposed to high irradiance. Furthermore, Björkman and others (1972a, 1981) conclude that shade plants tend to have a lower $t_{1/2}$ due to larger light harvesting antenna and smaller e^- pool size. Based on these results, I conclude that in the chloroplasts of shade-grown Acer seedlings, there was light-acclimation in light harvesting pigment levels but not in e^- transport carrier pool size.

Given that $t_{1/2}$ represents the photosystem activities of the leaf, a negative relationship between $t_{1/2}$ and total fluorescence quenching (Q_T) indicates a trade off between the light and dark reaction components (Figure 7). The same pattern is also evident between total chlorophyll and Q_T (not shown). Total fluorescence quenching in a healthy plant is a measure of the reoxidation rate of electron acceptors (Q_A) in Photosystem II (Schreiber and Bilger 1987, Bolhàr-Nordenkempf 1989, Krause and Weis 1991). And since the reoxidation of Q_A is associated with the consumption of ATP and NADPH in CO_2 fixation, Q_T is an indirect measure of how quickly and efficiently the chemical energy induced by light is shuttled to the dark reaction centres for CO_2 fixation (Schreiber and Bilger 1987). Q_T, therefore, is a useful parameter estimating the rate of energy utilization in the PCR cycle and indirectly the Rubisco concentration. Direct comparisons between sun and shade leaves of Arbutus unedo over a wide range of light intensities have found consistently lower photochemical quenching in the shade leaf (Shreiber and Bilger 1987); and the degree of quenching was linearly related to the steady-state assimilation rate. Greater photosynthetic capacity in gap-grown plants was also attributed to higher levels of Rubisco (Terashima and Evans 1988). It would appear that Q_T, Rubisco and A_{max} are three closely linked expressions of the carboxylation process in the chloroplast as demonstrated in this study and that gap-grown seedlings showed the expected acclimation with high rates of Q_T and A_{max}.

Based on the distribution of light and dark reaction components in Acer seedlings, we would expect higher costs of respiration in gap-grown plants and in turn lowering of their ability to utilize low PPFD. However, dim light (29 μmol m^{-2} s^{-1}) assimilation rates were only marginally lower in gap-grown plants. Furthermore, when these seedlings were exposed to a sudden onset of saturating PPFD simulating a sunfleck, assimilation rates rose more rapidly in gap-grown plants even after only 30 s (Figure 1,4 of Chapter 3). The advantages inferred at the chloroplast-level for shade plants were not substantiated by carbon uptake at the leaf level. It appears that we cannot estimate the lightfleck responses of Acer seedlings from chloroplast-level traits alone. Functionally, greater light harvesting pigments and e$^-$ transport carrier pool size should allow a leaf to capture brief sunflecks more effectively. However, since the activation of the light-harvesting centre and e$^-$ transport chain require little time (within seconds versus the full induction of photosynthesis at 20-30 min) (Chazdon and Pearcy 1986a,b; Stein et al 1990), these traits should not pose a significant assimilation constraint to the utilization of sunflecks longer than 10s in duration. But with higher chlorophyll levels and greater e$^-$ pool sizes, shade-grown Acer seedlings are capable of a more effective use of shorter light pulses, particularly if they are able to maintain a higher state of photosynthetic induction (Chazdon and Pearcy 1986a,b). Since over 90% of the sunflecks can be less than 32 s long in a closed-canopy forest (Chazdon 1988), the selective advantage of such a chloroplast construction is apparent. Further work is necessary to verify this interpretation. Light harvesting components play a minor role in sunflecks of longer durations where the carboxylation capacity and stomatal conductance predominate (Pearcy 1990). Under these conditions, gap-grown plants displayed a consistent advantage from higher Q_T to high steady-state photosynthesis. Despite the trade off demonstrated in the chloroplast components, gap-grown seedlings appeared to be better adapted in both the gap and the shade environments. These results also serve as a caution to the inference of shade adaptation in a trait without considering its functional relationship within the plant's larger design.

CHAPTER 3: The effect of simulated gap and shade treatments on photosynthetic response patterns and stomatal properties in seedlings of eight Acer species

Abstract

Seedlings of 4 canopy and 4 subcanopy Acer species (two populations each) were grown under two light treatments simulating forest shade (photosynthetic photon flux density (PPFD)=30 μmol m^{-2} s^{-1}; R:FR=0.6) and forest gap (PPFD=400 μmol m^{-2} s^{-1}; R:FR=1.12). The aim was to investigate the effect of growth irradiance on steady-state and transient (i.e., lightfleck response) photosynthesis among species and between canopy and subcanopy growth forms. Maximum photosynthetic rate (A_{max}, based on species mean) was increased from as little as 20% (A. saccharum) to as much as 138% (A. ginnala) from shade- to gap-grown seedlings. A_{max} differed significantly among species (2.3 to 12.3 μmol m^{-2} s^{-1}) but assimilation rates under dim light (30 μmol m^{-2} s^{-1}) were more similar (0.6 to 1.4 μmol m^{-2} s^{-1}). There were no physiological differences between canopy and subcanopy species, reflecting the generally similar leaf level structural traits such as SLM, chlorophyll and leaf nitrogen between the two growth forms. Contrary to expectation, photosynthetic lightfleck response was quicker in gap-grown plants than in shade-grown plants, although photosynthetic induction rates show trends consistent with other reports. These results suggest that the actual rates of assimilation may be more relevant in whole plant performance than the induction states. Although the loss of photosynthetic induction in darkflecks was greater in gap-grown A. macrophyllum, it appeared to have only minor effects on maintaining high gas exchange performance. The higher steady-state and transient photosynthetic response in gap-grown seedlings suggest that leaf properties such as greater SLM and area-based leaf N that permit greater A_{max} may also confer an advantage responding to sunflecks. No consistent relationship was found between stomatal conductance and stomatal density and stomatal pore diameter. A consistent negative relationship between stomatal density and stomatal pore diameter

found in this and other interspecific studies seem to indicate the stabilizing selection of an optimal level of conductance area.

Introduction

In the temperate forest, many *Acer* species must complete their juvenile stage growing in the forest understory. Some, like *A. saccharum*, require periodic gaps to reach maturity in the forest crown (Canham 1985) while others (eg. *A. pensylvanicum*) remain in the subcanopy through life. Seedlings of both canopy and subcanopy species show significant growth response to forest gaps (Wilson and Fischer 1977, Canham 1988a) and there are some indications that canopy species may be developmentally constrained even in the juvenile stage with higher wood density and tougher leaves that are more beneficial in the adult stage (Lei and Lechowicz 1990). Since subcanopy trees must complete their life cycle in the forest understory, selection for shade-adapted characters should be stronger than in canopy species. Canopy seedlings should possess traits more compatible with accelerated vertical growth when they encounter a forest gap. At present, little is known about the morphological and physiological variations among closely related canopy and subcanopy species such as the *Acer* and how these two growth forms respond to high and low growth irradiance environments.

Maximum photosynthetic rate (A_{max}) within a species varies directly with the photosynthetic active photon density (PPFD) regime in which a plant was grown (Björkman 1981). At the leaf-level, shade-acclimated individuals undergo several alterations such as increased chlorophyll content and reduced levels of photosynthetic carbon reduction (PCR) cycle components (Boardman 1977). In this configuration, the shade leaf is considered better able to capture limited quantum energy while minimizing the respiratory cost of maintaining cellular systems for carbon reduction (e.g. Crookston *et al* 1975, Welander and Hellgren 1988). Recent studies of the photosynthetic response to sunflecks in tropical forest understory plants further demonstrate the acclimation potential of plants grown in light-limited environments

(Pearcy 1983, 1990). One such acclimation is the photosynthetic induction rate, the time required for a shaded leaf to attain high, steady-state photosynthetic rates after exposure to high irradiance. This induction involves an initial phase of PCR cycle substrate (ribulose-1,5-bisphosphate) synthesis in the first minute of a lightfleck, while the second phase lasting about 5 minutes involves the activation of the major carboxylation enzyme Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) (Chazdon and Pearcy 1986a,b, Woodrow and Mott 1989, Pearcy 1990). For a dim-light acclimated leaf, both biochemical and stomatal limitations contribute to the rise in assimilation rate (Kirschbaum and Pearcy 1988, Kirschbaum et al 1988). Since stomatal conductance relaxes slowly after a lightfleck (Kirschbaum et al 1988), short intervals between lightflecks could maintain high conductance and substantially reduce the lag in response to full induction. For a shade-acclimated plant, we would expect a quicker attainment of full induction and slower loss of induction between sunflecks.

Chazdon and Pearcy (1986a,b) found that Alocasia macrorrhiza (an Australian understory herb) showed higher rates of photosynthetic induction after exposure to short duration lightflecks than the less shade tolerant tree seedling Toona australis. But because of the phylogenetic divergence and differences in light requirements in these two species, there is a need to examine the photosynthetic induction response of plants more closely related and grown under similar light regimes. In this way, a direct link between variations in sunfleck response and whole plant performance can be made with less confounding effect of phylogeny or developmental stage. Given the importance of sunflecks in the understory environment, transient rates of gas exchange during pulses of saturating irradiance can have a significant influence on the growth and survival of the whole plant (Chazdon 1988). This chapter addresses the deficiency in our understanding in the dynamic physiological responses in temperate forest trees using eight Acer species.

Stomatal density is among the leaf morphological traits affected by irradiance levels during leaf ontogeny (Holmgren 1968, Miskin and Rasmusson 1970, Abrams and

Kubiske 1990). In Atriplex patula, plants grown in high light had twice the stomatal density as those in low light while stomatal pore length remained unchanged (Björkman et al 1972a). An increase in stomatal conductance through high stomatal density is considered advantageous in open environments (Mott et al 1982). Although there is a positive correlation between density and pore size of stomates and maximum stomatal conductance (Maruyama and Tajima 1990), stomatal conductance is considered of minor importance in the steady-state photosynthesis under low diffuse light (Björkman et al 1972b). But during the brief exposure to sunflecks, Pearcy and others (1987, 1989, 1990) estimate stomatal limitation accounts for 10-25% of the suppressed assimilation. To better utilize sunflecks, diffusion limitation can be improved in two ways: by maintaining high stomatal conductance in dim light (Pearcy 1987) and by having high stomatal density. Are these patterns supported by forest maple seedlings?

In this study, I examine the variation in transient and steady-state photosynthesis in eight Acer species and test the consistency of seedling physiology with expected shade-adaptation in sunfleck response and stomatal characteristics.

Methods and Materials

The experimental design and statistical methods used in this chapter are given in Chapter 2. Photosynthetic and conductance results were based on August 1990 measurements. In 1991, I made a more detailed analysis of photosynthetic induction rate and the subsequent decrease in induction state during darkflecks using two species A. macrophyllum (canopy) and A. pensylvanicum (subcanopy) grown in the same two light treatments. Three replicate plants per species-treatments were measured. The initial induction procedure follows the method described in Chapter 1, the subsequent darkflecks (4 min each) were imposed on the plant by shielding the leaf with shade cloth. Photosynthesis after a darkfleck was determined during a 1 min period under saturating light.

Results

Photosynthesis and stomatal conductance

In all species, gap-grown plants achieved higher A_{max} than shade-grown plants (Figure 1, Table 1). Acer macrophyllum attained the highest A_{max} (12.2 μmol m^{-2} s^{-1}) in gap while another canopy species (A. saccharum) showed the lowest at 3.4 μmol m^{-2} s^{-1}. The same two species defined the high (9.2 μmol m^{-2} s^{-1}) and the low (2.3 μmol m^{-2} s^{-1}) A_{max} in the shade treatment. Among populations, variations in A_{max} were generally low (eg. A. palmatum) except in A. macrophyllum and A. platanoides. In most cases, photosynthesis 0.5 and 4.5 min after onset of bright light was higher for the gap-grown plants than for shade-grown plants. The rise in photosynthetic rate was greater in the first 5 min of exposure to bright light than in the subsequent 20 min. Photosynthesis in dim light ranged between 0.55 (A. saccharum-gap) and 1.41 (A. macrophyllum-shade) μmol m^{-2} s^{-1}. The overall mean photosynthesis in dim light was 0.9 μmol m^{-2} s^{-1}. This is similar to the value (1.3 μmol m^{-2} s^{-1}) of saplings of three maple species measured in the forest understory (Lei and Lechowicz 1990).

Variations in photosynthetic activities resided mainly among species within canopy and subcanopy classes but no differences between classes (Table 1). Despite the complexity underlying the photosynthetic system, gas exchange activities between populations in a species seem highly consistent (population(species, class):NS) for these Acer species.

The mean stomatal conductance (g_s) in dim light was 60 (40-100) mmol m^{-2} s^{-1} and at A_{max} was 100 (40-240) mmol m^{-2} s^{-1} (Figure 2). The coupling of g_s and A_{max} was weak when plants were exposed to low diffused light but became progressively stronger from a 0.5 min exposure to saturating light to the steady-state at 24.5 min. High g_s was maintained from dim light to A_{max} for A. macrophyllum, A. platanoides,

Figure 1. Photosynthetic response patterns of 4 canopy and 4 subcanopy Acer species (two populations per species) grown under gap (open symbol) and shade (closed symbol) treatments. Values given were mean (±1SE) of 5 plants. Photosynthesis of the same leaf was first measured on dim-light (30 μmol m^{-2} s^{-1}) acclimated plants, then under bright light (1260 μmol m^{-2} s^{-1}) after 0.5, 4.5 and 24.5 min of exposure. Seed sources for the species and populations used are given in Appendix 1.

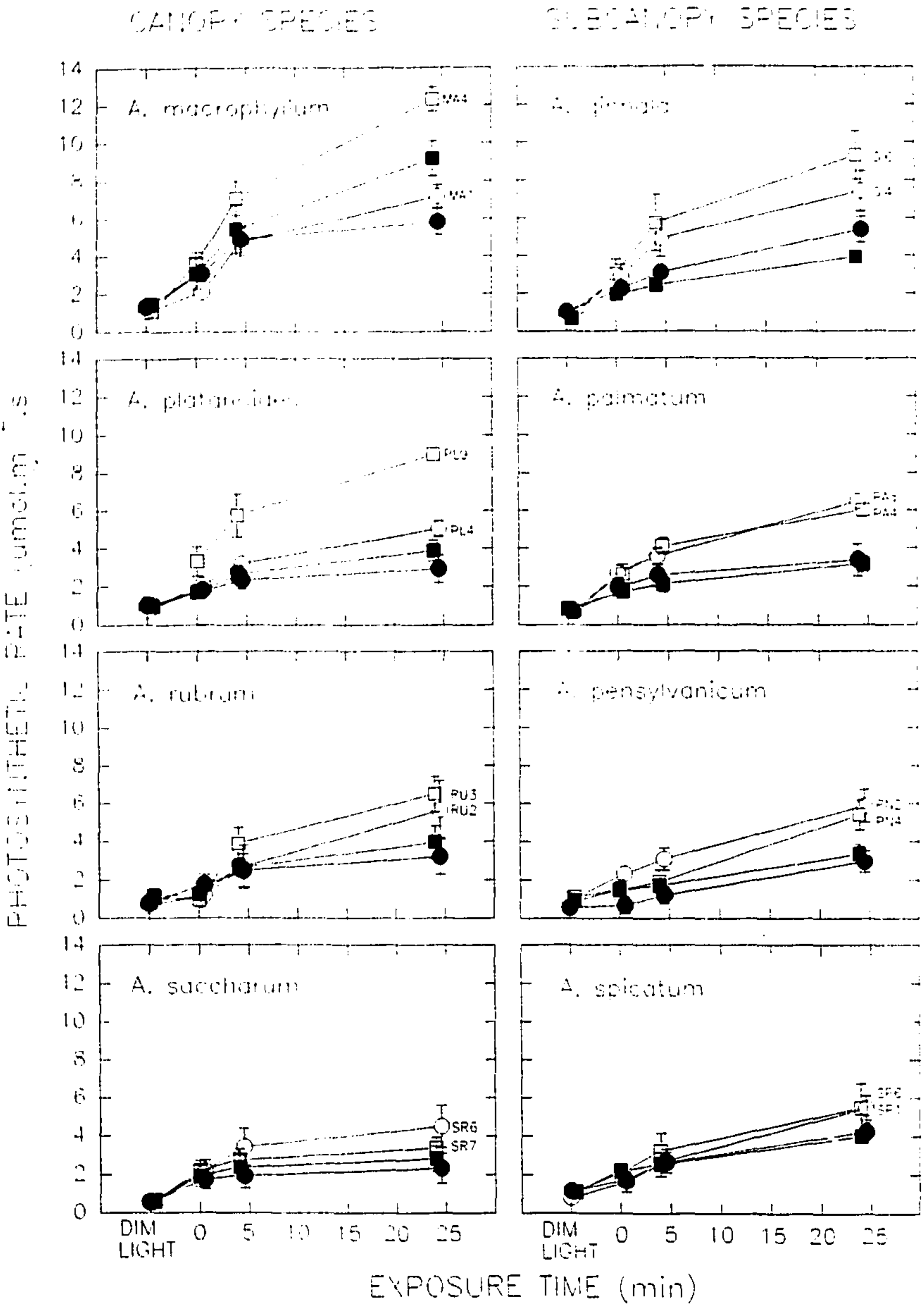
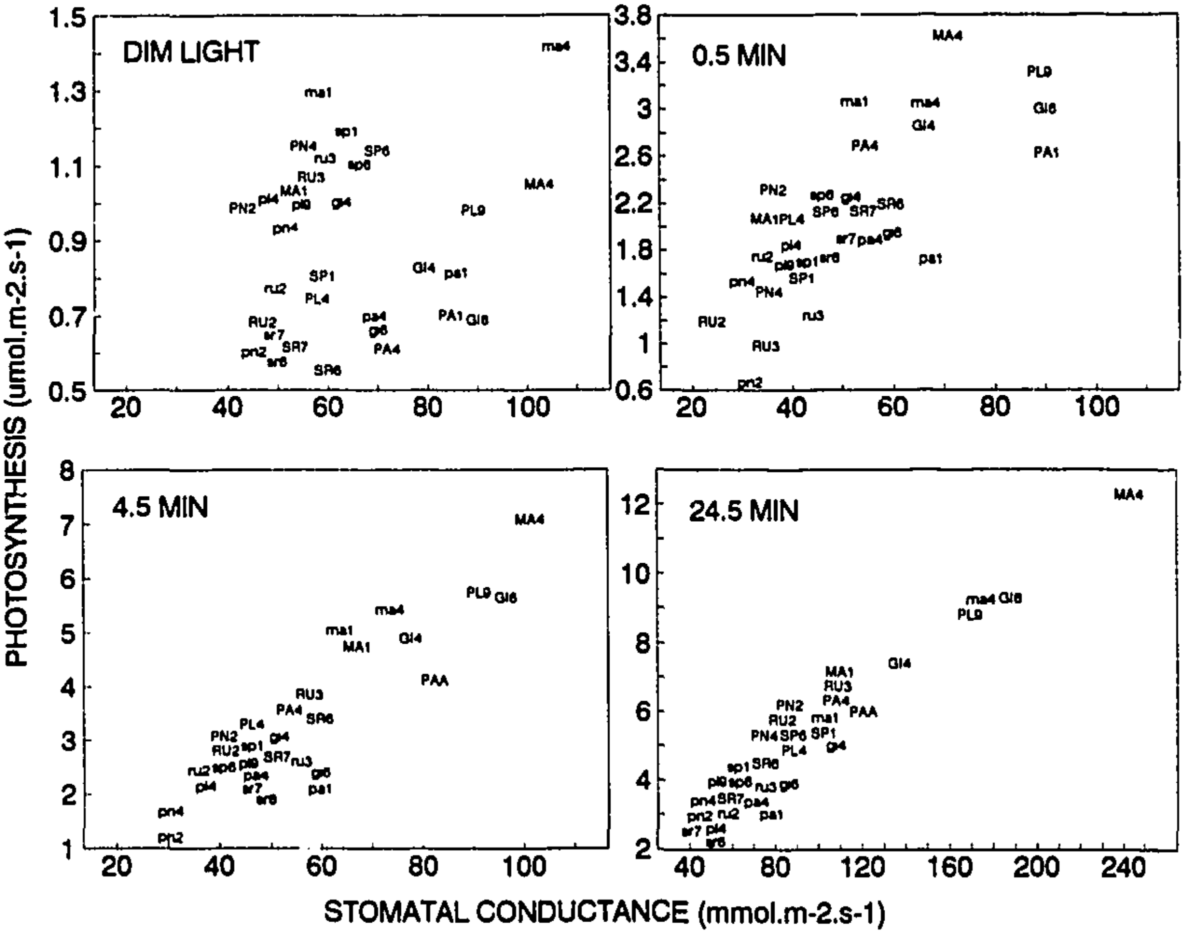

CANOPY SPECIES
SUBCANOPY SPECIES
A. macrophyllum
MA4
MA1
A. ginnala
A. platanoides
PL9
PL4
A. palmatum
PA3
PA4
A. rubrum
RU3
RU2
A. pensylvanicum
PN2
PN4
A. saccharum
SR6
SR7
A. spicatum
SP6
SP1
PHOTOSYNTHETIC RATE (µmol.m⁻².s⁻¹)
0
2
4
6
8
10
12
14
DIM LIGHT
0
5
10
15
20
25
EXPOSURE TIME (min)

Table 1. Analysis of variance results of physiological and stomatal traits of the 8 Acer species. Physiological measurements were taken in August 1990. Variances are partitioned among treatment (gap, shade), class (canopy, subcanopy), species (SP) and populations (P). Species and populations used are given in Figure 1 (Chapter2). Appropriate MS error terms derived from Winer (1971) and is shown in Table 1 (Chapter2). NS P>.05; * P=0.05; ** P=0.01; *** P=0.001.

TRAIT	SOURCE OF VARIATION						
	TREAT	CLASS	T*C	SP(C)	P(SP,C)	T*SP(C)	T*P(SP,C)
PHOTOSYNTHESIS							
DIM LIGHT	NS	NS	NS	*	NS	NS	NS
BRIGHT LIGHT - 0.5 MIN	NS	NS	NS	**	NS	NS	NS
4.5 MIN	**	NS	NS	**	NS	NS	NS
24.5 MIN	***	NS	*	***	NS	NS	NS
STOMATA							
STOMATAL DENSITY	NS	NS	NS	***	NS	NS	NS
STOMATAL APERTURE DIAMETER	NS	NS	NS	***	**	NS	NS

Figure 2. Relationship between photosynthesis and stomatal conductance in dim light and at the three exposure times under bright light. Measurements taken in August 1990. Species codes are canopy growth form: MA=A. macrophyllum, PL=A. platanoides, RU=A. rubrum and SR=A. saccharum; subcanopy growth form: GI=A. ginnala, PA=A. palmatum, PN=A. pensylvanicum and SP=A. spicatum; lowercase represents the shade treatment and uppercase the gap treatment. Standard errors on the species means was 15-22% for photosynthesis and 16-20% for stomatal conductance.


PHOTOSYNTHESIS (umol.m-2.s-1)
STOMATAL CONDUCTANCE (mmol.m-2.s-1)
DIM LIGHT
1.5
1.3
1.1
0.9
0.7
0.5
20
40
60
80
100
ma4
ma1
sp1
PN4
ru3
SP6
sp6
RU3
MA1
MA4
PN2
pl4
pl9
gi4
PL9
pn4
GI4
pa1
SP1
ru2
PL4
pa4
RU2
sr7
gi6
PA1
GI6
SR7
PA4
pn2
sr6
SR6
0.5 MIN
3.8
3.4
3
2.6
2.2
1.8
1.4
1
0.6
20
40
60
80
100
MA4
PL9
ma1
ma4
GI6
GI4
PA4
PA1
PN2
sp6
gi4
SR6
MA1PL4
SP6
SR7
sr7
pa4
gi6
pl4
ru2
pl9
sp1
sr6
pa1
pn4
SP1
PN4
ru3
RU2
RU3
pn2
4.5 MIN
8
7
6
5
4
3
2
1
20
40
60
80
100
MA4
PL9
GI6
ma4
ma1
MA1
GI4
PAA
RU3
PA4
PL4
SR6
PN2
gi4
RU2
sp1
SR7
ru3
ru2
sp6
pl9
pa4
gi6
pl4
sr7
pa1
sr6
pn4
pn2
24.5 MIN
12
10
8
6
4
2
40
80
120
160
200
240
MA4
ma4
GI6
PL9
GI4
MA1
RU3
PA4
PN2
PAA
RU2
ma1
PN4
SP6
SP1
PL4
gi4
sp1
SR6
pl9
sp6
ru3
gi6
pn4
SR7
pa4
pn2
ru2
pa1
sr7
pl4
sr6

A. ginnala and A. palmatum while both parameters were consistently low in A. pensylvanicum.

Internal CO_2 partial pressure

Leaf internal CO_2 partial pressure (C_i) in dim light was 340 ppm and shows negative relationship with photosynthesis (Figure 3). After a 30 s exposure to saturation , C_i dropped to a mean of 280 ppm. Mean C_i remained at 250 ppm in the two subsequent measurement times. The negative relationship between photosynthesis and C_i was evident at 0.5 min and 4.5 min but indistinct at 24.5 min, indicating that maximum g_s was reached. At 4.5 min, gap-grown seedlings clearly showed lower C_i and higher photosynthesis with higher g_s (Figure 2,3), suggesting that gap-grown seedlings had both more rapid stomatal opening and quicker biochemical response to onset of saturating irradiance.

Photosynthetic induction properties

In 1991, I examined, in greater detail, the pattern of photosynthetic induction rise to steady state from dark-acclimated seedlings and subsequent loss of induction after prolonged dark periods. Using the two species having a large contrast in A_{max}, Results in Figure 4 indicates that the induction pattern to steady-state for A. macrophyllum and A. pensylvanicum was similar to measurements taken in 1990 (Figure 1). While I referred to steady-state photosynthesis at 24.5 min determined in the previous season, this experiment showed that A_{max} was reached after only 12 minutes of exposure to saturating irradiance. After 24.5 min, the seedlings were shaded to 40 μmol m^{-2} s^{-1} (a level similar to that of the dim light condition before the lightfleck) for 4 min to simulate a "darkfleck". Photosynthetic rate after the darkfleck was determined under saturating light again by removing the shading for one minute. Lost of photosynthetic induction during the three periods of 4-min darkfleck was greatest in gap-grown

Figure 3. Relationship between photosynthesis and internal CO_2 in dim light and at the three exposure times under bright light. Measurements taken in August 1990. Species codes follows Figure 2; lowercase codes represent the shade treatment and uppercase the gap treatment. Standard errors on the species means was 15-22% for photosynthesis and 3-6% for leaf internal CO_2 partial pressure.

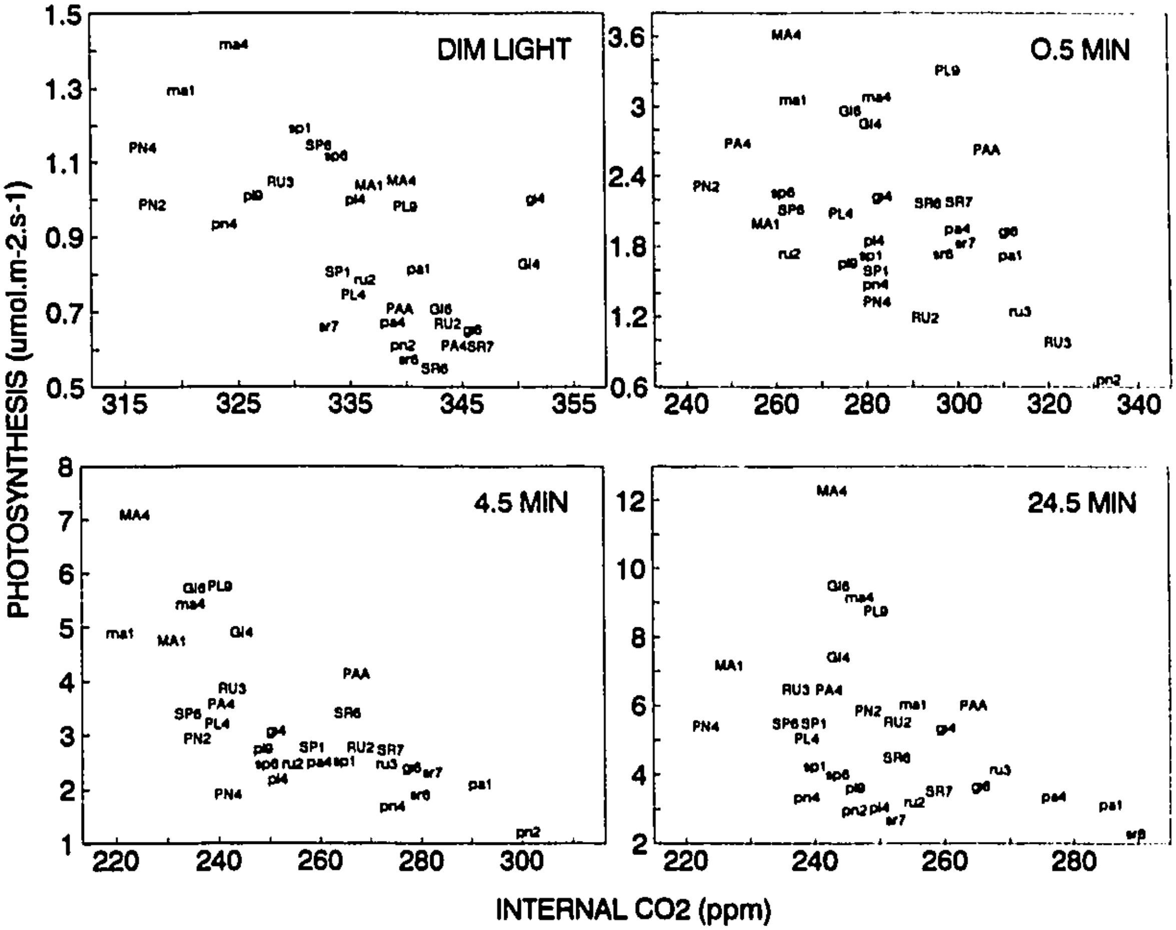
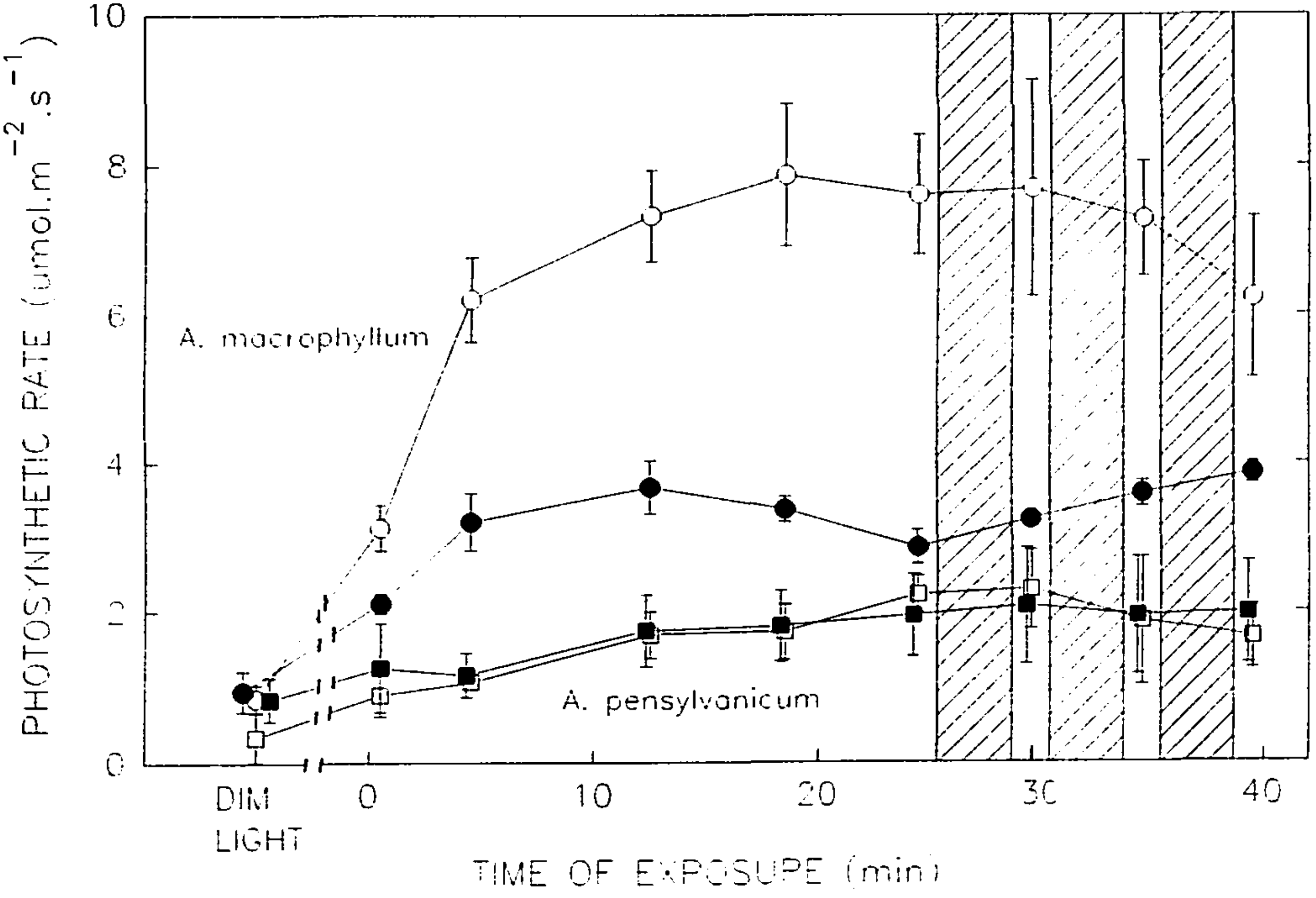

PHOTOSYNTHESIS (umol.m-2.s-1)
INTERNAL CO2 (ppm)
DIM LIGHT
1.5
1.3
1.1
0.9
0.7
0.5
315
325
335
345
355
ma4
ma1
sp1
SP6
sp6
PN4
RU3
MA1
MA4
pl9
pl4
PL9
gl4
PN2
pn4
SP1
ru2
pa1
Gl4
PL4
PAA
Gl6
sr7
pa4
RU2
gl6
pn2
PA4SR7
sr6
SR6
0.5 MIN
3.6
3
2.4
1.8
1.2
0.6
240
260
280
300
320
340
MA4
PL9
ma1
ma4
Gl6
Gl4
PA4
PAA
PN2
sp6
gl4
SR6 SR7
SP6
PL4
MA1
pa4
gl6
pl4
sr7
ru2
sp1
sr6
pa1
pl9
SP1
pn4
PN4
RU2
ru3
RU3
pn2
4.5 MIN
8
7
6
5
4
3
2
1
220
240
260
280
300
MA4
Gl6 PL9
ma4
ma1
MA1
Gl4
PAA
RU3
PA4
SP6
SR6
PL4
gl4
PN2
pl9
SP1
RU2 SR7
sp6 ru2 pa4 sp1
ru3
gl6
sr7
pl4
pa1
PN4
sr6
pn4
pn2
24.5 MIN
12
10
8
6
4
2
220
240
260
280
MA4
Gl6
ma4
PL9
Gl4
MA1
RU3 PA4
PN2
ma1
PAA
PN4
SP6 SP1
RU2
gl4
PL4
SR6
sp1
sp6
ru3
pl9
SR7
gl6
pn4
pa4
pn2 pl4
ru2
pa1
sr7
sr6

Figure 4. Patterns of photosynthetic induction rise to steady-state rate from dark-acclimated seedlings and the subsequent loss of induction after three successive 4-min darkflecks (hatched region). Each point is the mean (±1SE) of 3 replicate plants. Two representative species of canopy (A. macrophyllum) and subcanopy (A. pensylvanicum) growth forms were chosen for this detailed determination made in 1991. Measurements between darkflecks were made with bright light on (1260 μmol m^{-2} s^{-1}) for one minute.


PHOTOSYNTHETIC RATE (umol.m^{-2}.s^{-1})
0
2
4
6
8
10
A. macrophyllum
A. pensylvanicum
DIM LIGHT
0
10
20
30
40
TIME OF EXPOSUPE (min)

A. macrophyllum while A. pensylvanicum showed little loss of induction during the same period.

Dim light photosynthesis, leaf N and stomata

All Acer species were able to maintain a positive mean seasonal assimilation at the 30 μmol m^{-2} s^{-1} irradiance level (Figure 5). Overall, dim light photosynthesis (A_{dim}) decreased with increasing leaf nitrogen (r=-0.36, P=0.16, n=16) suggesting that there is a photosynthetic cost to high leaf N in dim light. This relationship is significant (r=-0.56, P=0.03, n=15) when shade-grown A. macrophyllum is excluded. There is a strong positive relationship between stomatal pore diameter and A_{dim}. In view of the overall negative relationship between stomatal density and stomatal pore diameter, larger pore size appears to have a stronger influence on A_{dim}. Within species in general, stomata become smaller and leaf N higher in gap- versus shade-grown seedlings (Figure 5) and overall, mean stomatal size decreased with increasing area-based leaf nitrogen. These results indicate that those species with larger stomata (A. macrophyllum and A. rubrum) had inherently lower carboxylation cost (i.e., leaf N) which allowed them to attain higher A_{dim}, perhaps through a lower leaf light compensation point. Gap-grown A. saccharum suffered the most in terms of nitrogen cost in A_{dim}, this is likely the result of N allocation to its small total leaf area (Table 2 in Chapter 4).

Stomata

Within a species, stomatal pore diameter remained a stable character both among replicates (indicated by the relatively small variance) and between treatments (Figure 6: the connections between two treatments is generally flat, i.e., no treatment effect [Table 1]). However, much greater variation in stomatal density was observed. Stomatal density was generally higher in gap-grown plants with A. palmatum showing no difference between treatments. The gap- and shade-treatment effect was not

Figure 5. The relationship among leaf nitrogen, stomatal pore diameter and dim light photosynthesis (measured at 30 μmol m^{-2} s^{-1}). The bivariate plots of the three traits are shown as projected surfaces along the respective axes. Species means calculated from 10 replicates. Species codes same as Figure 2.

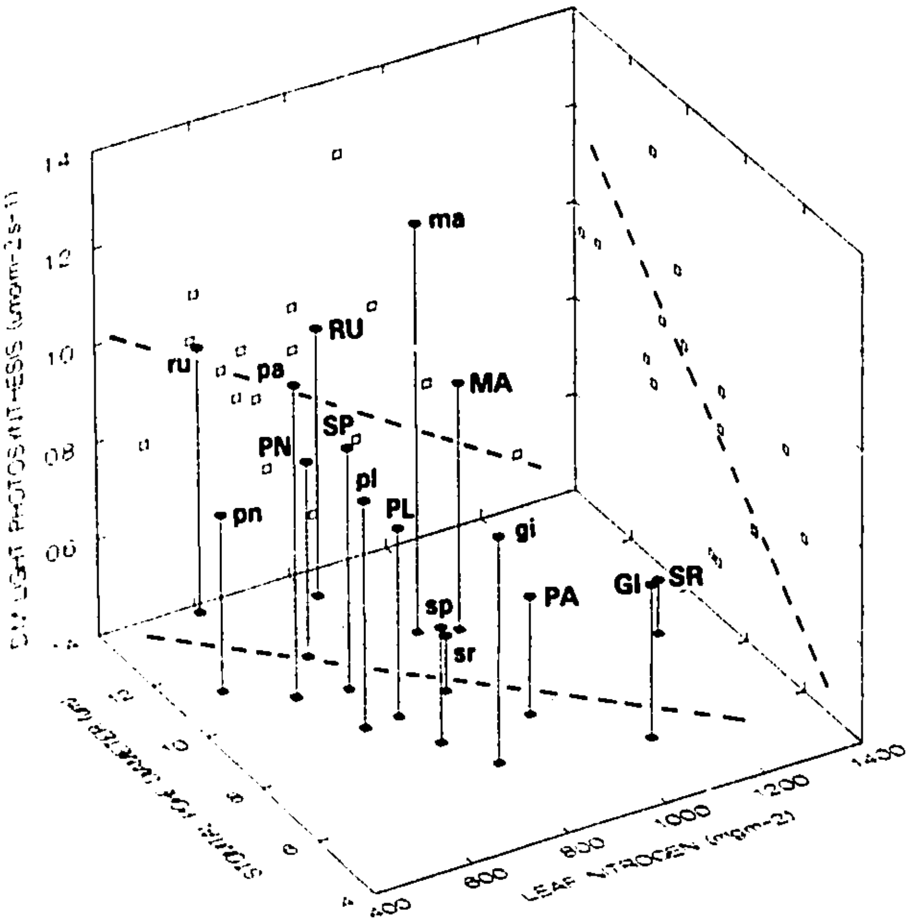
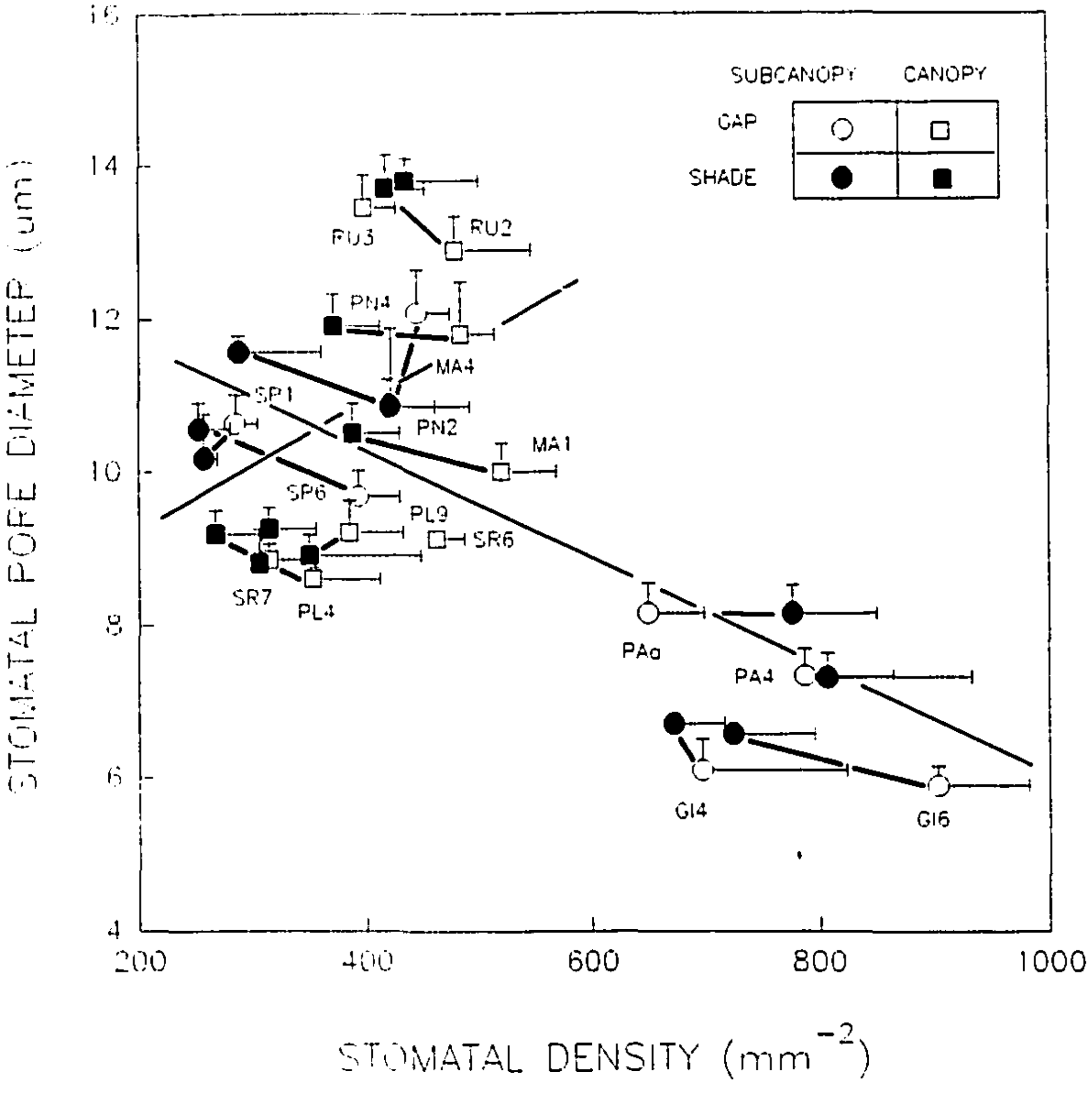

DAYLIGHT PHOTOSYNTHESIS (umgm-2s-1)
14
12
10
08
06
04
12
10
8
6
4
400
600
800
1000
1200
1400
LEAF NITROGEN (mgm-2)
ma
RU
ru
pa
MA
SP
PN
pl
PL
pn
gi
PA
GI
SR
sp
sr

Figure 6. Mean (+1SE) stomatal density and stomatal pore diameter of 4 canopy and 4 subcanopy Acer species grown under gap and shade light treatments. Heavy line connects the same species-population in the two treatments. There was a significant overall negative relationship ($r=-0.59$, $P<0.001$, $N=32$) and a positive trend among species in the upper left cluster ($r=0.40$, $P=0.054$, $N=24$). Each value represents the mean of 5 plants. Species codes follows Figure 2, population codes correspond to seed sources given in Table 1 of Appendix 1.


SUBCANOPY
CANOPY
GAP
○
□
SHADE
●
■
16
14
12
10
8
6
4
200
400
600
800
1000
STOMATAL PORE DIAMETER (um)
STOMATAL DENSITY (mm^{-2})
RU3
RU2
PN4
MA4
SP1
PN2
MA1
SP6
PL9
SR6
SR7
PL4
PAa
PA4
GI4
GI6

statistically significant (Table 1) due to a large error term among replicates. Among species differences were mainly attributable to the distinct separation between A. palmatum and A. ginnala and all the other species. While the high stomatal density in these two subcanopy species showed a concordance with high g_s, this was not the case for A. macrophyllum and A. platanoides (Figure 2). These results suggest that conductance was not affected within the range of stomatal density and pore diameters of these species. In general, these stomatal traits are conservative within species as the among population differences are smaller than those among species. The two subcanopy species, A. palmatum and A. ginnala, were distinctly different from other species by having smaller stomatal pore diameter and higher stomatal density (Figure 6). This leads to an overall negative relationship between stomatal density and pore diameter ($r=-0.59$, $P<0.001$, $n=32$; Figure 6). However, within the large cluster of six species, there is a positive relationship ($r=0.40$, $P=0.054$, $n=24$) indicating a subgeneric variation in stomatal properties in the forest maples. This variation may be geographically based as stomatal density in the four Asian species: A. palmatum, A. ginnala, A. buergerianum and A. rufinerve (the last two species were examined in Chapter 1) were all greater than 580 mm^{-2}.

Discussion

While all forest Acer seedlings were above the light compensation point at 30 μmol m^{-2} s^{-1}, those species with larger stomatal pores and low leaf N tend to have higher A_{dim}. These results imply that A_{dim} is facilitated by species-specific stomatal conductance associated with stomatal size (but not stomatal density), and the amount of investment in carboxylation (determined by leaf N and its maintenance respiration cost). If we infer shade acclimation based only on dim light photosynthesis, A. macrophyllum and A. rubrum, two canopy species, would be most successful in persistence in the shade. However, other properties such as poorer leaf display, less efficient wood and root investment (Chapter 4- Table 1) could negate the whole plant advantage A_{dim} alone may confer. A. macrophyllum is a species that seemed to suffer less N cost of A_{dim}, perhaps mediated by its high stomatal conductance in dim light (Figure 2). For most of the Acer species, additional cost of cambial expansion and root respiration (Poorter et al 1991) require additional light to maintain an overall positive carbon budget (Pearcy 1983).

Lightfleck responses

Plants acclimated to the understory environments should take greater advantage of sunflecks due to the general paucity of photon energy. This can be achieved in two ways: first, architecturally through increasing the light intercepting surface area by creating a monolayer of foliage (Horn 1971); this aspect of Acer ecology is discussed in Chapter 4. Second, physiologically by leaves having a quick photosynthetic induction rate where a steady state can be attained within a shorter time exposure to high irradiance and then lose induction more slowly between sunflecks (Chazdon and Pearcy 1986a,b, Chazdon 1988, Pearcy 1990). This also implies that high irradiance-grown plants ought to show less efficiency in physiological sunfleck response. In this study, photosynthetic induction state after 0.5 min of saturation light exposure was 37% and 38% for gap-grown plants (in canopy and subcanopy species respectively) and 58% and 47% for shade-grown plants. After 4.5 min of exposure, the induction state was increased to 68% and 55% for gap-grown canopy and subcanopy plants and 79% and 61% for shade-grown plants. These findings are consistent with the expectation that shade-grown plants are acclimated to attain higher states of induction than gap-grown plants (also shown in Figure 5, Chapter 1). However, based on actual photosynthesis, gap-grown plants consistently out-performed the corresponding shade-grown plants (Figure 1). The higher induction states in shade-grown plants were achieved by virtue of their lowered steady-state assimilation rate. In terms of carbon uptake then, gap-grown plants appeared to be better adapted to lightfleck utilization in most Acer seedlings. Gross (1982) found similar results in Fragaria virginiana. In a simulated model of photosynthetic response to sunflecks, he found high-light-grown (290 μmol m^{-2} s^{-1}) plants performed consistently better than those grown in low-light

(80 μmol m^{-2} s^{-1}). The proportion of carbon uptake during a single sunfleck of 0.5-, 1- and 2-min durations to the total in an hour (at 24-182 μmol m^{-2} s^{-1}) was 30-40% higher for high-light-grown plants. Despite the lower slope of initial light response curve (i.e. lower dim light photosynthesis), high-light plants attained higher rates during the sunfleck.

Chazdon and Pearcy (1986a,b) reported higher photosynthetic induction response in *Alocasia macrorrhiza*, an Australian rainforest herb (shade-adapted) than *Toona australis* seedlings, a canopy tree less tolerant of shade. They described the more rapid attainment of steady-state assimilation and slower loss of photosynthetic induction in the *A. macrorrhiza* as consistent with its light-limited environment. However, since *T. australis* was grown under a higher light regime, it was difficult to evaluate the relative patterns of photosynthetic induction of the species with different shade tolerance. Although the high-light-grown *T. australis* showed slower induction rate in lightfleck response, its transient photosynthetic rate was in fact consistently higher than *A. macrorrhiza* during the induction process. Even with its greater stomatal and biochemical limitations in sunfleck response, *T. australis* is capable of higher CO_2 assimilation. These findings raise a question how important the pattern of photosynthetic induction actually is to shade-adaptation when the actual assimilation rates contradict the adaptive argument based on relative rates. In considering the growth and survival of understory plants, the actual rates of transient photosynthesis ought to be the more relevant measure of physiological performance. In this study, gap-grown plants not only possessed the capacity for high A_{max}, they could also overcome stomatal and biochemical limitations sufficiently rapidly to show higher carbon gain in the first 5 minutes of a lightfleck. Coupled with comparable dim light photosynthetic rates (Figure 1) and dark respiration (Table 1, Chapter 4) to shade-grown plants, I infer that maple seedlings in the gap can well withstand the light condition in a closed canopy. Greater maximum assimilation capacity in this case appears not to be a disadvantage for gap plants.

Sunfleck response by understory plants is affected by stomatal conductance to varying degrees (Pearcy et al. 1985, Pearcy 1990). Severe depression of C_i during onset of sunflecks can hinder the induction rate of photosynthesis. However, if modest levels of stomatal conductance is maintained in low diffuse light, then assimilation during the onset of sunflecks will be largely limited (>85%) by carboxylation factors (Pearcy et al. 1985; Chazdon and Pearcy 1986a). In this study, dim light stomatal conductances (>40 mmol m^{-2} s^{-1}) were higher for all species (Figure 2), resulting in a modest drop of C_i from 315-350 ppm in dim light to 220-300 ppm after 4.5 min in high (Figure 3). These conductance levels impose only a small limitation on transient assimilation rates and are considered an adaptive feature of understory plants (Pearcy 1987). While water loss in the closed canopy posed little concern to the shade-grown seedlings, it may be a more important factor for gap-grown plants. Some gap plants such as A. macrophyllum and A. ginnala reached very high conductances at steady-state (Figure 2). Such behaviour could conceivably induce severe loss of leaf water potential during prolonged insolation in the gap. The maintenance of stable photosynthesis in A. macrophyllum after 25 min in saturating light (Figure 4) suggests that modest lengths of sunflecks do not impose an appreciable constraint on the water balance of the leaf.

The conservative nature of stomatal aperture diameter between light treatments and the tendency for stomatal density to increase under higher irradiance in the maples is consistent with other reports (Björkman et al 1972a, Eliáš 1988). The significant relationship between stomatal density and stomatal conductance in steady-state condition under saturating light (Mott et al 1982; this study: $r=0.26$, $P<0.001$, $N=160$) implies that stomatal density is an important parameter in maximizing assimilation even for understory plants, particularly during bouts of prolonged sunflecks.

The negative relationship between stomatal density and stomatal pore length in Acer seedlings is found in other herbaceous and woody species (Miskin and Rasmusson

1970, Carpenter and Smith 1975, Eliás 1988, Abrams and Kubiske 1990, Bongers and Pompa 1990). Although this relationship can be associated with epidermal cell size (Miskin and Rasmusson 1970) and ecological status (Carpenter and Smith 1975), its functional significance remains unclear. In the Acer seedlings, stomatal density was low and pore diameter high in species with larger leaves, the opposite of smaller-leaved species (Figure 3). Small-leaved species appeared to maintain higher levels of stomatal conductance than other species (A. macrophyllum was an exception, Figure 2). It is likely that higher stomatal density plays a greater role in determining stomatal conductance than pore diameter given similar regulation in stomatal opening and closure. Stomatal regulation in A. macrophyllum maintains a much higher opening (i.e. conductance) than the other species and may be one factor in its superior photosynthetic performance.

Conclusions

In this study, I have shown that among 8 maple species, both transient and steady-state photosynthetic rates appear to be species-specific. These rates are higher in gap-grown plants than shade-grown seedlings, indicating that although rates of attaining full induction state was slower for gap-grown plants, they are able to respond with higher assimilation rates even in the first minutes of lightfleck. These results suggest that lightfleck response of gap-grown plants are not compromised by their greater photosynthetic capacity when compared with shade-acclimated plants. These maple species maintain high stomatal conductance in dim light allowing them to minimize diffusion limitation at the onset of high irradiance. This character is considered advantageous for seedlings surviving in the closed canopy but may exact a cost in water loss for plant growing in forest gaps.

CHAPTER 4: Functional design and relative growth rate of forest Acer species grown under simulated shade and gap light regimes

Abstract

Eight species (two populations each) of 3- to 4-year-old Acer seedlings were grown under two light regimes simulating a natural forest gap and a closed forest canopy. The objectives were 1) to identify a suite of morphological and physiological traits underlying the juvenile growth of forest maple species and 2) to assess the effect of the two light regimes on the functional relationships among traits. I constructed a model of functional design based on aboveground plant form, leaf structures and physiology, and the carbon sink variables of wood density and fine root growth. The path model used to assess the contribution of these traits to variation in the relative growth rate in vertical height (RGRVH) shows that the functional design explained 95% and 66% of the variance in RGRVH (gap and shade treatments, respectively). These findings suggest that the proposed design is a reasonable integration of traits that influence whole plant performance in forest maple seedlings. Photosynthesis traits alone cannot explain variation in growth but must be considered in concert with carbon sink variables. Maximum photosynthetic capacity has a strong negative influence on RGRVH suggesting that there is a cost to those species that maintain high photosynthetic potential which is underutilized under these two irradiance treatments. Canopy and subcanopy species did not differ in leaf level structural and photosynthetic traits but they showed distinct patterns of carbon allocation to wood strength and shoot growth. Canopy species invested the additional carbon resource acquired in the gap treatment towards increasing wood strength while carbon investment in subcanopy species was to increasing plant size. These results show the functional basis for observations that subcanopy species are competitively superior under an intact forest crown or small gaps and that canopy species can only make substantial vertical ascent under large persistent forest gaps.

General Introduction

In a light limited environment, traits involved in photon capture such as plant architecture (Horn 1971, Hallé et al 1978, Chazdon 1985,1986c Küppers 1985), leaf chlorophyll content (Boardman 1977, Koike 1988, 1990), leaf nitrogen (Terashima and Evans 1988, Evans 1989a) and photosynthesis (Björkman 1981, Pearcy 1990) can all play a role in plant performance. Typically, the light regime in a forest varies from >30% full sun for several hours a day in a modest gap (Runkle 1984, Canham 1988b) to <5% full sun punctuated only occasionally by sunflecks under a full canopy (Chazdon 1988). The limitation of light represents a dominant controlling factor in understory plant growth and survival and is particularly critical for woody seedlings. Juvenile trees must persist in the closed canopy for several years using the energy from low diffuse light and pulses of sunflecks (see General Introduction).

Once a forest gap is created, woody seedlings such as Acer saccharum (a canopy species), and A. pensylvanicum (a subcanopy species) respond with accelerated growth critical to attaining reproductive size (Canham 1985, Hibbs et al 1980). A canopy seedling generally requires several gap episodes to reach the forest crown (Runkle and Yetter 1987, Runkle 1990) indicating that persistence through the period between gaps is also an important component of reaching maturity. Subcanopy species attain adult size in the forest understory and may be more shade-adapted than canopy species. For example, subcanopy maple species tend to have a more effective light-intercepting branching structure than canopy species (Sakai 1990a,b). Investment in wood strength may also be lower in the subcanopy growth form given its adult size but little is known about the patterns of biomass allocation between Acer species. It is clear that these plants must survive and reach maturity in a fluctuating light regime both in the short-term (i.e., sunflecks and deep shade) and in the long-term (forest gap and closed canopy). We would expect a strong selection for plant characters that confer persistence in deep shade but that can also respond effectively to the periodic gap openings. We would also expect some variation in biomass allocation to growth and wood strength between canopy and subcanopy seedlings because of their contrasting life history priorities.

Competitive ability and reproductive success are often associated with juvenile growth rate (Maddox and Antonovics 1983, Lechowicz and Blais 1988), plant size (Reekie and Bazzaz 1989) and time to reach maturity (Chazdon 1991). Therefore, in the forest understory, relative growth rate (RGR) appears to be a robust character for the assessment of whole plant performance in juvenile trees. Early life history of trees involves significant mortality due to herbivore attack and pathogen infection (Augspurger 1984a,b, Khan and Tripathi 1991) and self-thinning through negative carbon budget (Harper 1977, Hett and Loucks 1971). Relative growth rate can serve as an indicator of the general health of the seedling and its chances of future survival. While studies of influence of plant traits on RGR are available in herbaceous species (Poorter and Remkes 1990, Hirose 1987), such an analysis on woody species is lacking (William and Buxton 1989, Atipanumpai 1989, Ceulemans 1990).

Recent studies have demonstrated that no single trait predicts plant growth and reproductive success and that there is the need to consider the integrated effect of key functional traits (Maddox and Antonovics 1983, Chapin et al 1987, Lechowicz and Blais 1988, Atipanumpai 1989, Ceulemans 1990, Evans 1990, Farris and Lechowicz 1990). While photosynthetic traits may represent the potential carbon pool available to the plant, it is the partitioning of carbon to shoot extension, wood strength (i.e., wood density) and root that determines whole plant performance (Grime and Hunt 1975, Calow and Townsend 1981, Poorter and Bergkotte 1992). A similar paucity of information exists regarding the integrated effect of light-mediated traits on whole plant performance. Despite the rich experimental evidence demonstrating phenotypic acclimation in plants to reduced irradiance (e.g., Wylie 1951, Jackson 1967, Logan and Krotkov 1968, Wild 1979, Björkman 1981, McClendon and McMillen 1982, Osmond 1987, Givnish 1988), only a few studies have linked the adaptive value of these changes under shading to variations in whole plant performance. For example, Shirley (1929) described the correlated effect of thicker leaves and higher root:shoot ratio to increased growth under high irradiance. In an European hedgerow community, Küppers (1984a,b,c, 1985) demonstrated the potential contribution of physiology and biomass allocation to the competitive ability of species at various successional stages of community development. For woody plants, a quantitative evaluation of the effect of high and low light on the interactions among plant processes and their influence on growth is an essential next step in our understanding of the functional basis of shade adaptation (Atipanumpai 1989, Ceulemans 1990).

In this study, I examined the light-induced responses of a suite of plant traits and their integrated effect on whole-plant performance measured as the relative growth rate (RGR) in vertical height. I constructed a model of functional design for a group of forest Acer L. species that share similar ecological requirements in the juvenile stage but vary in growth forms and life histories. The model includes leaf level and whole plant level characters that can influence height growth directly or indirectly. This was done using path analysis (Wright 1921, Li 1975, Pedhazur 1982) where the strength of trait interactions can be assessed by the direction and magnitude of path coefficients. The irradiance effect on the functional relationships in the seedlings was analyzed by treating gap- and shade-grown plants separately.

This study will be presented in two parts. Part 1 focuses on the the justification for the traits included in the path model, the path structure, and the outcome of the path analysis. Part 2 explores various ramifications of the path model, especially additional aspects of branching architecture and shade acclimation in traits germane to the ecology of maple seedlings. This includes an evaluation of biomass allocation to wood strength (i.e., wood density) versus relative growth rates in height, total twig length and stem basal diameter that can lead to significantly different seedling survival, particularly under dense canopy shade. Each part will have its own brief introduction, methods and results but the interpretation of the results will be combined in a single concluding discussion.

Part 1. The path model

Introduction

Path analysis, first introduced by Sewall Wright in 1921, is similar to a multiple regression analysis in that a suite of characters are used to explain the variance of a determinant trait. But path analysis has the advantage of allowing the partitioning of direct and indirect effects of one variable on another in a hypothetical causal structure (a path diagram). The path diagram also resembles the mechanistic design used in simulation growth models (e.g., Reynolds and Acock 1985, Thornley and Johnson 1990) but the complexity is reduced to a more parsimonious set of key traits. Path analysis provides a test for consistency between expected and observed interactions among variables and unusual linkages can offer new insights into the functional relationships in the system (Schemske and Horvitz 1988). Path analysis can be used as an inductive tool (Mentis 1988) to generate novel functional structures through the modification and testing of existing models (Li 1975). The model presented in this study is a "forest maple" model where key plant traits of eight forest Acer species were used to construct a functional design by which the relative growth rate of height in juvenile maples is determined.

Methods and the Path Model Structure

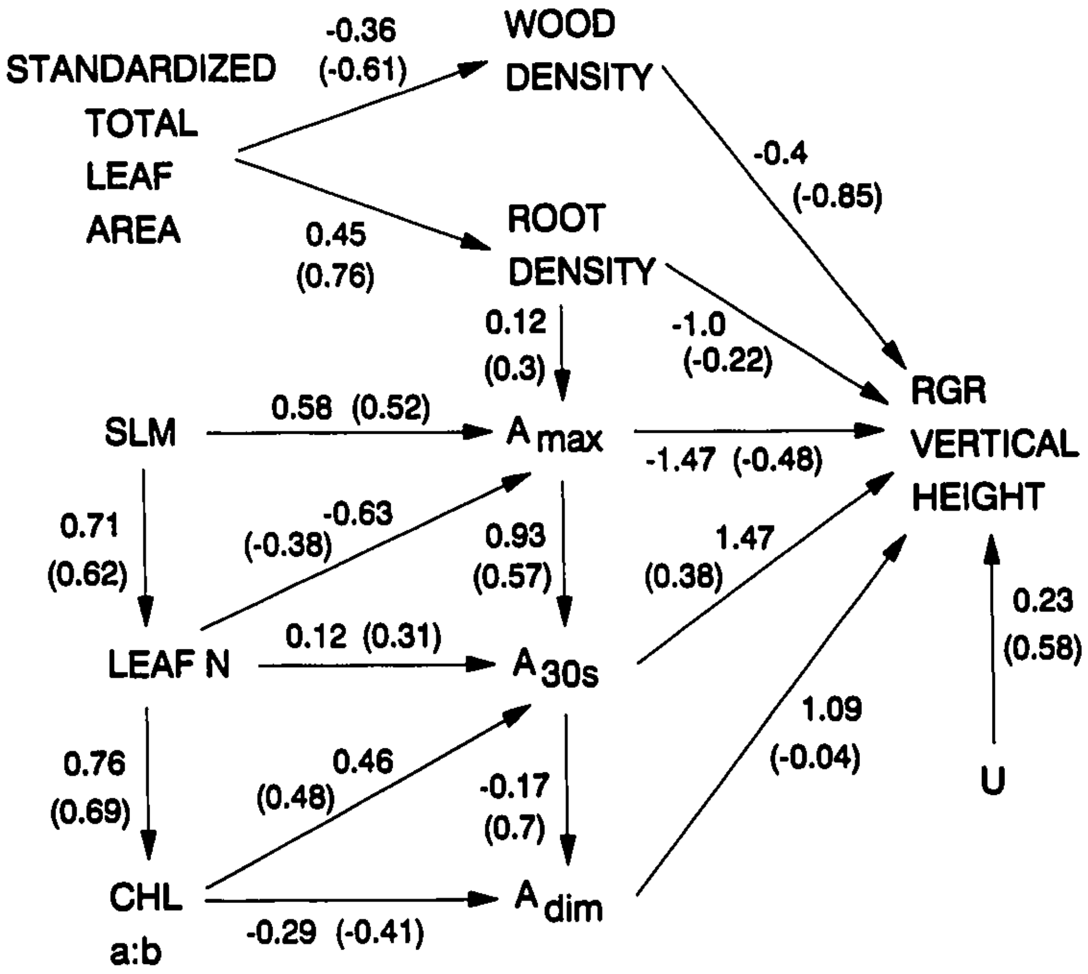
The path coefficients specified in the functional model were estimated using EzPath (SYSTAT Inc, Evanston, Illinois, Wilkinson 1990). Model specification procedure follows Steiger (1989). To circumvent possible violation of normality among variables (required for the Pearson Product Moment correlation analysis), I used a Spearman correlation matrix as the input data for EzPath. While the path coefficients in the model presented here was estimated using a Spearman correlation matrix, similar results were obtained in variants of the present model using Pearson coefficient matrices. The Maximum Likelihood method in EzPath was chosen to estimate the path coefficients because it generates the same coefficients as those independently derived from procedures given in Li (1975).

Path model structure

The model of functional design in Acer (Figure 1) is composed of four distinct components. **1.** The aboveground plant structure is represented by total leaf area standardized against total length of twigs in the crown. **2.** Whole plant carbon sinks are represented by wood density and fine root density. Both these traits share the available carbon pool with shoot extension growth. **3.** Leaf structural traits are represented by specific leaf mass (SLM), leaf N and chlorophyll a:b. All three traits are highly responsive to growth irradiance (Chapters 1,2). **4.** Carbon assimilation potential is represented by the steady-state rate at saturating irradiance [1260 μmol m^{-2} s^{-1}, A_{max}], transient rate after a 30 s exposure to saturating irradiance [A_{30s}] and steady-state rate in dim light [30 μmol m^{-2} s^{-1}, A_{dim}]). Based on functional relationships (given below), the linkages among the four components represent a plausible causal sequence of traits affecting growth in the forest maples. Justification of the path connections is given in following text.

I used relative growth rate in vertical height (RGRVH) as the dependent variable to represent whole-plant performance. This traditional growth parameter is also significantly correlated with RGR in total twig length ($r=0.46$, $P<0.001$, $n=160$) and in stem basal diameter ($r=0.47$, P,0.001, $n=160$). Height growth is important in maintaining a competitive advantage in light over neighbouring plants and the vertical ascent to the forest crown is critical to the future reproductive success of canopy seedlings. Among-species variation in the relationship among RGR in vertical height, total twig length, basal diameter and wood density are further assessed. This allows the identification of trade offs among contrasting patterns of biomass allocation.

Figure 1. Path diagram depicting the functional design of the eight forest Acer species: A. macrophyllum, A. platanoides, A. rubrum and A. saccharum (canopy form); A. ginnala, A. palmatum, A. pensylvanicum and A. spicatum (subcanopy form). The path analysis was run on the input of Spearman correlation matrix derived from species means. Gap and shade treatments were analysed separately, the two path coefficients for each link represent gap and shade (in brackets). U= residual path coefficient where $R^2_{(MODEL.VGRO)}+R^2_{(U.VGRO)}=1$.


STANDARDIZED TOTAL LEAF AREA
-0.36
(-0.61)
WOOD DENSITY
0.45
(0.76)
ROOT DENSITY
-0.4
(-0.85)
-1.0
(-0.22)
0.12
(0.3)
SLM
0.58 (0.52)
A max
-1.47 (-0.48)
RGR VERTICAL HEIGHT
0.71
(0.62)
-0.63
(-0.38)
0.93
(0.57)
1.47
(0.38)
0.23
(0.58)
LEAF N
0.12 (0.31)
A 30s
1.09
(-0.04)
0.76
(0.69)
0.46
(0.48)
-0.17
(0.7)
U
CHL a:b
-0.29 (-0.41)
A dim

The architecture of the aboveground plant structure is represented by the residual total leaf area (LA_{RES}). This parameter is derived by estimating, for each seedling, the residual leaf area from a regression of total leaf area on total twig length of all seedlings. LA_{RES} is, in effect, total leaf area standardized to unit twig length. Using this parameter in the path analysis instead of the raw leaf area values removes the possible confounding effect of allometry between size-dependent leaf area and relative growth rate in plant height. As the leaf area standardized to total twig length, LA_{RES} also represents the proportion of total production surface area to the total supporting structure, an estimate of the leaf display efficiency (LDI) of the maple species. Discussions of the relationships between LA_{RES} and alternate measures of LDI among maples are given in Part 2.

Wood density represents the seedling's investment in both structural strength (King 1991) and in barriers to pathogen attack (Loehle 1988). We would expect a direct trade off between high investment in wood fibre and low shoot extension growth. The amount of total leaf area represents the potential carbon income whose contribution to growth is amortized through its allocation to wood and root investment. Production of fine roots is the principal belowground carbon sink (Marshall and Waring 1985, Fitter 1987, Van Den Driessche 1987). There is a direct demand function of total leaf area on fine root density for the supply of water and nutrients required in photosynthesis. Since fine root density is highly correlated with fine root production rate ($r=0.97$, $N=16$), it also represents the short-term carbon cost. High root density then is expected to inversely affect overall growth rate.

Specific leaf mass represents both the investment to photosynthetic apparatus and the structural and respiratory costs of this function. High SLM generally leads to higher photosynthetic capacity under saturating irradiance (McClendon 1962, Ledig and korbobo 1983, Jurik 1986, Koike 1988, Reich et al 1991) but will also impose greater carbon cost in dim light when the photosynthetic apparatus is underutilized.

Therefore, the carbon return in unit leaf investment (i.e., SLM) could affect seasonal carbon uptake and influence season growth.

Leaf N (area-based) is indicative of the carboxylation potential of the leaf directly affecting the assimilation rate (Field 1983, Field and Mooney 1986) and should have a direct effect on photosynthesis under saturating light level: A_{max} and A_{30s} (these are leaves previously kept in the shade for >30 min then exposed to saturating light for 30 s).

Chlorophyll a:b represents leaf acclimation to the growth irradiance where lower Chl a:b in shade-grown plants acts to increase the light harvesting capacity of Photosystem (PS) II to maintain energy balance with PSI (Chow et al 1990a,b). Chl a:b and total chlorophyll content (the two are negatively correlated) could affect the efficient use of dim light and shade-grown seedlings are expected to show a negative link between Chl a:b and A_{dim} (photosynthetic rate under 50 μmol m^{-2} s^{-1} irradiance).

A_{max} is the steady-state photosynthesis after a 24.5 min exposure to saturating irradiance (1260 μmol m-2 s-1). The ability to utilize high light should be greater for those plants with greater amounts of photosynthetic apparatus as indicated by SLM (Walters and Field 1987, Pompa and Bonger 1988, Sims and Pearcy 1991, Turnbull 1991) and carboxylation potential as indicated by leaf N (Sage et al 1987, Seemann et al 1987, Suzuki et al 1987, Evans and Terashima 1988, Evans 1989b) and A_{max} represents the carbon acquisition potential of the leaf under sustained high light. Similarly, A_{dim} is the production variable that most contributes to growth under low irradiance levels. The ability to maintain carbon uptake under the ambient diffused light of the forest understory should be high in those plants that are "shade-tolerant" or show leaf-level acclimation in leaf N and SLM and chlorophyll to the shade treatment. A_{30s} is the transient photosynthetic rate of the dim light-acclimated plant at 30 s after exposure to saturating light. This variable estimates the influence of the sunfleck response on growth. Since the influence of sunflecks on growth is more critical in shade plants (Pearcy 1983), we would expect the link between A_{dim} and growth to be strong. This trait is assumed to be dependent of both the light (Chl a:b) and dark (Leaf N) reaction centre properties. The sequence of A_{dim}->A_{30s}->A_{max} is in essence a depiction of the species-specific light response curve under the two light treatments. Variation in the linkage strength between the two growth irradiance levels may be interpreted as photosynthetic acclimation. I used the seasonal mean (of four censuses taken in June-September 1990) of the three assimilation traits in the path analysis.

Results

Overall, the functional model accounts for 95% (gap treatment) and 66% (shade treatment) of the variance among seedlings for relative growth rate in vertical height (RGRVH, Figure 1). The relatively high unexplained variance in the shade-grown plants may be associated with the largely determinant extension growth during the spring flush and the smaller effect current-year functional traits have on the current-year measurement of RGRVH in the slower growing, shaded plants.

Those species with a high total leaf area leading to a lower wood density (negative path coefficients for both treatments, Figure 1) suggest there is a partitioning of available carbon pool between leaf biomass and wood strength. In contrast, there is a positive allometric relationship between total leaf area and total root density, which supports the expected supply function of leaves on root activity. Root density also contributes to the maintenance of high maximum photosynthetic rate at the single leaf level as indicated by the positive coefficients in both light environments.

Specific leaf mass has a positive effect on leaf N, chlorophyll a:b and A_{max} (Figure 1). High SLM is generally associated with greater photosynthetic capacity through increased leaf N per unit area and Chl a:b. Contrary to this expectation, the indirect effect of SLM on A_{max} through leaf N is negative. If we examine the bivariate relationship between leaf N and A_{max}, the trend in both the gap- and shade treatments is positive except for A. saccharum (Figure 2). The anomalous negative coefficients from leaf N to A_{max} in the path model is thus attributed to an exceptionally poor nitrogen use efficiency of photosynthesis (μmol s^{-1} of CO_2 uptake per gram nitrogen) in A. saccharum. The effect of leaf N in A. saccharum on A_{30s} ("lightfleck" response) is also weaker than the other species (Figure 2, A_{dim} versus leaf N in both treatments), but the overall path effect from leaf N to A_{30s} was positive, supporting the functional importance of carboxylation capacity (represented by leaf N) even in short duration exposure to high light. The positive influence of the effect of chlorophyll a:b on dim light photosynthesis is negative, consistent with the adaptive expectation that those species with proportionally higher chlorophyll b attain higher dim light photosynthetic rates. Interestingly the higher Chl a:b ratio is maintained in the gap-grown plants supporting its functional advantage even under moderate levels of growth irradiance. The positive effect of chlorophyll a:b on A_{30s} indicate that the level of light harvesting pigments covary with leaf N where high chlorophyll a:b promotes high lightfleck response. Chlorophyll a:b has a contrasting effect on dim light and transient photosynthetic rates.

There is a positive sequential influence from A_{dim} to A_{30s} to A_{max} in the shade treatment indicating a correlated light response at the three irradiance conditions. There does not appear to be a trade off between dim light and steady-state photosynthesis at saturating light in shade plants. This could be attributed to the modest increase from A_{dim} to A_{max} (Table 1) in shade-grown plants being insufficient to reveal a trade off (there are "shade" leaves that have low A_{max} which does not warrant a trade off). In contrast, gap plants show a negative relationship between A_{dim} and A_{max} through A_{30s} consistent with the expected trade off in high-light-grown leaves. The high magnitude of path coefficient from A_{30s} to A_{max} indicate that properties that promote efficient lightfleck response also lead to higher steady-state rates in saturating light.

Figure 2. The scatterplot matrix of plant traits used in the construction of the path diagram (Figure 1). Each plotted point is the mean for the species designated by the letter: M=A. macrophyllum, L=A. platanoides, R=A. rubrum and C=A. saccharum; subcanopy growth form: G=A. ginnala, A=A. palmatum, P=A. pensylvanicum and S=A. spicatum. Plots within a heavy frame have Spearman correlation coefficients at $P<0.1$.

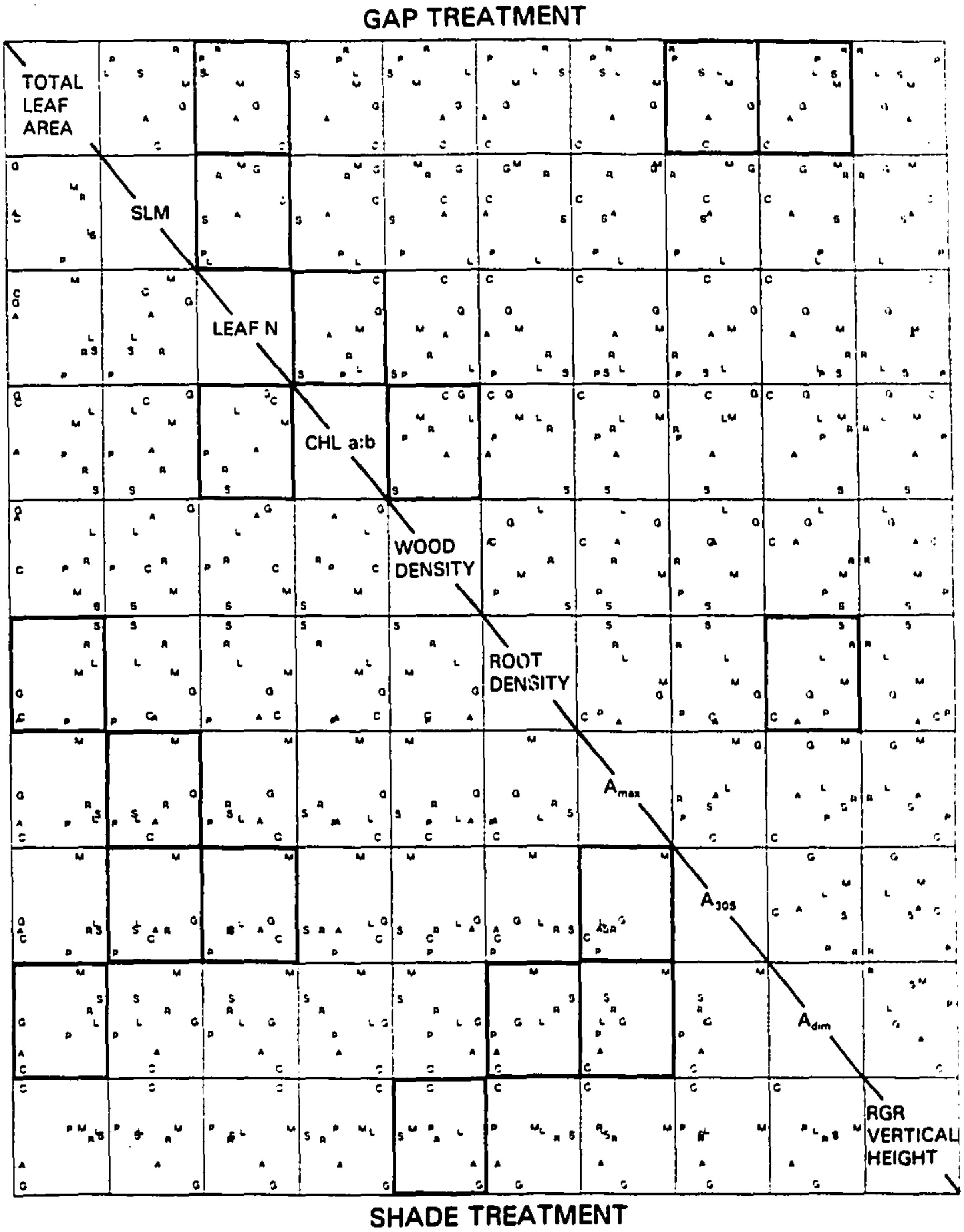

GAP TREATMENT
TOTAL LEAF AREA
SLM
LEAF N
CHL a:b
WOOD DENSITY
ROOT DENSITY
A_{max}
A_{305}
A_{dim}
RGR VERTICAL HEIGHT
SHADE TREATMENT

Table 1. Summary of plant traits in the eight _Acer_ species (mean±1SE, n=10) in the gap and shade treatments. Traits in bold are used in the path model. LDI$_L$ is the leaf display index expressed as the total leaf area (cm^2) per cm twig length (cm) and LDI$_W$ the total leaf area per g twig dry mass. For each trait, the upper 4 are canopy species and the lower 4 subcanopy species. Species codes are canopy growth form: MA=_A. macrophyllum_, PL=_A. platanoides_, RU=_A. rubrum_ and SR=_A. saccharum_; subcanopy growth form: GI=_A. ginnala_, PA=_A. palmatum_, PN=_A. pensylvanicum_ and SP=_A. spicatum_.

LEAF TRAITS

SP	LEAF MASS (g)		LEAVES PER PLANT		**TOTAL LEAF AREA (cm^2)**	
	GAP	SHADE	GAP	SHADE	GAP	SHADE
MA	8.6±0.7	7.4±0.7	13.0±1.2	17.2±2.2	1674±183	1759±221
PL	7.3±0.5	6.6±1.2	34.4±5.1	27.1±3.5	1849±162	2079±366
RU	10.3±0.7	8.3±0.5	53.6±4.2	57.1±3.2	2211±117	2203±135
SR	3.0±0.9	1.0±0.3	23.7±5.5	8.6±0.9	720±225	331±86
GI	5.1±0.4	3.4±0.4	128.2±11.2	99.6±9.8	1380±123	927±114
PA	4.8±0.7	2.5±0.4	126.0±19.4	76.1±9.3	1182±156	729±105
PN	7.3±1.2	4.0±1.0	20.4±3.4	18.6±4.0	2048±321	1525±376
SP	8.1±0.4	6.7±0.6	43.8±6.8	50.7±5.9	1843±150	2422±196

	SPECIFIC LEAF MASS (g.m^{-2})		**LEAF N (g.m^{-2})**	
	GAP	SHADE	GAP	SHADE
MA	44.3±2.4	32.6±2.6	0.975±0.084	0.905±0.055
PL	29.8±1.4	26.1±0.5	0.732±0.049	0.661±0.030
RU	42.5±1.5	30.9±0.8	0.810±0.036	0.597±0.035
SR	39.0±0.9	28.1±0.9	1.278±0.076	0.849±0.033
GI	43.6±1.8	35.7±1.4	1.088±0.043	0.810±0.035
PA	36.8±1.0	28.9±1.0	0.940±0.039	0.754±0.035
PN	30.9±1.6	21.9±1.5	0.692±0.035	0.500±0.034
SP	36.0±1.3	25.5±0.9	0.702±0.032	0.606±0.019

SHOOT TRAITS

	TWIG MASS (g)		TOTAL TWIG LENGTH (cm)		LDI$_L$ (cm^2.cm^{-1})		LDI$_W$ (cm^2.g^{-1})	
	GAP	SHADE	GAP	SHADE	GAP	SHADE	GAP	SHADE
MA	24.2±2.7	20.6±1.2	96±6	100±4	19.1±3.1	17.9±2.4	82±15	89±13
PL	17.9±1.7	14.9±2.9	100±6	98±16	19.4±1.7	20.5±2.6	114±10	158±15
RU	28.0±1.6	22.8±1.9	182±8	186±8	12.3±0.8	11.8±0.7	82±7	100±6
SR	4.0±1.5	1.3±0.4	44±14	24±4	16.1±2.6	12.3±1.5	197±25	266±31
GI	13.2±1.5	9.4±1.1	286±27	234±20	4.9±0.2	4.1±0.5	109±9	101±10
PA	18.5±2.8	6.9±1.1	265±36	176±25	4.5±0.2	4.2±0.4	69±7	114±8
PN	21.5±5.4	14.3±4.2	133±26	108±26	18.0±2.0	14.6±0.6	157±30	197±39
SP	24.0±1.7	18.6±1.6	161±6	191±16	11.3±0.7	12.8±0.7	79±6	139±16

WHOLE PLANT TRAITS

	VERTICAL PLANT HEIGHT (cm)		TOTAL ABOVEGROUND MASS (g)		ROOT:SHOOT		**WOOD DENSITY (g.m^{-3})**	
	GAP	SHADE	GAP	SHADE	GAP	SHADE	GAP	SHADE
MA	89.1±5.6	91.4±3.1	32.7±2.3	28.1±1.7	1.19±0.11	0.78±0.07	0.61±0.01	0.57±0.01
PL	60.6±5.6	60.6±11.2	23.9±1.6	21.3±3.8	1.28±0.13	0.69±0.06	0.71±0.01	0.65±0.02
RU	98.4±5.3	107.8±7.0	38.3±1.9	31.1±2.4	0.80±0.03	0.65±0.04	0.63±0.01	0.61±0.01
SR	23.5±5.2	17.0±3.7	7.0±2.4	2.3±0.6	0.69±0.08	0.68±0.07	0.66±0.02	0.60±0.05
GI	56.5±4.0	56.2±3.9	18.3±1.8	12.8±1.4	1.21±0.10	1.07±0.11	0.69±0.02	0.68±0.01
PA	53.0±7.9	37.7±6.9	23.2±3.5	9.3±1.4	0.32±0.02	0.31±0.03	0.66±0.02	0.67±0.02
PN	89.0±15.2	71.6±17.5	28.8±6.6	18.3±5.2	0.50±0.03	0.47±0.02	0.58±0.01	0.60±0.04
SP	115.5±5.0	105.0±8.5	32.1±2.0	25.2±2.0	0.63±0.04	0.54±0.04	0.56±0.01	0.55±0.01

ROOT TRAITS

	ROOT MASS (g)		**FINE ROOT DENSITY (cm^{-1})**		FINE ROOT PRODUCTION RATE (day^{-1} x 0.01)	
	GAP	SHADE	GAP	SHADE	GAP	SHADE
MA	36.9±1.7	21.5±1.6	0.77±0.09	0.56±0.02	2.03±0.43	1.05±0.15
PL	34.8±3.7	15.5±3.1	1.15±0.10	0.65±0.13	2.76±0.30	1.75±0.33
RU	30.5±0.8	19.8±1.1	1.33±0.11	0.81±0.06	3.59±0.55	2.31±0.18
SR	5.1±1.9	1.7±0.5	0.23±0.07	0.16±0.02	0.81±0.42	0.57±0.13
GI	22.3±2.7	13.9±1.9	0.57±0.08	0.38±0.06	1.88±0.31	1.19±0.23
PA	7.6±1.2	2.7±0.4	0.16±0.01	0.14±0.02	0.44±0.05	0.41±0.08
PN	15.1±3.6	8.9±2.6	0.28±0.04	0.11±0.03	1.11±0.15	0.35±0.06
SP	20.9±2.3	13.8±1.7	1.64±0.19	0.96±0.16	4.38±0.33	2.43±0.34

In both treatments, relative growth rate in vertical height (RGRVH) was negatively affected by increasing wood density, root density and A_{max}. Both wood density and root density act as drains on carbon in the assimilate pool and are expected to behave inversely with growth. The path coefficient of root density to RGRVH was greater in the gap treatment (-1 versus -0.22 in shade, Figure 1). These results are consistent with the earlier findings that proportional investment to root versus shoot growth was greater in gap-grown seedlings (i.e., higher root:shoot ratio, Table 1) leading to a greater trade off between the two structural components. The negative path from A_{max} to RGRVH (in both treatments) may first appear anomalous but is in fact biologically consistent with the experimental design. The method used to measure A_{max} (under saturating artificial light at 1260 μmol m^{-2} s^{-1}) was not typical of the growth irradiance experienced in both treatments. Exposure to saturating PPFD at 24.5 min was necessary to fully induce the steady-state rate in these seedlings but high response to this condition may represent a costly but underutilized photosynthetic apparatus that draws resources away from growth, lead to a negative link between the two variables. Transient assimilation rate (A_{30s}) has a positive direct affect on growth in both treatments. This is consistent with the expectation that sunfleck utilization contributes significantly to growth. Transient response could also benefit gap-grown seedlings experiencing fluctuating light through the lath roof. The direct effect of dim light assimilation (A_{dim}) on growth is positive in the gap treatment but has no effect in the shade. In the path modelling exercise, I found that this path link was particularly sensitive to changes in the specification of other connected traits, suggesting that the direct influence of A_{dim} to growth is weak and unstable. The bivariate plot shows A_{dim} negatively correlated with RGRVH in the gap treatment. This is consistent with the expectation that improved A_{dim} trades off with more efficient high light photosynthesis (negative path coefficient from A_{dim} to A_{30s}) that has a stronger effect on growth.

In general, the interactions of traits used in the path model are consistent with the functional basis of plant processes stated earlier in the path model structure. While the connecting path coefficients vary indicating a treatment effect, the basis of this variation in treatment response among maple species requires additional analysis. The following section provides this analysis on key components that can be linked to additional variables not in the present model. I will also assess the use of RGR in vertical height as the performance trait in relation to functionally related variation in the RGRs of total twig length and stem diameter.

Part 2. Shade acclimation and RGR in maple seedlings

Introduction

This section deals with functionally important plant traits that have not been addressed in detail in the path analysis or in the previous chapters. Traits such as branching architecture and leaf display index can reveal variations among species affecting whole plant fitness (Chazdon 1985, Canham 1988a). These traits are not included in the path model because their estimates (using overall plant size parameters) can confound the path analysis where relative growth rate in height is the determinant variable. Leaf level traits included in this section such as SLM and photosynthesis are represented in the path model but here I explore in more detail the patterns of acclimation to gap and shade among species.

Traditionally, relative growth rate is estimated as changes in vertical height or in overall size but these may not be the only relevant measures in the case of juvenile trees. Variations in lateral shoot growth represent strategies in biomass allocation that will affect growth form and light capture. Investment to wood density represents another share of the available carbon pool closely linked to overall growth. While there is variation in wood density among maple saplings (Lei and Lechowicz 1990), the consequences of this trait on growth has not been clearly established (Zobel and Buijtenen 1989).

Materials and Methods

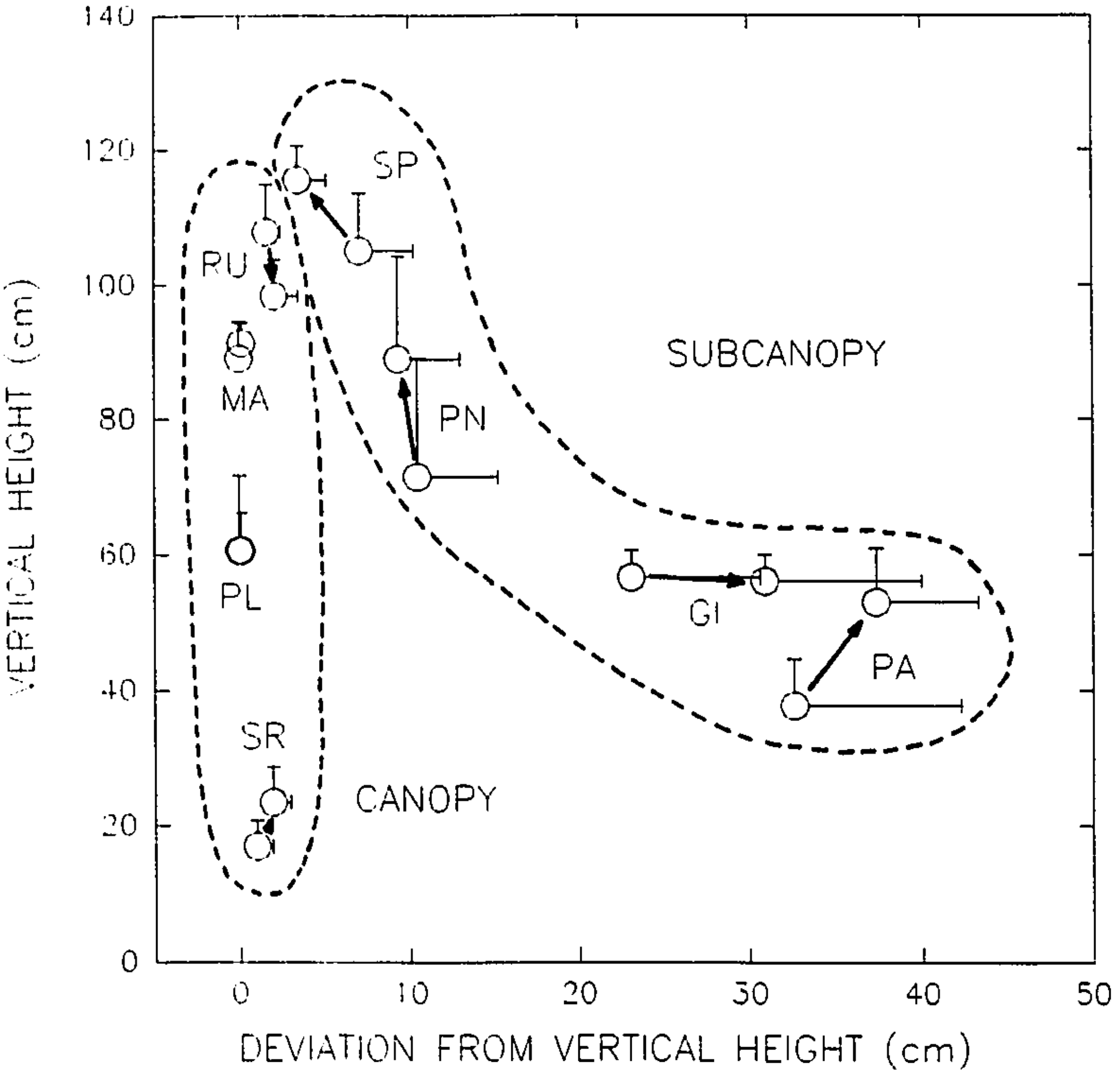
The eight Acer species examined in this chapter include four canopy species: Acer macrophyllum Pursh., A. platanoides L., A. rubrum L. and A. saccharum Marsh.; and also four subcanopy species: A. ginnala Maxim., A. palmatum Thumb., A. pensylvanicum L. and A. spicatum Lam. The experimental design is given in Chapter 2 (Figure 1) and a description of the simulated gap and shade light treatments for the seedlings in Chapter 1. Plant traits measured include leaf characters (specific leaf mass, chlorophyll and nitrogen levels), physiology (steady-state photosynthesis at low and saturating irradiance levels, dynamic photosynthesis simulating sunfleck response), and whole plant characters (leaf display index- leaf area/twig length or mass, branching structure, wood density, fine root production rate). The wood density of oven-dried twigs (total sample) was determined by weighing and volumetric displacement of water. Other traits and the harvesting procedure were given in Chapter 1. Seasonal relative growth rate in vertical height and total twig length (cm cm^{-1} yr^{-1}) and stem basal diameter(mm mm^{-1} yr^{-1}) were estimated as $Ln(h_2)-Ln(h_1)$ (from eq. 10.7, p. 349, Šesták et al 1971) where h_1 was determined in April 1990 and h_2 in October 1990. For most traits examined, the between population variation was small relative to differences among species and treatments; therefore, the following results will largely show only species means derived from pooling the two populations.

Results

Plant form

In general, subcanopy species showed a greater light-mediated response in growth than the canopy species (e.g., apical shoot length and total aboveground mass in A. palmatum and A. ginnala versus A. macrophyllum and A. rubrum). This growth response is solely due to the effect of PPFD and not influenced by R:FR ratio as demonstrated in Chapter 1. As the flushing of spring leaves is associated with a predetermined number of leaves and an associated amount of shoot extension, no height difference would be expected if production of neoform leaves was absent. Although most species showed a stronger determinant height growth in the shade- relative to the gap treatment, A. macrophyllum did not show further growth extension even in the gap treatment (Table 1). Similarly, the total leaf number and total leaf area of A. macrophyllum were not different between the two treatments but total leaf biomass was higher in the gap because of greater leaf density (SLM). Among the species, A. saccharum seedlings were smallest in size but (along with A. platanoides, A. palmatum and A. ginnala) showed significantly greater neoform leaf production in the gap treatment (Table 1). The latter two species had the smallest mean leaf size (9.3-10.8 cm^2), about 1/10 that of A. macrophyllum (102.3-128.8 cm^2). There was no discernible treatment effect on mean leaf area within species. To support the large number of leaves, A. palmatum and A. ginnala also had long twigs. The twigs in these two species were lighter per unit length (cf. total twig length and twig mass in Table 1) than the other species but with comparable wood density; these results mean that, among the maples, twigs of these two species were more slender and flexible, forming an arching stem with numerous lateral shoots (Figure 3). Seedlings of all species increased belowground growth in under the gap irradiance treatment (root:shoot ratio, Table 1) and the response was generally stronger in canopy species (except A. saccharum). At 0.68, the root:shoot ratio in A. saccharum is higher than the 0.35 reported by Marks (1975) for forest-grown seedlings. I estimated the allocation of additional biomass (to root versus shoot) gained in the gap treatment (the difference in total plant mass between gap- and shade-grown seedlings) and found that canopy species invested 75% of the additional biomass to root while it was only 27% in subcanopy species. Clearly, when subcanopy species experienced a modest increase in light resource, they place greater priority in growth to the aboveground part and the priority in canopy species appeared to be increased water and nutrient uptake potential.

Figure 3. The extent of arching in the main stem of seedlings measured as the difference between the linear stem length and the vertical distance from the soil surface to the highest point on the main stem. Species means (+1SE) calculated from 10 replicate plants. Arrows indicate the change from shade to gap treatment in each species. Species codes are canopy growth form: MA=A. macrophyllum, PL=A. platanoides, RU=A. rubrum and SR=A. saccharum; subcanopy growth form: GI=A. ginnala, PA=A. palmatum, PN=A. pensylvanicum and SP=A. spicatum.



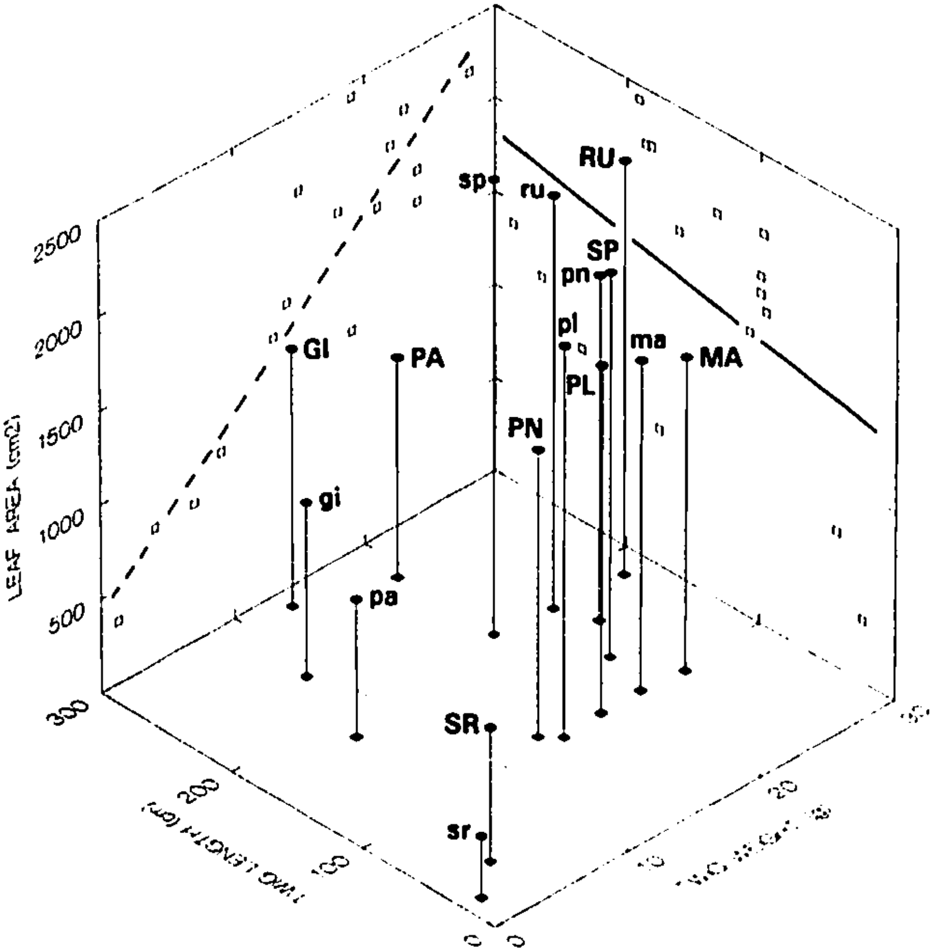
SP
RU
MA
PL
SR
PN
SUBCANOPY
CANOPY
GI
PA
VERTICAL HEIGHT (cm)
DEVIATION FROM VERTICAL HEIGHT (cm)
0
20
40
60
80
100
120
140
0
10
20
30
40
50

Canopy and subcanopy plants are fundamentally different in architecture. During the growing season, subcanopy plants produced more lateral branches than canopy plants. Sixty percent of canopy seedlings remained single-stemmed at the end of the season while only 18% of subcanopy seedlings did so. Subcanopy plants produced significantly more lateral shoots (frequency distribution between classes: $D=0.375$, $P<0.001$, $n1=80$, $n2=80$, Kolmogorov-Smirnov two-sample test). Treatment did not affect the changes in the number of lateral shoots within species. All four canopy species showed little stem curvature (more erect) and tended to be determinant in growth with small vertical height increases (Figure 3). The difference between vertical and linear plant height represent the degree of bending in a seedling. Stems of subcanopy species tended to be more flexed especially in A. ginnala and A. palmatum. They tended to be more indeterminant by having greater height growth from shade to gap than canopy species. A. ginnala has strongly curved stems where greater stem elongation in the gap was masked by bending of the terminal shoot. Module number was generally higher in the subcanopy species (4-16 vs. 1-13 in canopy species). High module number in A. rubrum is due to the high irradiance in the common garden where the plants were grown previous to the experiment (lateral branching proliferates in high light, Pickett and Kempf 1980). Increased arching in concert with the greater number of lateral shoots, allowed the subcanopy seedlings to display a monolayer of leaf area with less self-shading while canopy plants tended to be multilayer with greater apical dominance and self-shading.

Leaf Display Index

The efficiency of leaf display can be quantified by estimating the cost of structural tissue (as total length of twigs or as dry mass) supporting the photosynthetic surface area (i.e., the leaf display index or LDI). Figure 4 shows the parameters used to estimate LDI among maple species and Table 1 gives the derived values of LDI. In terms of leaf area per unit length of twig (LDI_L), A. ginnala and A. palmatum leaves were the least efficiently displayed and the two canopy species A. macrophyllum and

Figure 4. Twig length, twig mass and total leaf area are three aboveground structural traits used to estimate leaf display efficiencies (LDI_L, LDI_W) and the standardized leaf area (LA_{RES}) among maple species. Seedling size can be derived from the location of the species on the 3-D space where the small size of A. saccharum is evident. Species codes same as Figure 3, uppercase= gap treatment and lowercase= shade treatment.


LEAF AREA (cm2)
2500
2000
1500
1000
500
300
200
100
0
TWIG LENGTH (cm)
0
10
20
30
TWIG WEIGHT (g)
sp
RU
ru
SP
pn
pl
PL
ma
MA
GI
PA
PN
gi
pa
SR
sr

A. platanoides were the most efficient (Table 1). The estimation of aboveground structural trait L[illegible]$_{as}$ used in the path analysis is derived from the relationship between leaf area and twig length (Figure 4). Those species below the regression line (leaf area= 1342+1.43*twig length) have lower standardized leaf area. No treatment effect is detected with this estimate of leaf display (Table 2). When LDI is expressed as area per unit twig dry weight (LDI_W), the difference among these species became marginal. The allometric relationship between leaf area and twig mass is strong ($R^2=0.72$) among the species (Figure 4). The high values of LDI_W in A. saccharum may be indicative of its low structural investment to leaf area that aids in maintaining a positive carbon budget in the forest understory. Within species, there was a significant improvement in weight-based leaf display index under gap treatment associated with proportional greater leaf versus twig growth (Table 1). These results illustrate that estimates of leaf display efficiency can vary significantly depending on the unit of measure for leaf support, LDI_L relates stronger to the physical configuration of the light-intercepting surface while LDI_W is a better estimate of the relative carbon costs of leaf to support structures.

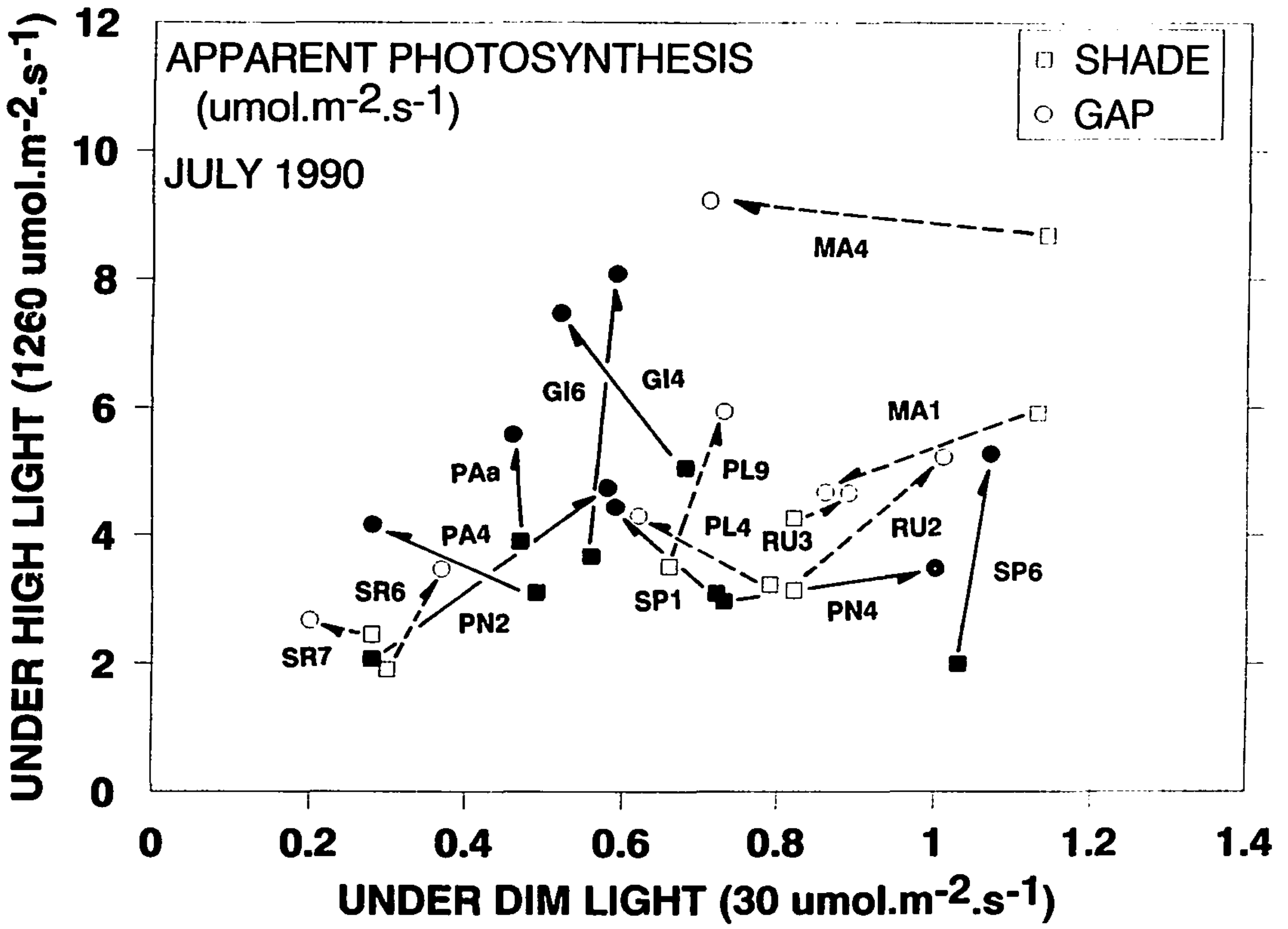
Physiological performance

There was significant among-species variation in photosynthetic acclimation to light treatments (Table 2, Figure 5). For most species, A_{max} was higher in gap-grown seedling (arrow pointing upwards), but no such increase was apparent in dim light photosynthesis. For example, A. macrophyllum with the highest A_{max} showed a decrease in dim light photosynthesis when grown in the gap. In Figure 5 both the magnitude and the angle (e.g., from the vertical) represent acclimation in photosynthesis for each species. Overall, between-population variation in a species was low but there were significant differences among species, even within a growth form class (Figure 5). In two canopy species, A_{max} in A. saccharum was only between 2.3 and 4.5 μmol m^{-2} s^{-1}, while rates were three times greater in A. macrophyllum. Only six species-population (out of 16) showed photosynthetic response patterns

Table 2. Analysis of variance results of plant characters partitioned among treatment (gap, shade), class (canopy, subcanopy), species (SP) and populations (P). Species and populations used are given in Figure 1 (Chapter 2). Appropriate MS error terms derived from Winer (1971) and is shown in Table 1 (Chapter 2). NS P>.05; * P=0.05; ** P=0.01; *** P=0.001. Leaf display indices are LDI_L- total leaf area/ total twig length, LDI_W- total leaf area/ twig mass. Fine root production rate is expressed as number per day.

TRAIT	SOURCE OF VARIATION						
	TREAT	CLASS	T*C	SP(C)	P(SP,C)	T*SP(C)	T*P(SP,C)
LEAF TRAITS							
LEAF MASS	***	NS	NS	NS	***	NS	NS
LEAVES PER PLANT	NS	NS	NS	***	NS	*	NS
TOTAL LEAF AREA	NS	NS	NS	NS	***	NS	NS
SPECIFIC LEAF MASS	***	NS	NS	*	***	**	NS
LEAF N (area-based)	***	***	NS	***	***	***	NS
CHLOROPHYLL a	**	NS	NS	**	NS	NS	NS
CHLOROPHYLL b	***	NS	NS	NS	NS	NS	NS
TOTAL CHLOROPHYLL	**	NS	NS	**	NS	NS	NS
CHLOROPHYLL a:b	***	NS	NS	***	NS	NS	NS
SHOOT TRAITS							
TWIG MASS	***	NS	NS	NS	***	NS	NS
TOTAL TWIG LENGTH	NS	NS	NS	*	***	NS	NS
LDI_L	NS	NS	NS	NS	***	NS	NS
LDI_W	*	NS	NS	NS	***	**	NS
WHOLE PLANT TRAITS							
VERTICAL PLANT HEIGHT	NS	NS	NS	*	***	NS	NS
TOTAL ABOVRGROUND MASS	***	NS	NS	NS	***	NS	NS
ROOT-TO-SHOOT RATIO	*	NS	NS	**	***	**	NS
WOOD DENSITY	*	NS	**	**	*	NS	NS
ROOT TRAITS							
ROOT MASS	**	NS	NS	*	***	*	NS
FINE ROOT DENSITY INDEX	*	NS	NS	***	*	***	NS
FINE ROOT PRODUCTION RATE	**	NS	NS	***	NS	*	NS

Figure 5. Photosynthetic response to dim and saturating lights in eight Acer species (2 population each) grown in gap and shade treatments. Open symbols are canopy species and closed symbols subcanopy species. The average standard error for dim light and high light photosynthesis was 26% and 17% of the respective means. Length and angle of the connecting line represent the magnitude and direction of photosynthetic acclimation. Species codes same as Figure 3; population codes correspond to seed sources given in Table 1 of Appendix 1.


APPARENT PHOTOSYNTHESIS
(umol.m-2.s-1)
JULY 1990
SHADE
GAP
MA4
GI6
GI4
MA1
PAa
PL9
PA4
PL4
RU3
RU2
SR6
SP1
SP6
PN2
PN4
SR7
UNDER HIGH LIGHT (1260 umol.m-2.s-1)
UNDER DIM LIGHT (30 umol.m-2.s-1)
0
2
4
6
8
10
12
0
0.2
0.4
0.6
0.8
1
1.2
1.4

consistent with shade acclimation: higher dim light rates and lower high light rates in shade-grown versus gap-grown plants of each species (i.e., arrow pointing towards upper left corner).

"Sunfleck" photosynthesis, leaf N and total chlorophyll

Forest maples demonstrated a rapid response to the onset of saturating light after being acclimated in dim light. At 2.20±0.18 and 1.96±0.19 μmol m^{-2} s^{-1} (in gap and shade treatment respectively), photosynthesis after a 30 s exposure (A_{30s}) was 2.9- and 2.3-fold higher than A_{dim}. A_{30s} was positively correlated with leaf N and chlorophyll content (Figure 6), suggesting that high levels of both contribute to an improved sunfleck response. A. macrophyllum and A. ginnala responded more quickly to A_{30s} while A. pensylvanicum, A. rubrum and A. spicatum were more sluggish. Although leaves of gap-grown A. saccharum were well endowed with chlorophyll and N, this did not lead to high A_{30s}. A_{dim} and A_{max} were also low in this species. Chlorophyll fluorescence showed that A. saccharum had the lowest quantum use efficiency (F_v/F_m) and total fluorescence quenching (Q_T) suggesting a deficiency in the photochemical transfer mechanism (see Chapter 2). Gas exchange in A. saccharum does not appear to be more limited by stomatal conductance than other species (Figure 2, Chapter 3); both stomatal density and mean stomatal pore diameter fall within the median values among the Acer species (Table 1). Leaf N and chlorophyll content are positively correlated indicating a biological coupling in the investment to the overall photosynthetic apparatus that is partly mediated by SLM (Figure 2).

Relative growth rates

The architectural difference among species (Figure 7) warrants a consideration of the relative growth rate of vertical height, total twig length and basal diameter.

Figure 6. The relationship among leaf nitrogen, total chlorophyll and transient photosynthesis (determined on shade-acclimated leaves after a 30 s exposure to saturating light). The bivariate plots of the three traits are shown as projected surfaces along the respective axes. Species means calculated from 10 replicate plants. Species codes same as Figure 3, uppercase= gap treatment and lowercase= shade treatment.

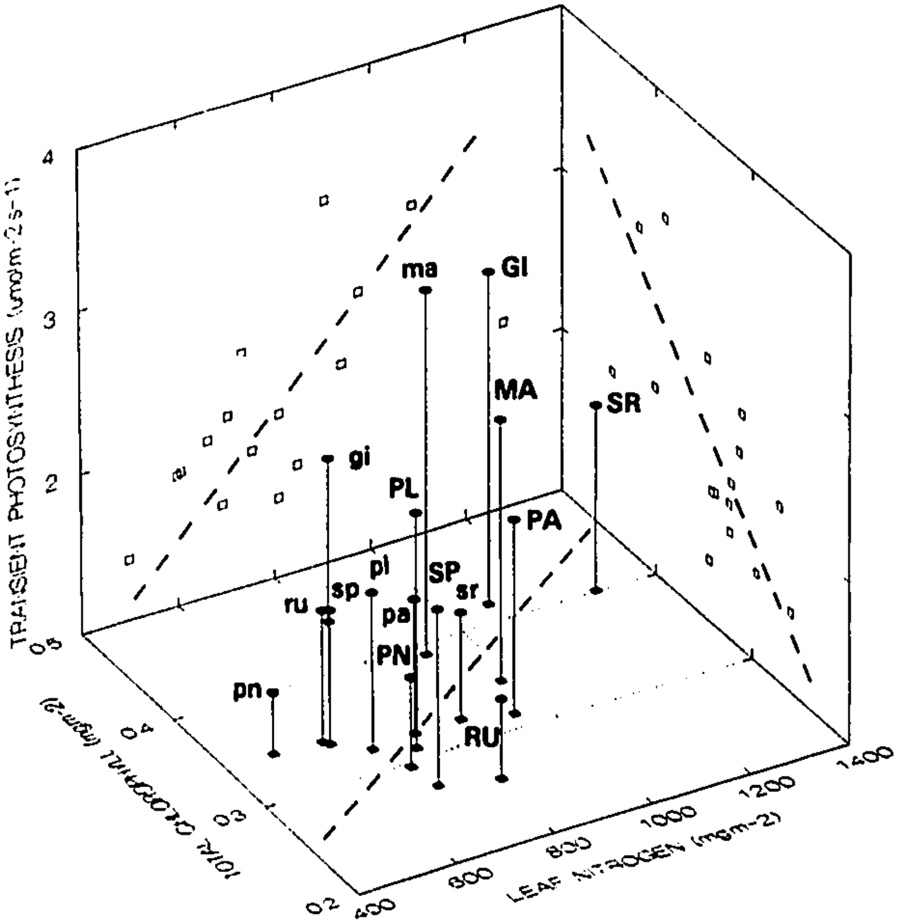
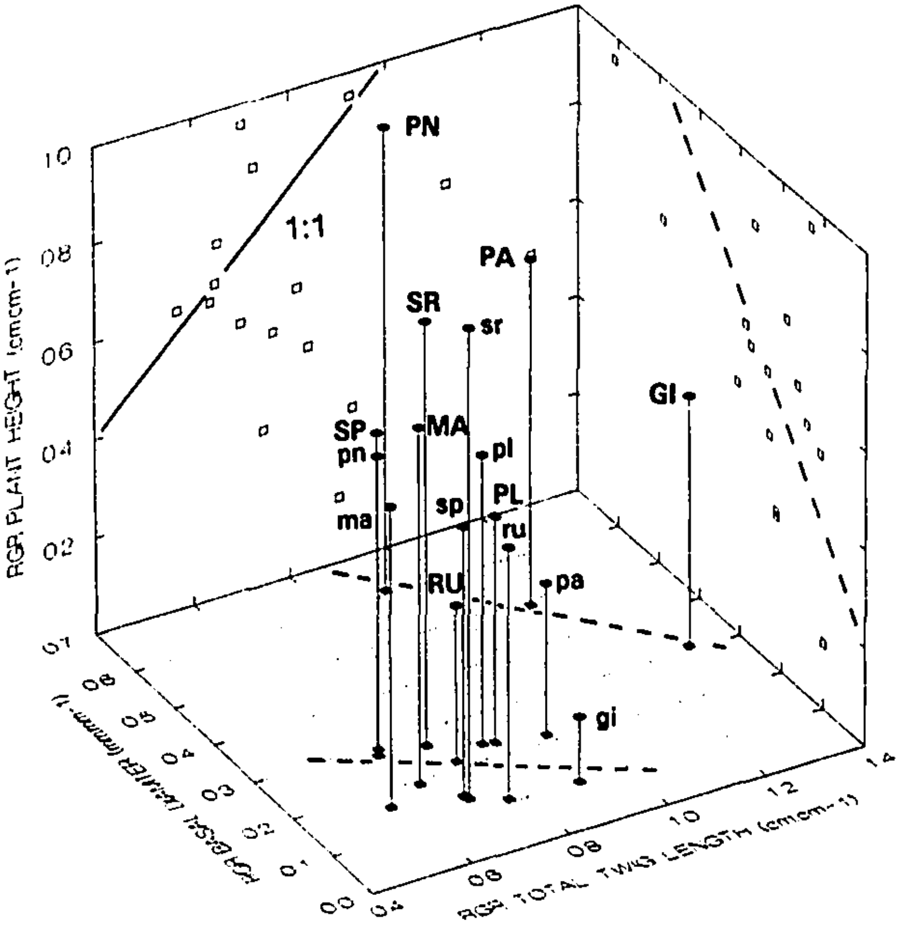

TRANSIENT PHOTOSYNTHESIS (umol m-2 s-1)
4
3
2
TOTAL CHLOROPHYLL (mgm-2)
0.5
0.4
0.3
0.2
LEAF NITROGEN (mgm-2)
400
600
800
1000
1200
1400
ma
GI
MA
SR
gi
PL
PA
pl
SP
sp
sr
ru
pa
PN
pn
RU

Figure 7. The relationship among the three seasonal relative growth rates (RGR) in total twig length, stem basal diameter and vertical plant height. The bivariate plots of the three traits are shown as projected surfaces along the respective axes. Species means (+1SE) calculated from 10 replicate plants. Species codes same as Figure 3, uppercase= gap treatment and lowercase= shade treatment. The 1:1 line on the RGR plant height vs. RGR twig length plot separates those with greater vertical growth rate (above the line) from those with greater lateral shoot growth.


RGR PLANT HEIGHT (cmcm-1)
1.0
0.8
0.6
0.4
0.2
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
RGR BASAL DIAMETER (mmmm-1)
0.4
0.6
0.8
1.0
1.2
1.4
RGR TOTAL TWIG LENGTH (cmcm-1)
1:1
PN
PA
SR
sr
GI
SP
MA
pn
pl
sp
PL
ma
ru
RU
pa
gi

Differential investment to terminal versus lateral growth maintains a growth form that could influence light interception (i.e. leaf display index) and rate of ascent to the forest crown. RGR in height growth (RGRVH) is coordinated with RGR in stem basal diameter (RGRBD), a size parameter that reflects both aboveground and belowground growth (Figure 7). A weaker positive relationship is found between total twig growth rate (RGRTL) and RGRBD. Within this plot, we find two clusters of negatively correlated species indicating that the production of lateral shoots is inversely related to the increases in basal diameter and that the trend is mediated by the wood density of the species. For example, the negative trend in the three gap-grown subcanopy species, A. ginnala, A. palmatum and A. pensylvanicum corresponds to a decreasing wood density from A. ginnala to A. pensylvanicum (Figure 7, Table 1). A. ginnala therefore, can show greater total shoot growth without increasing basal diameter because it makes denser and more slender woody axes. The same explanation applies to the other cluster nearer the origin of the plot.

An inverse relationship is also evident between RGRTL and RGRVH. The species that invested more to total twig growth trades off with its vertical height growth. Although total twig growth rate includes the terminal shoot, most of the species have more than 4 total shoots (to 16 in A. ginnala). A. saccharum and A. macrophyllum are the two species with the strongest apical dominance (mean shoot number is 1-2.6). The values in the RGRVH versus RGRTL plot for these two species lie above the 1:1 line indicating that they either lack lateral shoots (RGRVH=RGRTL) or invested more to vertical shoot growth. All other species showed greater lateral growth.

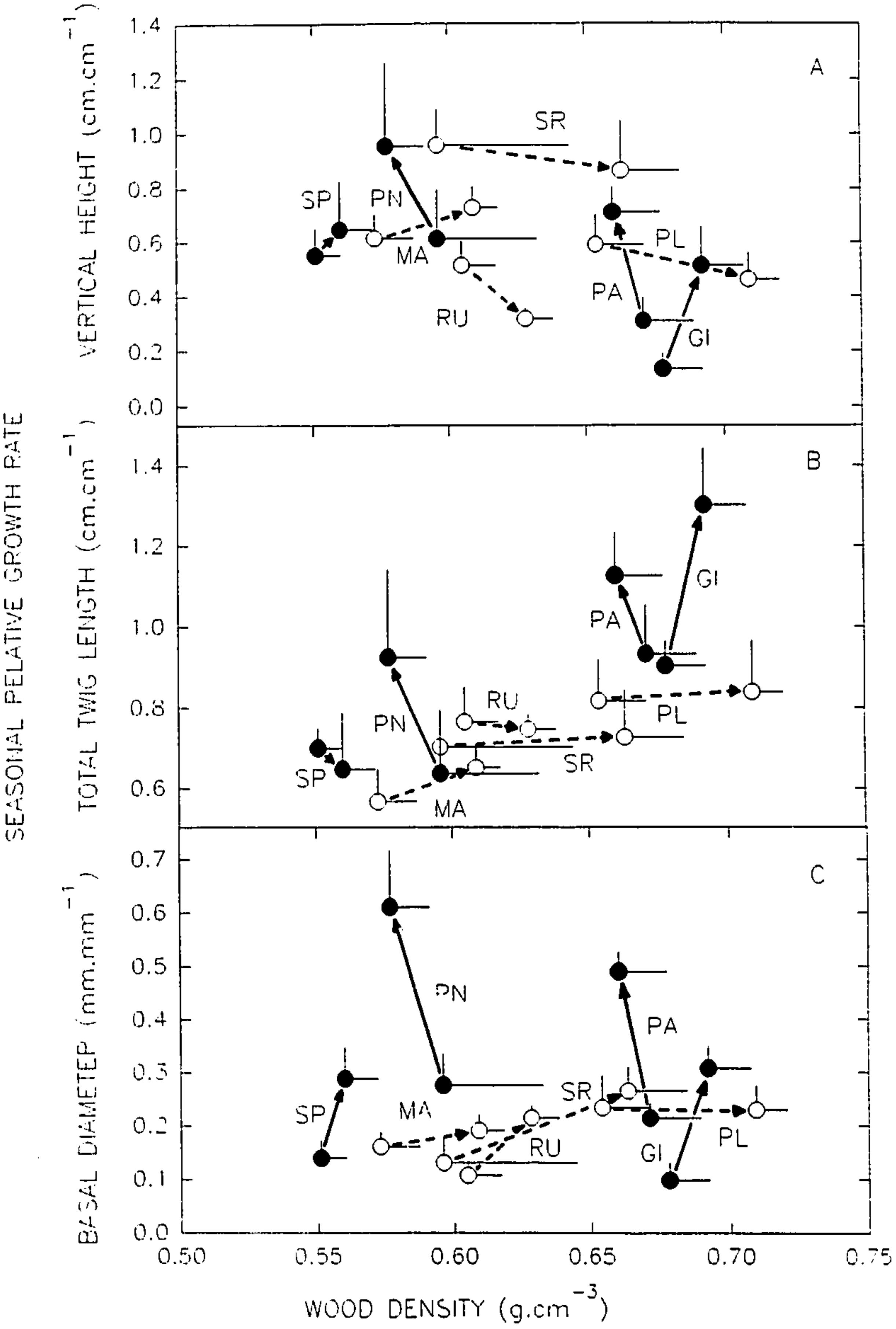
Wood density and relative growth rates

Overall, wood density between growth forms was only marginally different (P=0.06, Table 2) but significantly lighter (P=0.012) in the shade treatment. Within the canopy species, twigs of A. macrophyllum were lighter but more stout compared with the denser and more slender twigs of A. saccharum (Table 1). There is a distinct separation of the light-mediated change in wood density (Figure 8) indicated by the direction of the arrow between canopy and subcanopy species. This is also demonstrated by the significant (P=0.008) treatment by growth form class interaction effect in wood density. This indicates that, in each species, the additional carbon resource received when grown in the gap treatment is variously invested to increasing wood strength or basal diameter (an index of size as it increases with both aboveground and belowground growth) but not both. Canopy species did not have an inherently stronger wood than subcanopy species as demonstrated by the high wood density values of A. ginnala and A. palmatum. Variation in wood density among these Acer seedlings was partially influenced by the growth environment in the previous growing seasons and the relevant feature in wood density is the change within species from the shade to the gap treatment and its effect on vertical growth. Subcanopy seedlings trade off wood strength for size (arrow pointing up) while canopy seedlings sacrifice size for wood strength (arrows pointing to the right).

Discussion

The major aim of this study has been to provide an integrated assessment of the traits important to the juvenile growth of forest maple seedlings. This effort has led to the present path model that satisfactorily describes the interactions among traits and their overall effect on seedling growth. While this functional model represents a useful and parsimonious synthesis of the processes involved in maple seedling growth, it is also an abridgement of somewhat more complex processes that warrant a closer view. In the next sections, I will first interpret the functional meaning of the path model as it has been developed here, followed by a discussion of processes at the levels of the leaf, root, wood and whole plant growth. These discussions provide a more complete consideration of parts of the functional design not fully represented in the path model. The patterns of biomass allocation to wood and to the three growth parameters (i.e., vertical height, total twig length and stem basal diameter) will receive special attention since the response of these patterns to gap and shade treatments among

Figure 8. Variation in the seasonal relative growth rate of a) vertical plant height, b) total twig length and c) stem basal diameter as a function of wood density. Canopy (open circle) and subcanopy (filled circle) species means (+1SE) calculated from 10 replicate plants. Arrow points from shade to gap treatment. Seasonal growth rates are expressed as $\ln(h_2)-\ln(h_1)$ (from eq. 10.7, p. 349, Šesták et al 1971) where h_1 is trait measured in April 1990 and h_2 the same trait measured in October 1990. Species codes same as Figure 3, uppercase= gap treatment and lowercase= shade treatment.



SEASONAL RELATIVE GROWTH RATE
A
VERTICAL HEIGHT (cm.cm^{-1})
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
SR
SP
PN
MA
RU
PL
PA
GI
B
TOTAL TWIG LENGTH (cm.cm^{-1})
1.4
1.2
1.0
0.8
0.6
GI
PA
RU
PN
PL
SR
SP
MA
C
BASAL DIAMETER (mm.mm^{-1})
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
PN
PA
SR
SP
MA
RU
GI
PL
0.50
0.55
0.60
0.65
0.70
0.75
WOOD DENSITY (g.cm^{-3})

forest maple seedlings reveal life history strategies not previously appreciated in the ecology of trees. In other cases the discussion does not involve traits outside the present model but only a more complete consideration of trait variation among species and between treatments.

Variation in functional design in the genus Acer

Many traits interact to affect whole plant performance (Figure 2). The significant associations in some functional traits shown in this scatter plot matrix represent linked processes, intermediate to their effect on relative growth rate. Leaf level acclimation to the shade treatment in lower SLM, chlorophyll a:b ratio and maximum assimilation rates, and higher leaf N are consistent with other reports (e.g., Wild 1979, Björkman 1981, Givnish 1988). But those species that exhibited the most acclimated characters did not always show the greatest increase in height (Figure 2). While leaf level traits are important in carbon acquisition, they explain only a small portion of the vertical growth in Acer species. In a separate path analysis with only the three photosynthesis traits (and excluding wood density and root density) affecting RGRVH, the residual path coefficients (U) on RGRVH were 0.80 and 0.81 in gap and shade treatments respectively. This suggests that the assessment of whole plant performance must also include traits that function as carbon sinks to the total assimilation pool. These results agree with Ramos and Grace's (1990) conclusion that "it is the influence of light on the distribution of assimilated carbon rather than the rate of production of assimilates per area of leaf, that is the most diagnostic attribute for distinguishing the ecological status of the tree species". The strength of the present path model (i.e., % variance explained) indicates that the putative structure of plant process components adequately captures the functional design of the Acer seedlings. This model illustrates the importance of including both the productive (i.e., leaf structure to photosynthesis) and the cost (whole plant structure to above- and belowground carbon sinks) aspects of the plant when growth is assessed. While leaf level traits such as leaf N can enhance maximum photosynthetic performance, this functional path actually represents a maladaptation to the experimental light regimes. Whole plant growth is better described as the difference between carbon uptake potential under ambient irradiance regimes (e.g., lightflecks and dim light) and the carbon expenditure on wood and root activities. The next sections examine components of this functional design in more detail.

Leaf level traits

The seasonal carbon budget of the maple seedlings indicates that persistent shade alone will not sustain seedling survival. The seasonal mean dim light photosynthesis (A_{dim}) and dark respiration are 0.77±0.05 and 0.46±0.04 μmol m^{-2} s^{-1} (gap), and 0.86±0.08 and 0.45±0.03 μmol m^{-2} s^{-1} (shade). Given the length of daylight (assuming a mean of 9 hours of light when solar altitude is >30°, List 1951) and the presence of cloud cover (30%), a leaf level carbon deficit might result for these plant under a closed forest canopy without additional light sources such as sunflecks (Loach 1967). However, characters that confer a higher A_{dim} will still be advantageous in shade-grown seedlings by increasing the margin of carbon gain. The lack of a strong direct association between A_{dim} and RGRVH in shade-grown seedlings (Figure 1,2) suggest that the assimilates thus acquired during the growing season are allocated to maintenance and storage processes and not to height growth.

Given the large proportion of total light energy shade plants receive as sunflecks (Chazdon 1988, Canham et al 1990), phenotypic acclimation should enhance the photosynthetic response of shade-grown plants to light pulses. The induction of transient assimilation rate is dependent of Rubisco activation, carboxylation substrate level and stomatal conductance (Chazdon and Pearcy 1986a,b, Pearcy 1990). Since about 75% of leaf N is allocated to the photosynthetic apparatus (Chapin et al 1987), its positive correlation with A_{30s} (Figure 6) is expected.

Although the induction process does not involve chlorophyll levels alone because of the rapid transfer of chemical energy within the light harvesting pigments (Bolhàr-Nordenkempf et al 1989, Chapter 2), higher total chlorophyll combined with a larger electron transport pool could contribute to a more rapid onset of CO_2 fixation (Ireland et al 1984, 1989) and lead to higher A_{30s}. Among the Acer species, there was a twofold range in investment in leaf N and total chlorophyll representing a substantial cost differential. With the positive direct influence of A_{30s} to plant height in the functional path design (Figure 1), investment in leaf traits that resulted in improved "sunfleck" response is considered adaptive in forest maple seedlings.

Greater investment in leaf nitrogen is not necessarily adaptive (i.e. resulting in higher growth rates) even for gap-grown seedlings. For example, A. macrophyllum had the highest A_{max} in both treatments but showed only low to modest RGR relative to other species. For these species, the growth irradiance in both treatments was less than 20% full sun with periodic sunflecks while the saturation light used to generate A_{max} was 55% full sun. Those species capable of reaching high A_{max} must maintain a "high performance" photosynthetic apparatus with the associated respiratory costs. Under an environment where the photosynthetic capacity is underutilized such as in both the shade and gap treatments, a cost in whole plant performance would be expected as demonstrated by the negative path coefficient from A_{max} to RGR plant height.

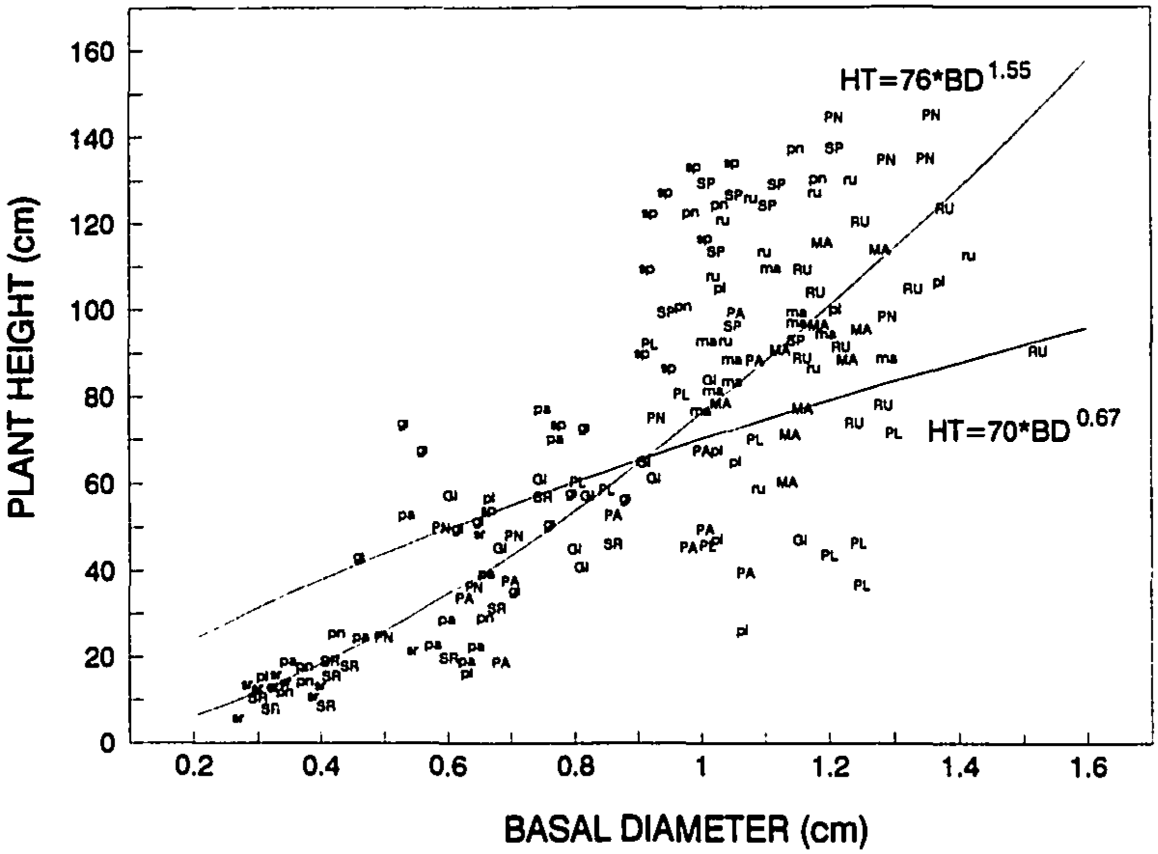
Root growth

As indicated by the path diagram, root activity represents a major carbon sink in these seedlings. These seedlings had higher root:shoot ratio (Table 1) than other forest trees (<0.37, Marks 1975) and forest herbs (<0.22, Cid-Benevento and Werner 1986) suggesting a greater drain on available carbon for growth. The greater proportional carbon investment to root growth in gap-grown plants is consistent with seedlings of a tropical shade-tolerant tree (Fisher et al 1991) and with herbaceous species reported by Poorter et al (1991). Allocation to belowground growth appears to be secondary to shoot growth in subcanopy species. Their greater increase in shoot versus root from shade to gap is in direct contrast to canopy species. Such growth form differences suggest that a developmental constraint in canopy species for anchorage that will be important when they reach adult size. Similar to the investment to wood density, growth form appears to have a strong influence on the allocation of carbon that will have considerable growth consequences.

Wood density

Wood density and growth trade off between canopy and subcanopy species is evident even at the juvenile stage. There was a priority placed in increasing wood strength (highly correlated with wood density, Zobel and van Buijtenen 1989) in canopy species (Figure 8). While resistance to buckling and windthrow are important adult characters for canopy trees, the tendency for building strong wood appears to be expressed in the seedling stage (Lei and Lechowicz 1990). At this age, the Acer seedlings in this study were clearly not limited by the theoretical upper bound established for adult trees (McMahon 1973) (Figure 9) with a positive exponential increase in height with larger basal diameter. But King (1986) found that while small A. saccharum sapling stems are closer to the critical buckling point than larger saplings, carbon demand towards wood strength in the adult severely constrained its continued growth (King 1990a). The tendency to increase wood strength with age is also observed in the seedlings of Pinus patula (Ladrach 1986). When additional assimilate became available in the gap treatment, it is used to build thicker secondary cell wall in the stem instead of other functions such as extension growth (Zobel and Buijtenen 1989). Among 6 provenances of a tropical tree Acacia mangium, Atipanumpai (1989) found a negative relationship between net photosynthesis and plant height and dbh. Although he did not relate wood strength to height growth, the large range in wood density (420-680 kg m^{-2}) among provenances that could account for the observed relationship where high photosynthesis provenances have denser

Figure 9. Scatterplot of plant vertical height versus stem basal diameter. Growth equation Height=70*Diameter$^{0.667}$ was taken from McMahon (1973) and Height=76*Diameter$^{1.55}$ was derived from the least-square regression line using log-transformed values. Species codes are canopy growth form: MA=A. macrophyllum, PL=A. platanoides, RU=A. rubrum and SR=A. saccharum; subcanopy growth form: GI=A. ginnala, PA=A. palmatum, PN=A. pensylvanicum and SP=A. spicatum; uppercase codes represent gap-grown plants and lowercase shade-grown plants.


PLANT HEIGHT (cm)
0
20
40
60
80
100
120
140
160
BASAL DIAMETER (cm)
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
HT=76*BD 1.55
HT=70*BD 0.67

wood. This would be consistent with the results of canopy Acer where excess carbon is invested in increased wood strength.

From a functional perspective, it may be more reasonable to expect Acer seedlings to allocate additional carbon towards growth in height or lateral spread to improve their competitive advantage for light. This is the option subcanopy species have chosen. For these subcanopy species, there appears to be an inherent priority for growth over durability or longevity. Since subcanopy species remain relatively short throughout their life, the size advantage gained in light interception outweighs the safety considerations. As wind stress is low in the understory, the marginal gain in safety against damages caused by falling debris (Chazdon 1986a) appears to be an insufficient selection factor for greater wood strength. From this we may conclude that for canopy seedlings, only large gaps persisting for several years will sustain sufficient height growth from the carbon residual of investment to wood strength. In the shade and small gap, subcanopy species channel more carbon resource to shoot extension both vertically and laterally. This allows for greater competitive ability (from the height) and improved light interception (from the width of crown defined by lateral branches) in a light-limited environment. There was a negative relationship between stem diameter growth rate and age of first reproduction ($r=-0.63$) and a positive relationship between wood specific gravity and mean life span (22 species, $r=0.64$) among 17 Japanese woody species (Koike T, unpublished). The demand for greater wood strength in canopy trees appears to pose a strong developmental constraint that delays maturation. Free of this constraint, subcanopy species can devote more resource to reach adult size quickly and at an earlier time.

Plant architecture

While overall aboveground structure was represented by the residual of leaf area (LA_{RES}) in the functional model to avoid possible autocorrelation with relative growth rate, this parameter is also linked to the variation in leaf display efficiency among maples (Figure 4). The two subcanopy species (A. palmatum and A. ginnala) have low LA_{RES} that correspond to a poor leaf display per unit twig length (LDI_L, Table 1) indicating a greater demand for support structure when leaves are small and numerous. But the additional cost of this branching structure may be compensated by a strongly reflexed stem (Figure 3) and numerous lateral shoots, giving these two species an advantage in light interception over other species. A. macrophyllum demonstrated a different strategy where fewer, larger leaves are displayed on a single stem. This high LDI_L and LDI_W in A. macrophyllum (Table 1) is economical but is associated with greater self shading from the multilayered erect stem. Growth and persistence in this species appears to be achieved by compensating higher self shading with a lower cost of support and high photosynthesis in both high and low light conditions (Figure 1,2 in Chapter 3).

Like A. macrophyllum, A. saccharum seedlings remain mostly single stemmed that is consistent with the priority of canopy species in vertical versus lateral branching. But partly due to its small size, LA_{RES} was lower for A. saccharum. In this broad species comparison, A. saccharum is exceptional for being the slowest growing species. Logan (1965) and Grime (1966) also found this species to have the lowest growth rate among temperate woody species. This appears to be associated with its low photosynthetic activity. At 2.3-4.5 μmol m^{-2} s^{-1}, it is similar to other reports of 2.6 μmol m^{-2} s^{-1} (Ledig and Korbobo 1983) and 2.1 μmol m^{-2} s^{-1} (Weber et al 1985). In contrast, other maple species we analyzed had rates as high as 12 μmol m^{-2} s^{-1} in A. macrophyllum (Figure 1 in Chapter 3). With a high area-based leaf N, A. saccharum also has a relatively poor nitrogen use efficiency among the species. But similar to the understory palm (Geonoma cuneata, Chazdon 1985,1986a), A. saccharum has an advantage in low light environments by its small size and highly cost efficient leaf display (LDI_W, Table 1; Canham 1986a). While growth and competitive abilities will be limited by its low photosynthetic capacity, A. saccharum is able to survive for many years in the shade by minimizing carbon demand for growth (Bloom et al 1985). I suggest that these results provide the functional basis for the persistence of this species (Hett and Loucks 1971, Canham 1985) in the forest understory. It appears that seedlings of A. saccharum require large gaps of substantial duration (12-24 yrs, Canham 1985) to overcome the physiological constraint in gas exchange and nitrogen use efficiency.

Apart from the differences in the magnitude of some path links, the functional design is rather similar between gap and shade treatments (Figure 1). This suggests that the pattern of interactions among leaf level and whole plant level traits were not significantly altered by growth irradiance, rather, it is the investment to wood and to apical versus lateral shoot growth that carry significant adaptive consequences. In the forest, subcanopy species can begin reproduction at 1/3 to 1/10 the size of canopy trees (Fowells, 1965, Hosie 1979, Krüssmann 1979, Fang 1981; personal observation). Given equal RGR and equal response to a gap opening, a subcanopy plant will reach maturity sooner in the forest understory. The shorter age to maturity also reduces the number of periods of suppression between gaps a plant must endure, lessening the risk of mortality due to carbon deficit. Contrasting RGR between vertical height and lateral twigs serves to indicate the direction of biomass investment to becoming tall or broad. For subcanopy species, the imperative for height growth is small. Greater RGR in total twig length with a large module number can maintain a sympodial growth form and a monolayer leaf display (Horn 1971, Sakai 1987,1990a). The monolayer configuration of the plant canopy is accentuated by the greater stem curvature in subcanopy species (Figure 3). There is evidence that the accumulated intercepted solar radiation among poplar clones is genetically controlled through total leaf area and stem curvature (Ceulemans 1990). Similar species specific determination of shoot architecture among Acer species appears to be evolutionarily constrained (Sakai 1990b) but still ecologically functional. Kohyama (1987, 1990) observed lower height growth in sympodial broadleaf evergreen tree species than monopodial species under the tropical forest gap, suggesting a trade off between larger canopy size and the potential for vertical extension. These findings suggest that the trade off between light interception and of height gain is a strong determinant of survival in the forest understory (Chazdon 1986a,b,c, Kohyama 1991).

The average birth rate of gaps in temperate forests is between 0.5% and 3.6% per year (Runkle 1982). This means that only a small percentage of suppressed tree seedling will encounter release growth regimes and the rest must persist for many years. The best strategy for a canopy seedling appears to remain small and persist through to the next gap. The reduced growth may represent a sacrifice in competitive advantage for canopy seedlings, but it is balance by resource accumulation that will confer long-term persistence (Bloom et al 1985). Subcanopy species appear to adopt a different strategy of reinvesting acquired resources into new growth even in a modest gap. For these small trees, marginal increases in the competition for light through height or canopy breadth could mean reaching reproductive size earlier than neighbours. Selection in the subcanopy seedlings appears to favour compromising strong apical dominance and wood strength investment for rapid maturity in the forest understory.

Conclusions

I used an integrated approach to assess whole plant performance. By combining the effect of whole plant structure, leaf level morphology and physiology and above- and belowground carbon sinks, I identified a functional design that organized patterns of variation among traits in forest maple seedlings. This design shows that in the analysis of whole plant performance, it is insufficient to consider photosynthetic activities alone. The pattern of carbon allocational and respiratory costs incurred from structural and maintenance functions of wood and root are other critical elements that must be integrated into the overall assessment of the functional basis for variation in growth. The linking of process and performance is under active investigation in herbaceous species (e.g., Evans 1989, Farris and Lechowicz 1990, Poorter and Remkes 1990, Poorter et al 1990) and this study represents the first similar attempt evaluating woody seedlings. While a basic functional structure has been identified for the maples, future research challenges lie in an understanding of the long-term survival consequences of architecture versus carbon gain (Chazdon 1986c, Sakai 1990a, Kohyama 1991), wood strength in maintaining structural integrity (King 1990a) and in defense (Loehle 1988), and carbohydrate storage (Loescher et al 1990) in woody juveniles.

GENERAL CONCLUSIONS AND ORIGINAL CONTRIBUTIONS

1. An original contribution in the overall approach lies in the broad, quantitative comparison within a single "natural" genus of trees. Ecophysiology of trees in the past has always been based on comparisons of a small number of species (often intergeneric) or comparisons of only a few characters for many species. I combined: i) traits from all levels of functional importance, ii) twelve diverse maple species, and iii) two ecologically relevant treatment environments. The shade treatment specifically is the first reported attempt to simulate in concert the three essential elements of understory light: reduced PPFD, reduced R:FR and sunflecks. This approach offered the basis for a sound analysis of the functional ecology of the forest maples.

2. In maple seedlings, shade acclimation is mainly a response to light intensity and that R:FR plays only a minor role in induction of shade characteristics. This is consistent with other findings that only shade intolerant herbaceous and woody species exhibit a strong "shade avoidance" response to lowering R:FR ratio. The lack of R:FR response prevails regardless of differences in the adult size of canopy and subcanopy species and the associated contrasts in juvenile traits. Given that shade tolerance is critical to maple seedling survival in the forest understory, a shade avoidance response suited to species growing in open habitats may not have a selective advantage. Original contribution This is the first report on the partitioned effect of light quantity and quality on temperate hardwood species and demonstrates that light quality (R:FR) is of minor importance in the shade acclimation of forest trees.

3. In the chloroplast of Acer seedlings, there is a trade off between light and dark reaction processes. These seedlings invested more into functionally "adaptive" components appropriate to their light environment: an increase in carboxylation capacity in gap-grown plants and higher chlorophyll levels in shade-grown plants. However, chloroplast-level properties were not wholly corroborated by gas exchange

measurements as shade-grown plants did not show a better response to dim light photosynthesis and to lightflecks. These results caution against making adaptive interpretations based on only one functional level of plant character. An original contribution was made in demonstrating an empirical relationships between chlorophyll fluorescence kinetics and the levels of chlorophyll and leaf nitrogen across species and between high and low light treatments. This is the first report linking chloroplast-level acclimation to the ecologically important variations in steady-state photosynthesis and lightfleck responses in woody seedlings.

4. *Acer* seedlings responded to sunflecks in an unexpected fashion. While higher leaf N and SLM led gap-grown plants to reached higher steady-state assimilation rates, contrary to expectation, these plants also responded quicker to lightflecks. However, if estimates of the photosynthetic induction process (i.e., lightfleck response) expressed as % A_{max} (induction state) is used, gap-grown plants were slower in reaching full induction simply because of their higher A_{max}. These results indicate that: i) the ability to use dim light and also pulses of light was not compromised in gap-grown plants, ii) absolute assimilation rates may be a more ecologically relevant trait in assessing sunfleck response than induction state. Original contribution I established: i) the pattern of physiological acclimation to gap and shade for a diverse group of maples, ii) that variations in photosynthetic induction state may not be a good indicator of actual assimilation potential, and iii) that variations in stomatal traits alone cannot explain rates of steady-state and transient photosynthesis.

5. Maximum photosynthesis has a strong negative influence on height growth suggesting that there is a cost to those species that maintain high photosynthetic potential which is underutilized under these two irradiance treatments. Leaf display efficiency varied among species, and when considered with light interception, gas exchange and patterns of carbon allocation, can adequately account for the natural persistence of maple seedlings in the forest shade. Canopy and subcanopy species did not differ in leaf level structural and photosynthetic traits but they showed distinct

patterns of carbon allocation to wood strength and shoot growth. Canopy species invested the additional carbon resource acquired in the gap treatment towards increasing wood strength while carbon investment in subcanopy species was to increasing plant size. Original contribution While previous studies only alluded to the compromises woody plants make between carbon source and sink, this is the first experimental demonstration of i) the overall trade off between growth and wood strength, and ii) the influence of life history on woody juveniles where the subcanopy form trade off wood strength for size while the canopy form sacrifices size for wood strength.

6. I presented a template for the functional design of forest maples (i.e., a path model) that adequately explains the basis for interspecific variations in the seasonal growth rate of Acer seedlings. By integrating important plant processes at the leaf, shoot, and root levels, this design model accounts for both traits that contribute to carbon gain and those that share the carbon resource pool with height growth. This design, representing the key functional processes of forest maples, illustrates the importance of considering biomass allocation to wood and root when assessing whole plant performance. Original contribution Recent published reports using the integrated approach to plant performance are advancing our understanding of plant ecophysiology but none has previously addressed: i) the effect of structural support and belowground activity on fitness-related traits, or ii) the functional ecology of woody plants. This study represents the first attempted to combine the modelling of plant processes with experimental manipulation in an evaluation of the basis for variation in the growth of tree seedlings.

LITERATURE CITED

Abrams MD (1986) Physiological plasticity in water relations and leaf structure of understory versus open-grown *Cercis canadensis* in northeastern Kansas. Canadian Journal of Forest Research 16:1170-1174

Abrams MD, Kubiske ME (1990) Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade-tolerance rank. Forest Ecology and Management 31:245-253

Adamson HY, Chow WS, Anderson JM, Vesk M, Sutherland MW (1991) Photosynthetic acclimation of *Tradescantia albiflora* to growth irradiance: morphological, ultrastructural and growth responses. Physiologia Plantarum 82:353-359

Anderson JM, Chow WS, Goodchild DJ (1988) Thylakoid membrane organization in sun/shade acclimation. Australian Journal of Plant Physiology 15:11-26

Anderson JM, Osmond CB (1987) Shade-sun responses: compromises between acclimation and photoinhibition. pp 1-38 In: Kyle DJ, Osmond CB, Arntzen CJ (eds) *Photoinhibition*. Elsevier, Amsterdam, The Netherlands

Arnon D (1949) Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. Plant Physiology 24:1-15

Atipanumpai L (1989) *Acacia mangium: studies on the genetic variation in ecological and physiological characteristics of a fast-growing plantation tree species*. The Finnish Forest Research Institute, Helsinki, Finland

Axelsson L, Klockare B, Sundqvist C (1979) Oak seedlings grown in different light qualities. Physiologia Plantarum 45:387-392

Augspurger CK (1984a) Seedling survival among tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology 65:1705-1712

Augspurger CK (1984b) Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61:211-217

Augspurger CK (1984c) Light requirements of neotropical tree seedlings: a comparative study of growth and survival. Journal of Ecology 72:777-795

Ballaré CL, Sánchez RA, Scopel AL, Casal JJ, Ghersa CM (1987) Early detection of neighbour plants by phytochrome perception of spectral changes in reflected sunlight. Plant Cell and Environment 10:551-557

Björkman O (1981) Responses to different quantum flux densities. pp 57-107 In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) *Encyclopedia of plant physiology, Vol. 12A, Plant physiological ecology I*. Springer, Berlin, Germany

Björkman O, Boardman NK, Anderson JM, Thorne SW, Goodchild DJ, Pyliotis NA (1972a) Effect of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. Carnegie Institute of Washington Yearbook 71:115-135

Björkman O, Ludlow MM, Morrow PA (1972b) Photosynthetic performance of two rainforest species in their native habitat and analysis of their gas exchange. Carnegie Institute of Washington Yearbook 71:94-102

Blais PA, Lechowicz MJ (1989) Variation among populations of *Xanthium strumarium* (Compositae) from natural and ruderal habitats. American Journal of Botany 76:901-908

Bloom AJ, Chapin FS III, Mooney HA (1985) Resource limitation in plants- an economic analogy. Annual Review of Ecology and Systematics 16:363-392

Boardman NK (1977) Comparative photosynthesis of sun and shade plants. Annual Review of Plant Physiology 28:355-377

Bolhàr-Nordenkampf, Long SP, Baker R, Öquist G, Schreiber U, Lechner EG (1989) Chlorophyll fluorescence as a probe of the photosynthetic competence of leaves in the field: a review of current instrumentation. Functional Ecology 3:479-514

Bongers F, Pompa J (1988) Is exposure-related variation in leaf characteristics of tropical rain forest species adaptive? pp. 191-200. In: Werger MJA, van der Aart PJM, During HJ, Verhoeven JTA (eds) *Plant form and vegetation structure*. SPB Academic, The Hague

Bongers F, Pompa J (1990) Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico. Botanical Gazette 151:354-365

Brokaw NVL (1985) Treefalls, regrowth, and community structure in tropical forests. Pages 53-69 In: see Pickett STA and White PS (1985)

Bruinsma J (1963) The quantitative analysis of chlorophylls a and b in plant extracts. Photochemistry and Photobiololgy 2:241-249

Burnison BK (1980) Modified dimethyl sulfoxide (DMSO) extraction for chlorophyll analysis of phytoplankton. Canadian Journal of Fisheries and Aquatic Sciences 37:729-733

Calow P, Townsend CR (1981) Resource utilization in growth. pp 220-244 In: Townsend CR, Calow P (eds) *Physiological ecology, an evolutionary approach to resource use*. Sinauer Associates,Sunderland, Mass., USA

Canham CD (1985) Suppression and release during canopy recruitment in *Acer saccharum*. Bulletin of the Torrey Botanical Club 112(2):134-145

Canham CD (1988a) Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69:786-795

Canham CD (1988b) An index for understory light levels and around canopy gaps. Ecology 69:1634-1638

Canham CD, Denslow JS, Platt WJ, Runkle JR, Spies TA, White PS (1990) Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forestry Science 20:620-631

Carpenter SB, Smith ND (1975) Stomatal distribution and size in southern Appalachian hardwoods. Canadian Journal of Botany 53:1153-1156

Carpenter SB, Smith ND (1981) A comparative study of leaf thickness among southern Appalachian hardwoods. Canadian Journal of Botany 59:1393-1396

Casal JJ, Aphalo PJ (1989) Phytochrome control of chlorophyll content in mature attached leaves of *Petunia axillaris*. Annals of Botany 63:595-598

Casal JJ, Aphalo PJ, Sanchez RA (1987) Phytochrome effect on leaf growth and chlorophyll content in *Petunia axillaris*. Plant, Cell and Environment 10:509-514

Casal JJ, H Smith (1989) The function, action and adaptive significance of phytochrome in light-grown plants. Plant, Cell and Environment 12:855-862

Cavelier J, Goldstein G (1989) Mist and fog interception in elfin cloud forests in Colombia and Venezuela. Journal of Tropical Ecology 5:309-322

Ceulemans R (1990) *Genetic variation in functional and structural productivity determinants in poplar*. Dept. Biology. University of Antwerp, Amsterdam, The Netherlands

Chabot BF, Chabot JF (1977) Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca*. Oecologia 26:363-377

Chabot-Jacquety Y, Levacher P, Phelouzat R (1986) Croissance, ramification et stratégie adaptative d'un ligneux des terrains vagues: le *Buddleia variabilis* Hemsl. (Buddleiacées). Bull Soc Bot Fr 133:353-362

Chapin FS III, Bloom AJ, Field CB, Waring RH (1987) Plant responses to multiple environmental factors. Bioscience 37:49-57

Chazdon RL (1985) Leaf display, canopy structure, and light interception of two understory palm species. American Journal of Botany 72:1493-1502

Chazdon RL (1986a) The cost of leaf support in understory palms: economy versus safety. American Naturalist 127:9-30

Chazdon RL (1986b) Light variation and carbon gain in rain forest understory palms. Journal of Ecology 74:995-1012

Chazdon RL (1986c) Physiological and morphological basis of shade tolerance in rain forest understory palms. Principes 30:92-99

Chazdon RL (1988) Sunflecks and their importance to forest understory plants. Advances in Ecological Research 18:1-63

Chazdon RL (1991) Plant size and form in the understory palm genus *Geonema*: are species variations on a theme? American Journal of Botany 78:680 694

Chazdon RL, Fetcher N (1984) Photosynthetic light environment in a lowland tropical rain forest in Costa Rica. Journal of Ecology 72:553-564

Chazdon RL, Pearcy RW (1986a) Photosynthetic responses to light variation in rainforest species. I. Induction under constant and fluctuating light conditions. Oecologia 69:517-523

Chazdon RL, Pearcy RW (1986b) Photosynthetic responses to light variation in rainforest species. I. Carbon gain and photosynthetic efficiency during lightflecks. Oecologia 69:524-531

Chazdon RL, Pearcy RW (1991) The importance of sunflecks for forest understory plants. Bioscience 41:760-766

Chow WS, Anderson JM, Melis A (1990a) The photosystem stoichiometry in thylakoids of some Australian shade-adapted plant species. Australian Journal of Plant Physiology 17:665-674

Chow WS, Melis A, Anderson JM (1990b) Adjustments of photosystem stoichiometry in chloroplasts improve the quantum efficiency of photosynthesis. Proceedings of the National Academy of Sciences 87:7502-7506

Chow WS, Adamson HY, Anderson JM (1991) Photosynthetic acclimation of *Tradescantia albiflora* to growth irradiance: lack of adjustment of light-harvesting components and its consequences. Physiologia Plantarum 81:175-182

Cid-Benevento CR, Werner PA (1986) Local distributions of old-field and woodland annual plant species: demography, physiological tolerances and allocation of biomass of five species grown in experimental light and soil-moisture gradients. Journal of Ecology 74:857-880

Clapham AR, Tutin TG, Moore DM (1987) *Flora of the British Isles* (3rd ed). Cambridge University Press, Cambridge, UK

Corré WJ (1983) Growth and morphogenesis of sun and shade plants. I. The influence of light intensity. Acta Bot Neerl 32:49-62

Critchfield WB (1971) Shoot growth and heterophylly in *Acer*. Journal of the Arnold Arboretum 52:240-266

Crookston RK, Treharne KJ, Ludford P, Ozbun JL (1975) Response of beans to shading. Crop Science 15:412-416

Cronquist A (1981) *An integrated system of classification of flowering plants*. Columbia University Press, New York, USA

Dale MP, Causton DR (1992) Use of the chlorophyll *a/b* ratio as a bioassay for the light environment of a plant. Functional Ecology 6:190-196

De Jong PC (1976) Flowering and sex expression in *Acer* L. Mededelingen Landbouwhogeschool Wageningen 76-2. The Netherlands

Dunn A, Arditti J (1968) *Experimental physiology. Experiments in cellular, general and plant physiology*. Holt, Rinehart and Winston, New York, USA

Eliáš P (1988) Stomata in forest communities: density, size and conductance. Acta Universitatis Carolinae- Biologica 31:27-41

Erdmann GG, Crow TR (1988) Foliar nutrient variation and sampling intensity for *Acer rubrum* trees. Canadian Journal of Forestry Research 18:134-139

Eschrich W, Burchart R, Essiamah S (1989) The induction of sun and shade leaves of the European Beech (*Fagus sylvatica* L.): anatomical studies. Trees 3:1-10

Eskins K, Duysen M, Dybas L, McCarthy S (1985) Light quality effects on corn chloroplast development. Plant Physiology 77:29-34

Evans AS (1989) Phenotypic plasticity in leaf physiological and life history traits: evolutionary implications in rapid-cycling *Brassica campestris* L. Ph.D. Dissertation, The University of Chicago, Illinois, USA

Evans JR (1989a) Partitioning of nitrogen between and within leaves grown under different irradiances. Australian Journal of Plant Physiology 16:533-548

Evans JR (1989b) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9-19

Evans JR, Terashima I (1988) Photosynthetic characteristics of spinach leaves grown with different nitrogen treatments. Plant Cell Physiology 29:157-165

Evans JR, Caemmerer S von, Adams WW III (1988) Ecology of photosynthesis in sun and shade. CSIRO, Australia

Fang WP (1981) Aceraceae. Flora Reipublicae Popularis Sinicae, Tomus 46. pp 66-273 Beijing, People's Republic of China

Farris MA, Lechowicz MJ (1990) Functional interactions among traits that determine reproductive success in a native annual plant. Ecology 71:548-557

Field C (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. Oecologia 56:341-347

Field CB, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. pp 25-55 In: see Givnish T 1986

Fisher BL, Howe HF, Wright SJ (1991) Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understory. Oecologia 86:292-297

Fitter AH (1987) An architectural approach to the comparative ecology of plant root system. New Phytologist 106 (Suppl):61-77

Fitter AH, Ashmore CJ (1974) Response of two *Veronica* species to a simulated woodland light climate, New Phytologist 73:997-1001

Fork DC, Govindjee (1980) Chlorophyll a fluorescence transients of leaves from sun and shade plants. Naturwissenschaften 67:510-511

Fowells HA (1965) *Silvics of forest trees of the United States*. Agriculture Handbook No. 271. US Department of Agriculture, Washington DC, USA

Fredeen AL, Field CB (1991) Leaf respiration in *Piper* species native to a Mexico rainforest. Physiologia Plantarum 82:85-92

Fredeen AL, Griffin K, Field CB (1991) Effects of light quality and quantity and soil nitrogen status on nitrate reductase activities in rainforest species of the genus *Piper*. Oecologia 86:441-446

Fried JS, Tappeiner JC II, Hibbs DE (1988) Bigleaf maple seedling establishment and early growth in Douglas-fir forests. Canadian Journal of Forest Research 18:1126-1233

Gates DM (1980) Biophysical ecology. Springer-Verlag, Berlin, Germany

Givnish T (ed) (1986) *On the economy of plant form and function*. Cambridge University Press, Cambridge, UK

Givnish T (1988) Adaptation to sun and shade: a whole-plant perspective. Australian Journal of Plant Physiology 15:63-94

Goulet F, Bellefleur P (1986) Leaf morphology plasticity in response to light environment in deciduous tree species and its implication of forest succession. Canadian Journal of Forest Research 16:1192-1195

Grime JP (1966) Shade avoidance and shade tolerance in flowering plants. pp 187-207 In: Bainbridge R, Evans GC, Rackham O (eds) *Light as an ecological factor*. Wiley, New York

Grime JP, Jeffrey DW (1964) Seedling establishment in vertical gradients of sunlight. Journal of Ecology 53:621-642

Grime JP, Hunt R (1975) Relative growth-rate: its range and adaptive significance in a local flora. Journal of Ecology 63:393-422

Gross LJ (1982) Photosynthetic dynamics in varying light environments: a model and its application to whole leaf carbon gain. Ecology 63:84-93

Gulmon SL, Chu CC (1981) The effects of light and nitrogen on photosynthesis, leaf characteristics. and dry matter allocation in the chaparral shrub, *Diplacus aurantiacus*. Oecologia 49:207-212

Haberlandt G (1914) *Physiological plant anatomy*. Macmillan, London

Hagi G (1965) *Illustrierte flora von mittel-Europa*. Band V / 1. Teil. Carl Hanser Verlag, München, Germany

Hallé F, Oldeman RAA, Tomlinson PB (1978) *Tropical trees and forests: an architectural analysis*. Springer-Verlag, Berlin, Germany

Harper JJ (1977) *Population biology of plants*. Academic Press, London

Harrington RA, Brown BJ, Reich PB (1989) Ecophysiology of exotic and native shrubs in southern Wisconsin. 1. Relationship of leaf characteristic, resource availability, and phenology to seasonal patterns of carbon gain. Oecologia 80:356-367

Hett JM, Loucks OL (1971) Sugar maple (*Acer saccharum* Marsh.) seedling mortality. Journal of Ecology 59:1071-1074

Hibbs DE (1979) The age structure of a striped maple population. Canadian Journal of Forest Science 9:504-508

Hibbs DE (1982) Gap dynamics in a hemlock-hardwood forest. Canadian Journal of Forest Research 12:522-527

Hibbs DE, Fischer BC (1979) Sexual and vegetative reproduction of striped maple (*Acer pensylvanicum* L.). Bulletin of the Torrey Botanical Club 106:222-227

Hibbs DE, Wilson BF, Fischer BC (1980) Habitat requirements and growth of striped maple (*Acer pensylvanicum* L.). Ecology 61(3):490-496

Hicks DJ, Chabot BF (1985) Deciduous forest. pp 257-277 In: Chabot BF, Mooney HA (eds) *Physiological Ecology of North American plant communities*. Chapman & Hall, New York, USA

Hirose T (1987) A vegetative plant growth model: adaptive significance of phenopypic plasticity in matter partitioning. Functional Ecology 1:195-202

Hiscox JD, Israelstam GF (1979) A method for the extraction of chlorophyll from leaf tissue without maceration. Canadian Journal of Botany 57:1332-1334

Hoddinott J, Hall LM (1982) The responses of photosynthetsis and translocation rates to changes in the *zeta* ratio of light. Canadian Journal of Botany 60:1285-1291

Holmgren P (1968) Leaf factors affecting light-saturated photosynthesis in ecotypes of *Solidago virgaurea* from exposed and shaded habitats. Physiologia Plantarum 21:676-698

Horn HS (1971) *The adaptive geometry of trees*. Princeton University, Princeton, New Jersey, U.S.A.

Hosie RC (1979) *Native trees of Canada*. 8th edition. Fitzhenry & Whiteside, Don Mills, Ont., Canada

Hutchison BA, Matt DR (1977) The distribution of solar radiation within a deciduous forest. Ecological Monographs 47:185-207

Isanogle IT (1944) Effects of controlled shading upon the development of leaf structure on two deciduous tree species. Ecology 25:404-413

Igbuanogo ABI (1989) Adaptations to changes in illumination of chloroplast structure, chlorophyll content and light transmission of mature leaves of some deciduous tree seedlings. Botanical Bulletin of Academia Sinica 30:133-142

Igboanugo ABI (1990) Effects of shading on shoot morphology, wood production and structure of Quercus petraea seedlings. Forest Ecology and Management 38:27-36

Ireland CR, Long SP, Baker NR (1984) The relationship between carbon dioxide fixation and chlorophyll a fluorescence during induction of photosynthesis and carbon dioxide concentrations. Planta 160:550-558

Ireland CR, Long SP, Baker NR (1989) An integrated portable apparatus for the simultaneous measurement of photosynthetic CO2 and water vapour exchange, light absorption and chlorophyll fluorescence emission of attached leaves. Plant Cell and Environment 12:947-958

Jackson LWR (1967) Effect of shade on leaf structure of deciduous tree species. Ecology 48:498-499

Jurik TW (1986) Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. American Journal of Botany 73:1083-1092

Jurik TW, Chabot JF, Chabot BF (1979) Ontogeny of photosynthetic performance in Fragaria virginiana under changing light regimes. Plant Physiology 63:542-547

Kasperbauer MJ, Hamilton JL (1984) Chloroplast structure and starch grain accumulation in leaves that received different red and far-red levels during development. Plant Physiology 74:967-970

Khan ML, Tripathi RS (1991) Seedling survival and growth of early and late successional tree species as affected by insect herbivory and pathogen attack in sub-tropical humid forest stands of north-east India. Acta Œcologia 12:569-579

King DA (1986) Tree from, height growth, and susceptibility to wind damage in Acer saccharum. Ecology 67:980-990

King DA (1990a) The adaptive significance of tree height. American Naturalist 135:809-828

King DA (1990b) Allometry of saplings and understorey trees of a Panamanian forest. Functional Ecology 4:27-32

King DA (1991) Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. Functional Ecology 5:485-492

Kingsolver JG, Schemske DW (1991) Path analysis of selection. Trends in Ecology and Evolution 6:276-280

Kirschbaum MUF, Pearcy RW (1988) Gas exchange analysis of the relative importance of stomatal and biochemical factors in photosynthetic induction in Alocasia macrorrhiza. Plant Physiology 86:782-785

Kirschbaum MUF, Gross LJ, Pearcy RW (1988) Observed and modelled stomatal responses to dynamic light environments in the shade plant Alocasia macrorrhiza. Plant Cell and Environment 11:111-121

Kobza J, Seemann JR (1988) Mechanisms for light-dependent regulation of ribulose-1,5-bisphosphate carboxylase activity and photosynthesis in intact leaves. Proceedings of the National Academy of Science 85:3815-3819

Kohyama T (1987) Significance of architecture and allometry in saplings. Functional Ecology 1:399-404

Kohyama T, Hotta M (1990) Significance of allometry in tropical saplings. Functional Ecology 4:515-521

Koike T (1988) Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaf trees. Plant Species Biology 3:77-87

Koike T (1990) Autumn coloring, photosynthetic performance and leaf development of deciduous broad-leaved trees in relation to forest succession. Tree Physiology 7:21-32

Krause GH, Weis E (1984) Chlorophyll fluorescence as a tool in plant physiology. II. Interpretation of fluorescence signals. Photosynthesis Research 5:139-157

Krause GH, Weis E (1991) Chlorophyll fluorescence and photosynthesis: the basics. Annual Review of Plant Physiology and Molecular Biology 42:313-349

Kruckeberg AR (1983) Temperate floras: the north Pacific connection. Annals of the Missouri Botanical Garden 70:591-596

Krüssmann G (1979) Manual of cultivated broad-leaved trees and shrubs. Vol.1. Timber Press, Oregon

Küppers M (1984a) Carbon relations and competition between woody species in a central European hedgerow. I. Photosynthetic characteristics. Oecologia 64: 332-343

Küppers M (1984b) Carbon relations and competition between woody species in a central European hedgerow. II. Stomatal responses, water use, and hydraulic conductivity in the root/leaf pathway. Oecologia 64:344-354

Küppers M (1984c) Carbon relations and competition between woody species in a central European hedgerow. III. Carbon and water balance on the leaf level. Oecologia 65:94-100

Küppers M (1985) Carbon relations and competition between woody species in a central European hedgerow. IV. Growth form and partitioning. Oecologia 66:343-352

Kwesiga FR, Grace J (1986) The role of the red/far-red ratio in the response of tropical tree seedlings to shade. Annals of Botany 57:283-290

Kwesiga FR, Grace J, Sandford AP (1986) Some photosynthetic characteristics of tropical timber trees as affected by the light regime during growth. Annals of Botany 58:23-32

Ladrach WE (1986) Control of wood properties in plantations with exotic species. Inves For Carton de Colombia Cali, Colombia, Res Rept 106, 11p (quoted in Zobel R and van Buijtenen HS 1989)

Langenheim JH, Osmond CB, Brooks A, Ferrar PJ (1984) Photosynthetic responses to light in seedlings of selected Amazonian and Australian rainforest tree species. Oecologia 63:215-224

Lechowicz MJ (1984) Why do temperate deciduous tree leaf out at different times? Adaptation and ecology of forest communities. American Naturalist 124:821-842

Lechowicz MJ, Blais PA (1988) Assessing the contribution of multiple interacting traits to plant reproductive success: environmental dependence. Journal of Evolutionary Biology 1:255-273

Lechowicz ML, Blais PA (unpublished, 1990) Kjeldahl determination of nitrogen in plants. Dept Biology, McGill University, Montreal, Quebec

Ledig FT, Korbobo DR (1983) Adaptation of sugar maple populations along altitudinal gradients: photosynthesis, respiration. and specific leaf weight. American Journal of Botany 70:256-265

Lee DW (1985) Duplicating foliage shade for research on plant development. HortScience 20:116-118

Lee DW (1986) Unusual strategies of light absorption in rain-forest herbs. pp. 105-131 In: see Givnish TJ

Lee DW (1987) The spectral distribution of radiation in two neotropical rainforests. Biotropica 19(2):161-166

Lee DW (1988) Simulating forest shade to study the developmental ecology of tropical plants: juvenile growth in three vines in India. Journal of Tropical Ecology 4:281-292

Lei TT, Lechowicz MJ (1990) Shade adaptation and shade tolerance in saplings of three Acer species from eastern North America. Oecologia 84:224-228

Li CC (1975) Path analysis- a primer. Boxwood Press, Pacific Grove, California, USA

Li H-L (1952) Floristic relationships between eastern Asia and eastern North America. Transactions of the American Philosophical Society 42:371-429

Lichtenthaler HK (1985) Differences in morphology and chemical composition of leaves grown at different light intensities and quality. pp 201-221 In: Baker NC, Davies WJ, Ong CK (eds) Control of leaf growth. Cambridge University, London, UK

Lichtenthaler HK, Buschmann C, Döll M, Fietz H-J, Bach T, Kozel U, Meier D, Rahmsdorf U (1981) Photosynthetic activity, chloroplast ultrastructure, and leaf characteristics of high-light and low-light plants and of sun and shade leaves. Photosynthetic Research 2:115-141

Lieberman D, Lieberman M, Peralta R (1989) Forests are not just swiss cheese: canopy stereogeometry of non-gaps in tropical forests. Ecology 70:550-552

List RJ (1951) Smithsonian Meteorological tables. 6th revised edition. The Smithsonian Institution. Washington, DC, USA

Loach K (1967) Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. New Phytologist 66:607-621

Loehie C (1988) Treelife history strategy: the role of defenses. Canadian Journal of Forestry Research 18:209-222

Loescher WH, McCamant T, Keller JD (1990) Carbohydrate reserves, translocation, and storage in woody plant roots. Hortscience 25:274-281

Logan KT (1965) Growth of tree seedlings as affected by light intensity. I. White birch, yellow birch, sugar maple and silver maple. Dept of Forestry Publication No. 1121, Ottawa, Canada

Logan KT, Krotkov G (1968) Adaptation of the photosynthetic mechanism of sugar maple (Acer saccharum) seedlings grown in various light intensities. Physiologia Plantarum 22:104-116

Maddox GD, Antonovics J (1983) Experimental ecological genetics in Plantago: a structural equation approach to fitness components in P. aristata and P. patagonica. Ecology 64:1092-1099

Maeglin RR, Ohmann LF (1973) Boxelder (Acer negundo): a review and commentary. Bulletin of the Torrey Botanical Club 100(6):357-363

Mancinelli AL (1989) Interaction between phytochrome and cryptochrome in higher plant photomorphogenesis. American Journal of Botany 76(1):143-154

Marshall JD, Waring RH (1985) Predicting fine root production and turnover by monitoring root starch and soil temperature. Canadian Journal of Forest Science 15:791-800

Masarovičová E, Štefančík L (1990) Some ecophysiological features in sun and shade leaves of tall beech trees. Biologia Plantarum (Praha) 32:374-387

Marks PL (1975) On the relation between extension growth and successional status of deciduous trees of the northeastern United States. Bulletin of the Torrey Botanical Club 102:172-177

Maruyama S, Tajima K (1990) Leaf conductance in Japonica and Indica rice varieties. I. Size, frequency and aperture of stomata. Japanese Journal of Crop Science 59:801-808

Matsui K (1991) Pollination ecology of four Acer species in Japan with special reference to bee pollinators. Plant Species Biology 6:117-120

McClendon JH (1962) The relationship between the thickness of deciduous leaves and their maximum photosynthetic rate. American Journal Botany 49:320-322

McClendon JH, McMillen GG (1982) The control of leaf morphology and the tolerance of shade by woody plants. Botanical Gazette 143:79-83

McMahon TA (1973) Size and shape in biology. Science (Wash., DC) 179:1201-1204

McMillen GG, McClendon JH (1983) Dependence of photosynthetic rates on leaf density thickness in deciduous woody plants grown in sun and shade. Plant Physiology 72:674-678

Melancon S, Lechowicz MJ (1987) Differences in the damage caused by glaze ice on codominant Acer saccharum and Fagus grandifolia. Canadian Journal of Botany 65:1157-1159

Mentis MT (1988) Hypothetico-deductive and inductive approach to ecology. Functional Ecology 2:5-14

Messier C, Bellefleur P (1988) Light quantity and quality on the forest floor of pioneer and climax stages in a birch-beech-sugar maple stand. Canadian Journal of Forest Research 18:615-622

Minckler LS, Woerheide JD (1965) Reproduction of hardwoods 10 years after cutting as affected by site and opening size. Journal of Forestry 63:103-107

Miskin KE, Rasmusson DC (1970) Frequency and distribution of stomata in barley. Crop Science 10:575-578

Mitchell RJ (1992) Testing evolutionary and ecological hypotheses using path analysis and structural equation modelling. Functional Ecology 6:123-129

Mooney HA (1991) Plant physiological ecology - determinants of progress. Functional Ecology 5:127-135

Morgan DC, Smith H (1979) A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. Planta 145:253-258

Morgan DC, Smith H (1981) Non-photosynthetic responses to light quality. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology I. Response to the physical environment. Encyclopedia of Plant Physiology, New Series Vol. 12A:110-134. Springer-Verlag, New York

Morgan DC, Rook DA, Warrington IJ, Turnbull HL (1983) Growth and development of Pinus radiata D. Don: the effect of light quality. Plant Cell and Environment 6:691-701

Morikawa Y, Asakawa S, Sasaki S (1976) Growth of pine and birch seedlings under lights with different spectral compositions and intensities. Journal of the Japanese Forestry Society 58:174-178

Mott KA, Gibson AC, O'Leary JW (1982) The adaptive significance of amphistomatous leaves. Plant Cell and Environment 5:455-460

Nobel PS (1991) Physicochemical and environmental physiology. Academic Press, San Diego, USA

Oberbauer SF, Strain BR (1985) Effects of light regime on the growth and physiology of Pentaclethra macroloba (Mimosaceae) in Costa Rica. Journal of Tropical Ecology 1:303-320

Ogata K (1965) A dendrological study on the Japanese Aceraceae, with special reference to the geographical distribution. Bulletin of the Tokyo University Forests 60:1-99

Ogata K (1967) A systematic study of the genus Acer. Bulletin of the Tokyo University Forests 63:89-206

Öquist G, Wass R (1988) A portable, microprocessor operated instrument for measuring chlorophyll fluorescence kinetics in stress physiology. Physiologia Plantarum 73:211-217

Osmond CB (1987) Photosynthesis and carbon economy of plants. New Phytologist 106 (Suppl):161-175

Pearcy RW (1983) The light environment and growth of C_3 and C_4 tree species in the understorey of a Hawaiian forest. Oecologia 58:19-25

Pearcy RW (1987) Photosynthetic gas exchange responses of Australian tropical forest trees in canopy. gap and understory micro-environments. Functional Ecology 1:169-178

Pearcy RW (1990) Sunflecks and photosynthesis in plant canopies. Annual Review of Plant Physiology 41:421-453

Pearcy RW, Osteryoung K, Calkin HW (1985) Photosynthetic responses to dynamic light environment by Hawaiian trees. Plant Physiology 79:896-902

Pearcy RW, Pfitsch WA (1989) Daily carbon gain by Adenocaulon bicolor (Asteraceae), a redwood forest understory herb, in relation to its light environment. Oecologia 80:465-470

Pedhazur EJ (1982) Multiple regression in behavioral research. 2nd edition. Holt, Rinehart and Winston, New York

Penfound WT (1931) Plant anatomy as conditioned by light intensity and soil moisture. American Journal Botany 18:558-572

Pickett STA, Kempf JS (1980) Branching patterns in forest shrubs and understory trees in relation to habitat. New Phytologist 86:219-228

Pickett STA, White PS (1985) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, USA

Pieters GA (1960) On the relation between the maximum rate of photosynthesis and the thickness of the mesophyll in sun- and shade leaves of *Acer pseudoplatanus* L. Meded Landbouwhogeschool, Wageningen 60:1-6

Pliny, the Elder (ca. 60AD) <Naturalis Historia>. *The Natural History of Pliny, Volume 3*. Translated by Bostock J, Riley HT (1956). Henry G Bohn, London, UK

Pompa J, Bongers F (1988) The effect of canopy gaps on growth and morphology of seedlings of rain forest species. Oecologia 75:625-632

Poorter H, Remkes C (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia 83:553-559

Poorter H, Remkes C, Lambers H (1990) Carbon and nitrogen economy of 24 wild species differing in relative growth rate. Plant Physiology 94:621-627

Poorter H, Van der Werf A, Atkin OK, Lambers H (1991) Respiratory energy requirements of roots vary with potential growth rate of a plant species. Physiologia Plantarum 83:469-475

Poorter H, Bergkotte M (1992) Chemical composition of 24 wild species differing in relative growth rate. Plant Cell Environment 15:221-229

Post LJ (1965) Vegetative reproduction of mountain maple. Dept of Forestry Publication No. 1097, Ottawa, Canada

Post LJ (1969) Vegetative reproduction and the control of mountain maple. Pulp and Paper Magazine of Canada, October 17, 1969:115-117

Powers HO (1967) A blade tissue study of forty-seven species and varieties of Aceraceae. American Midland Naturalist 78:301-323

Ramos J, Grace J (1990) The effects of shade on the gas exchange of seedlings of four tropical trees from Mexico. Functional Ecology 4:667-677

Reekie EG, Bazzaz FA (1989) Competition and patterns of resource use among seedlings of five tropical trees grown at ambient and elevated CO_2. Oecologia 79:212-222

Reich PB, Walters MB, Ellsworth DS (1991) Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area and photosynthesis in maple and oak trees. Plant, Cell and Environment 14:251-259

Reichardt PB, Chapin FS III, Bryant JP, Mattes BR, Clausen TP (1991) Carbon/nutrient balance as a predictor of plant defense in Alaskan balsam poplar: potential importance of metabolite turnover. Oecologia 88:401-406

Reynolds JF, Acock B (1985) Predicting the response of plants to increasing carbon dioxide: a critique of plant growth models. Ecological Modelling 29:107-129

Röhrig E, Ulrich B (1991) Temperate deciduous forests. Elsevier, Amsterdam, The Netherlands

Runkle JR (1982) Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63:1533-1546

Runkle JR (1985) Disturbance regimes in temperate forests. in: Pickett STA and White PS

Runkle JR (1990) Gap dynamics in an Ohio Acer-Fagus forest and speculations on the geography of disturbance. Canadian Journal of Forestry Research 20:632-641

Runkle JR, Yetter TC (1987) Treefalls revisited: gap dynamics in the southern Appalachians. Ecology 68:417-424

Sage RF, Pearcy RW, Seemann JR (1987) The nitrogen use efficiency of C_3 and C_4 plants. III. Leaf nitrogen effects on the activity of carboxylating enzymes in Chenopodium album (L.) and Amaranthus retroflexus (L.). Plant Physiology 85:355-359

Sakai S (1987) Patterns of branching and extension growth of vigorous saplings of Japanese Acer species in relation to their regeneration strategies. Canadian Journal of Botany 65:1578-1585

Sakai S (1990a) Sympodial and monopodial branching in Acer: implications for tree architecture and adaptive significance. Canadian Journal of Botany 68:1549-1553

Sakai S (1990b) Sympodial and monopodial branching in Acer (Aceraceae): evolutionary trend and ecological implications. Plant Systematics and Evolution 171:187-197

Sanchez-Coronado ME, Rincòn E, Vazquez-Yanes C (1989) Growth responses of three contrasting Piper species growing under different light conditions. Canadian Journal of Botany 68:1182-11

Sand-Jensen K 1988 Photosynthetic responses ofUlva lactuca at very low light. Mar Ecol Prog Ser 50:195-201

SAS Institute Inc. (1988) SAS/STAT user's guide, Release 6.03 Edition. SAS Institute Inc., Cary, NC, USA

Schemske DW, Horvitz CC (1988) Plant-animal interactions and fruit production in a neotropical herb: a path analysis. Ecology 69:1128-1137

Schreiber U (1986) Detection of rapid induction kinetics with a new type of high-frequency modulated chlorophyll fluorometer. Photosynthetic Research 9:261-272

Schreiber U, Fink R, Vidaver W (1977) Fluorescence induction in whole leaves: differentiation between the two leaf sides and adaptation to different light regimes. Planta 133:121-129

Schreiber U, Bilger W (1987) Rapid assessment of stress effects on plant leaves by chlorophyll fluorescence measurements. pp 27-53 In: Tenhunen JD, Catarino FM, Lange OL, Oechel WC (eds) Plant response to stress. Springer-Verlag, Berlin, Germany

Seemann JR, Sharkey TD, Wang JL, Osmond CB (1987) Environmental effects on photosynthesis, nitrogen-use efficiency, and metabolite pools in leaves of sun and shade plants. Plant Physiology 84:796-802

Seemann JR, Kirschbaum MUF, Sharkey TD, Pearcy RW (1988) Regulation of ribulose-1,5-bisphosphate carboxylase activity in Alocasia macrorrhiza in response to step changes in irradiance. Plant Physiology 88:148-152

Senger H, Bauer B (1987) The influence of light quality on adaptation and function of the photosynthetic apparatus. Photochemistry and photobiology 45:939-946

Šesták Z, Čatský J, Jarvis PG (1971) Plant photosynthetic production. Manual of methods. W Junk, The Hague

Shirley HL (1929) The influence of light intensity and light quality upon the growth of plants. American Journal of Botany 16:354-390

Sims DA, Pearcy RW (1989) Photosynthetic characteristics of a tropical forest understory herb, Alocasia macrorrhiza, and a related crop species, Colocasia esculenta grown in contrasting environments. Oecologia 79:53-59

Sims DA, Pearcy RW (1991) Photosynthesis and respiration in Alocasia macrorrhiza following transfers to high and low light. Oecologia 86:447-453

Smith DW, Tumey PR (1982) Specific density and caloric value of the trunk wood of white birch, black cherry, and sugar maple and their relation to forest succession. Canadian Journal of Forestry Research 12:186-190

Smith H (1981) Light quality as an ecological factor. pp 93-110 In: Grace J, Ford ED, Jarvis PG (eds) Plants and their atmospheric environment. Blackwell Scientific, Oxford, UK

Smith H (1982) Light quality, photoperception, and plant strategy. Annual Review of Plant Physiology 33:481-518

Smith H (1986) The perception of light quality. pp 187-217 In: Kendrick RE, Kronenberg GHM (eds) Photomorphogenesis in Plants. W. Junk, Dordrecht, The Netherlands

Smith H, Morgan DC (1983) The function of phytochrome in nature. In: Shropshire W Jr, Mohr H (eds) Encyclopedia of plant physiology, Volume 16. Springer-Verlag, Berlin, Germany

Smith M, Martin CE (1987) Growth and morphological responses to irradiance in three forest understory species of the C_4 grass genus Muhlenbergia. Botanical Gazette 148:141-148

Spencer DF, Ksander GG (1987) Comparison of three methods for extracting chlorophyll from aquatic macrophytes. Journal of Freshwater Ecology 4:201-208

Steiger JH (1989) EzPath. Systat Inc, Evanston Illinois, USA

Stein U, Buschmann C, Blaich R, Lichtenthaler HK (1990) Induction kinetics of delayed fluorescence of sun and shade leaves of Fagus sylvatica in ms-range. Radiation and Environmental Biophysics 29:119-128

Strauss-Debenedetti S, Bazzaz FA (1991) Plasticity and acclimation to light in tropical Moraceae of different successional positions. Oecologia 87:377-387

Sullivan JR (1983) Comparative reproductive biology of Acer pensylvanicum and A. spicatum (Aceraceae). American Journal of Botany 70:916-924

Suzuki S, Nakamoto H, Ku MSB, Edwards GE (1987) Influence of leaf age on photosynthesis, enzyme activity, and metabolite levels in wheat. Plant Physiology 84:1244-1248

Tanai T. (1978) Taxonomical investigation of the living species of the genus Acer L., based on vein architecture of leaves. Journal of the Faculty of Science, Hokkaido University, Series IV 18(3): 243-282

Terashima I, Evans JR (1988) Effects of light and nitrogen nutrition on the organization of the photosynthetic apparatus in spinach. Plant Cell Physiology 29:143-155

Teskey RO, Shrestha RB (1985) A relationship between carbon dioxide, photosynthetic efficiency and shade tolerance. Physiologia Plantarum 63:126-132

Thayer SS, Björkman O (1990) Leaf xanthophyll content and composition in sun and shade determined by HPLC. Photosynthesis Research 23:331-343

Thompson WA, Stocker GC, Kriedemann PE (1988) Growth and photosynthetic response to light and nutrients of *Flindersia brayleyana* F. Muell., a rainforest tree with broad tolerance to sun and shade. Australian Journal of Plant Physiology 15:299-315

Thornley JHM, Johnson IR (1990) *Plant and crop modelling: a mathematical approach to plant and crop physiology*. Clarendon, Oxford, UK

Turnbull MH (1991) The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. Oecologia 87:110-117

Vaartaja O (1962) The relationship of fungi to survival of shaded tree seedlings. Ecology 43:547-549

Van Den Driessche R (1987) Importance of current photosynthate to new root growth in planted conifer seedlings. Canadian Journal of Forest Science 17:776-782

Vazquez-Yanes C, Smith H (1983) Phytochrome control of seed germination in the tropical rainforest pioneer trees *Cecropia obtusifolia* and *Piper auritum* and its ecological significance. New Phytologist 92:477-486

Veres JS, Pickett STA (1982) Branching patterns of *Lindera benzoin* beneath gaps and closed canopies. New Phytologist 91:767-772

Vidal D, Griera E, Marin P, Sabido J (1990) Anatomical and physiological acclimation of *Fatsia japonica* leaves to irradiance. American Journal of Botany 77:1149-1158

Vogelmann HW (1973) Fog precipitation in the cloud forests of eastern Mexico. Bioscience 23:96-100

Vrestiak P (1986) Development of the Norway maple (*Acer platanoides* L.) leaf biomass in urban greenery. Ekolódia (CSSR) 5:147-160

Wallace LL, Dunn EL (1980) Comparative photosynthesis of three gap phase successional tree species. Oecologia 45:331-340

Walters MB, Field CB (1987) Photosynthetic light acclimation in two rainforest *Piper* species with different ecological amplitudes. Oecologia 72:449-456

Warrington IJ, Rook DA, Morgan DC, Turnbull HL (1989) The influence of simulated shadelight and daylight on growth, development and photosynthesis of *Pinus radiata*, *Agathis australis* and *Dacrydium cupressinum*. Plant, Cell and Environment 12(4):343-356

Welander NT, Hellgren O (1988) Acclimation of *Codiaeum variegatum* L. 'Aucubaefolia' to changes in photon flux density. II. Net photosynthesis. dark respiration and chlorophyll content. Journal of Horticultural Science 63(2):279-286

White PS (1983) Eastern Asian-eastern North American floristic relations: the plant community level. Annals of the Missouri Botanical Garden 70:734-747

Whitney HE, Johnson WC (1984) Ice storms and forest succession in southwestern Virginia. Bulletin of the Torrey Botanical Club 111:429-437

Wild, A (1979) Physiologie der photosynthese höherer pflanzen die anpassung an die lichtbedingungen. Ber Deutsch Bot Ges Bd 92:341-364

Wilkinson L (1990) *SYSTAT: the system for statistics*. SYSTAT Inc, Evanston, Il, USA

Williams PA , Buxton RP (1989) Response to reduced irradiance of 15 species of native and adventitive shrub and tree seedlings from eastern Canterbury. New Zealand Journal of Ecology 12:95-101

Willmot A, Moore PD (1973) Adaptation to light intensity in *Silene alba* and *S. dioica*. Oikos 24:458-464

Wilson BF, Fischer BC (1977) Striped maple: shoot growth and bud formation related to light intensity. Canadian Journal of Forest Research 7:1-7

Winer BJ (1971) Statistical principles in experimental design, 2nd ed. McGraw-Hill, New York

Woodward FI (1990) From ecosystems to genes: the importance of shade tolerance. Trends in Ecology and Evolution 5:111-115

Woodrow IE, Mott KA (1989) Rate limitation of non-steady state photosynthesis by ribulose-1,5-bisphosphate carboxylase in spinach. Australian Journal of Plant Physiology 16:487-500

Woods DB, Turner NC (1971) Stomatal response to changing light by four tree species of varying shade tolerance. New Phytologist 70:77-84

Wooge JD, Barden JA (1987) Seasonal changes in specific leaf weight and leaf anatomy of apple. HortScience 22:292-295

Wright S (1921) Correlation and causation. Journal of Agricultural Research 20:557-585

Wylie RB (1951) Principles of foliar organization shown by sun-shade leaves from ten species of deciduous dicotyledonous trees. American Journal of Botany 38:355-361

Yamamoto S-I (1989) Gap dynamics in climax *Fagus cranata* forests. Botanical Magazine Tokyo 102:93-114

Young DR, Smith WK (1980) Influence of sunlight on photosynthesis, water relations, and leaf structure in the understory species *Arnica cordifolia*. Ecology 61:1380-1390

Yun JI, Taylor SE (1986) Adaptive implications of leaf thickness for sun- and shade-grown *Abutilon theophrasti*. Ecology 67:1314-1318

Zobel BJ, Buijtenen JP van (1989) *Wood variation, its causes and control*. Springer-Verlag, Berlin, Germany

Zon R, Graves HS (1911) Light in relation to tree growth. Forest Service Bulletin 92. U.S. Dept Agriculture, Washington DC, USA

APPENDIX 1

Seed sources of *Acer* species, and germination and rearing procedures

Table 1. Seed sources of *Acer* species and populations used in the experiments. Nomenclature follows Ogata (1967).

Species	Code	Seed Source	Seed acq. year	Date of germination
Subcanopy species				
A. buergerianum Miq.	BU1	Fujita, Japan[1]	1989	MAY 1989
A. ginnala Maxim.	GI4	F.W. Schumacher Co.[2] "domestic"	1987	DEC 1988
A. ginnala Maxim.	GI6	Sheffield Seed Co.[3]	1987	OCT 1988
A. ginnala Maxim.	GI8	Rogow Arboretum, Poland[4]	1988	DEC 1988
A. ginnala Maxim.	GI7	Gehölz, Germany[5]	1988	FEB 1989
A. palmatum Thunb.	PA1	F.W. Schumacher Co. (var. atropurpureum)	1987	JAN 1989
A. palmatum Thunb.	PA4	Sheffield Seed Co.	1988	JAN 1989
A. pensylvanicum L.	PN1	Mont St. Hilaire, Quebec	1986	JAN 1989
A. pensylvanicum L.	PN2	Nova Tree Seed Co.[6]	1987	NOV 1988
A. pensylvanicum L.	PN4	Mont St. Hilaire seedling transplants	1988	APR 1988
A. spicatum Lam.	SP1	Mont St. Hilaire, Quebec	1986	OCT 1988
A. spicatum Lam.	SP6	Guelph, Ontario	1987	OCT 1988
A. rufinerve Sieb. et Zucc.	RF1	TARC, Japan[7]	1988	OCT 1988
Canopy species				
A. macrophyllum Pursh.	MA4	Northern California coast	1989	FEB 1989
A. macrophyllum Pursh.	MA1	Univ. Washington, Seattle, Washington	1987	DEC 1988
A. nigrum Michx. f.	NI1	Beaconsfield, Quebec	1988	FEB 1989
A. platanoides L.	PL1	Bratislava Park, CSSR[8]	1988	FEB 1989
A. platanoides L.	PL4	Westonbirt Arboretum, UK[9]	1987	NOV 1988
A. platanoides L.	PL9	Gehölz, Germany	1988	DEC 1988
A. rubrum L.	RU2	F.W. Schumacher Co. "northern"	1987	DEC 1988
A. rubrum L.	RU3	Nova Tree Seed Co.[10]	1987	NOV 1988
A. saccharinum L.	SA1	Beaconsfield, Quebec	1989	JUN 1989
A. saccharinum L.	SA3	Guelph, Ontario	1989	JUL 1989
A. saccharum Marsh.	SR3	F.W. Schumacher Co. "northern"	1989	MAR 1989
A. saccharum Marsh.	SR6	Beaconsfield, Quebec	1988	FEB 1989
A. saccharum Marsh.	SR7	F.W. Schumacher Co. "northern"	1988	JAN 1989

Commercial seed sources:

1 Fujita Seed Co. Ltd. P.O. Box 211 Osaka C. 53091, 2-6-28 Kyomachibori, Nishi-ku, Osaka 550, Japan
2 F.W. Schumacher Co., Inc. 36 Spring Hill Road, Sandwich, Mass 02563-1023 USA
3 Sheffield's Seed Co., Inc. 273 Route 34; Locke. N.Y. 13092, USA
4 Szkola Glówna, Gospodarstwa Wiejskiego, Akademia Rolnicza, Leśny Zaklad Doświadczalny, Arboretum 96-135 Rogów, tel 20, Poland
5 Gehölz- Und Waldsamenproduktion, Conrad Appel KG. Beerfelden-Gammelsbach, Postfach 1123, D-6124 Beerfelden Germany
6 Nova Tree Seed Co., Inc. R.R. #2 Middle Musquodoboit, Nova Scotia B0N 1X0 Canada
7 Tropical Agriculture Research Centre, Ministry of Agriculture, Forestry and Fisheries, Ohwashi, Tsukuba, Ibaraki, 305 Japan
8 Dr. Viera Feráková, Univerzita Komenského, Nositeíka Radu Republiky, Prírodovedecká fakulta, Katedra botaniky, Geobotaniky a pedológie, CSSR
9 Forest Commission (Research) Westonbirt Arboretum, Tetbury, Glos. GL8 8QS, UK
10 Seed source: Kingston, Ontario

Germination and rearing procedures

I germinated the maple seeds that require stratifying (all except A. rubrum and A. saccharinum) by first soaking seeds in 50 μmol giberellic acid solution (17.32 mg GA l^{-1} distilled H_2O) overnight, then placing the soaked seeds in plastic bags with moist sphagnum moss. The bags were kept moist at 4°C until germination and the seedlings were then established in the phytotron as they germinated. Seedlings were grown in 60 cm deep plexiglas tubes (total soil volume=2.8 litres) in commercial potting soil (Fafard et Fréres Ltée, St. Guillaume, Quebec). They were watered as necessary and fertilized weekly with Hoagland's solution (Dunn and Arditti 1968, Version 2). The phytotron greenhouse compartment was programmed to track outdoor temperature regime and shaded to maintained a maximum of 50% full sun. The seedlings were allowed to become dormant normally during the fall and during winter months the greenhouse temperature was kept at a minimum temperature of 2°C. The seedlings therefore went through 2-3 years annual cycles of growth and dormancy prior to their use in these experiments. This avoided any potential maternal effect from resources stored in the seed.

APPENDIX 2

Description of Acer species

For each species the description follows the sequence of species (common name), leaf form and size range (scale: — = 5 cm), size at maturity, geographical range, habitat preference; and life history and phenology. Sources, unless otherwise stated, include Fang (1981), Fowells (1965), Hosie (1979), Krüssmann (1979) and Ogata (1965). Species listed in the same order as that in Table 1 of Appendix 1.

A. macrophyllum Pursh. (Bigleaf maple) 

Tree, 15-25 m. Coniferous forests of the Pacific coast from southern tip of Alaska to southern California below 300 m elevation. Humid, deep loams to thin rocky soils but prefers deep alluvial moist soils. Strongly limited by water availability in southern range. Sometimes pioneer species on disturbed land. Fastest growing western maple. Wood moderately strong, not hard. Shade tolerance seems to decrease with age. First reproduction at 10 yr. Anthesis in early April to May, concurrent with leafing out. Insect pollinated. Fruit maturation in late August to October. Seedlings can persist in Douglas-fir forest but survival rate increases with increased insolation to 60% open sky (Fried et al 1988). Sapling foliage palatable to black-tailed and mule deer, and elk. Mammal browsing strongly suppresses seedling growth (Fried et al 1988) in the forest understory.

A. nigrum Michx. f. (Black maple) 

Tree to 25 m, 1 m dbh. Eastern North America. Prefers wetter sites than A. saccharum on mesic well-drained loams, moist alluvial and calcarious soils. Occurs in regions of low relief (<800 m) such as river valleys. Wood heavy, hard and strong.

Anthesis in May, after 1/3 leaf expansion. Primarily bee-pollinated. Fruit maturation from Sept. to Oct. Hybridizes freely with A. saccharum.

A. platanoides L. (Norway maple)

Tree to 30 m, 1 m dbh with a broad spreading crown. Trans-Europe, east to the Urals and the Caucasus, south to Armenia (Hegi 1965); introduced to the British Isles in the 15th or 16th century (Clapham et al 1987). Preferring deep, moist, well-drained rich soils, but growing well on all but very poor soils (Clapham et al 1987). Wood hard, moderately elastic. Sugar content in sap 1.1-3.5%. Earliest reproduction at 20 yrs. Lifespan 150-200 yrs (Vrestiak 1986). Anthesis in April, before leaf expansion. Pollinated mainly by bees. Many cultivars.

A. rubrum L. (Red maple)

Tree to 40 m, 0.5-0.75 m dbh. Life span < 150 yr. Open crown. Wide climatic tolerance from eastern Canada west to Prairies and south to warm-temperate Florida. Occurs on a variety of soil types from rich loam to shallow lithosols. More common on extreme soil moisture conditions, either very wet or relatively dry, avoiding alkaline soils. Its litter poor in N and intermediate in Ca. Wood moderately heavy, hard and strong. Pioneer or subclimax species but more shade tolerant than Populus and Prunus pensylvanicum. Anthesis in March-April. Imperfectly dioecious, flowering begin as early as Feb. in south. Fruit maturation from March to June. Germination not light-dependent; dormancy absent in most seed. Taproot development in seedling strongly dependent on soil moisture. Readily produces basal sprouts.

A. saccharinum L. (Silver maple)

Tree to 40 m, 0.6-1.2 m dbh. Life span < 125 yr. Range similar to red maple but does not extend to the southern Atlantic coast and Florida. Grows on all soil types with sufficient moisture supply. Characteristically a bottom-land species. Fast-growing tree. Wood moderately hard, heavy, but not strong. Anthesis from Feb. to March, fruit maturation from April to June. Seeds viability highly sensitive to desiccation. Dormancy absent. Shade tolerance moderate on good sites to intolerant on poor sites. Subclimax species unable to survive prolonged suppression.

A. saccharum Marsh. (Sugar maple) 

Tree, to 40 m, 0.5-1 m dbh. Eastern North America. Grows on fertile, moist, well-drained soils of all types. Soil pH range: 3.7-7.3 but most common in pH 5.5-7.3. Occurs in 500-1300 m elevation. Wood heavy, hard and strong. Sap flow begins in March, 3% sugar content. Anthesis in late April to May, one week after leaf emergence. unstable monoecy: localized unisexual flower and unbalanced distribution of male and female flowers. Mostly bee-pollinated. Fruit ripens in 12 weeks. Mast year occurs in 2-5 yr intervals. Basal sprouting more frequent in younger trees. Seed germination requires stratification of 6-8 weeks, light not essential. Height and radial growth begin at budbreak and terminate in 15 weeks. Long-lived to 400 yrs. Windfirm i.e., high wood density.

A. buergerianum Miq. var. buergerianum (Three-toothed maple) 

Small tree, 5-10 m. Eastern China and Taiwan, introduced to Japan in ca. 1800. In broadleaf forests between 300 and 1000 m elevation. Anthesis in April, fruit maturation in August.

A. ginnala Maxim. subsp. ginnala (Amur maple) 

Shrub or small tree, 5-6 m. Crown broad. Northeastern China, Japan and Korea. In forests below 800 m, restricted to marshy sites. Occurs in clumps. Anthesis in May. Fruit maturation in Oct.

A. palmatum Thunb. var. palmatum (Japanese maple)

Small tree to 8 m. Found in eastern China, southern Korea, Japan and Taiwan. Occurs between 200-1200 m elevation in forest edge or open woodland over a wide range of soil conditions. Anthesis: mid-April to early May, concurrent with leafing out. Andro-monoecious. Fruit matures in early October, readily germinates. Ogata (1965) describes this species as a large tree to 1 m dbh, but this might be a rare occurrence (Sakai S, personal communication).

A. pensylvanicum L. (Striped maple)

Small tree 6-12 m. Eastern North America. Prefers well-drained moist soils in shaded cool, moist forest. Anthesis in late April-mid-May after leaves have fully expanded, inflorescence unisexual and trees often dioecious and undergo gender change (usually from male to female (De Jong 1976, Hibbs and Fischer 1979). Apomixis rare (De Jong 1976, Sullivan 1983). Fruit maturation in autumn. Wood moderately light, soft and low in strength. Seedling highly tolerant of shade, capable of surviving under closed forest canopy for 15 years (Hibbs 1979). Optimum height growth occurs in 32-58% full sun (Wilson and Fischer 1977).

A. rufinerve Siebold et Zuccarini

Small tree, 10-15 m, 10 cm dbh. Endemic to Japan. Occurs in mountain forests of rather dry soils from middle to upper slopes. Anthesis from early April to early May. Prefers open habitats such as roadside and large forest gaps (Matsui 1991).

A. spicatum Lam. (Mountain maple)

Shrub or small understory tree, 6 m. Eastern North America. Grows well of well-drained moist soils along moist rocky hillsides and ravines. Seldom thrives in the open. Prefers rocky, moist forest areas. Anthesis in May-June after leaves have fully expanded. Flowers unisexual but both genders occur on the same inflorescence. A high degree of apomixis (Sullivan 1983). Fruit maturation in Sept-Oct. Wood moderately light, soft, low in strength. A propensity to produce basal sprouts; stem layers readily (Post 1969, personal observation). Vegetative reproduction important in maintaining population (Post 1969).

APPENDIX 3

Protocol for chlorophyll extraction using dimethyl sulfoxide (DMSO)

Chlorophyll extraction of plant tissue using DMSO requires no maceration and takes less time and is more efficient (gives better yield of chlorophyll) than traditional acetone and ethanol methods (Burnison 1980, Spencer and Ksander 1987). The extract is also more stable and can be stored up to 4 days (Hiscox and Israelstam 1979). The disadvantage of this method is the mild skin irritation caused by DMSO exposure (consult chemical safety data sheet for more detail). Extraction must be done in a fume hood and protective clothing and gloves worn.

Materials

DMSO (dimethyl sulfoxide)
water bath (at 65°C)
vortex mixer
10 ml bottle-top dispenser
Parafilm
Latex gloves
spectrophotometer (a Milton-Roy Spectronic 1001 Plus was used for ease and precision of measuring multiple wavelengths, band width resolution= 1 nm)

Extraction

Chlorophyll extraction can be made from freshly harvested leaf material or from material stored in sealed bag and frozen in -18°C immediately after harvesting.

Prepare water bath at 65°C. I used a Precision Portable Circulator Model PH (GCA Corp. Chicago Illinois) in a 34 L picnic cooler.

Take about 0.025 g of leaf tissue, weigh and record fresh weight. Place tissue in test tube. Tougher tissue should be cut into 2 mm strips for more effective extraction. Avoid prolonged exposure of fresh or thawed material to strong light and room temperature.

Dispense 5 ml DMSO to test tube, cover top with Parafilm. Place tube in water bath.

Extraction time vary depending on tissue toughness. For maple leaves 30 min is sufficient for most samples while some required up to 2 hours extraction time. Mix sample tubes with vortex mixer after 15 min in water bath. Complete extraction can be visually determined when tissue appears transparent.

Let cool and take absorption readings. I did not filter the extract but if your sample appears cloudy this will be necessary.

Determination of chlorophyll a and b content

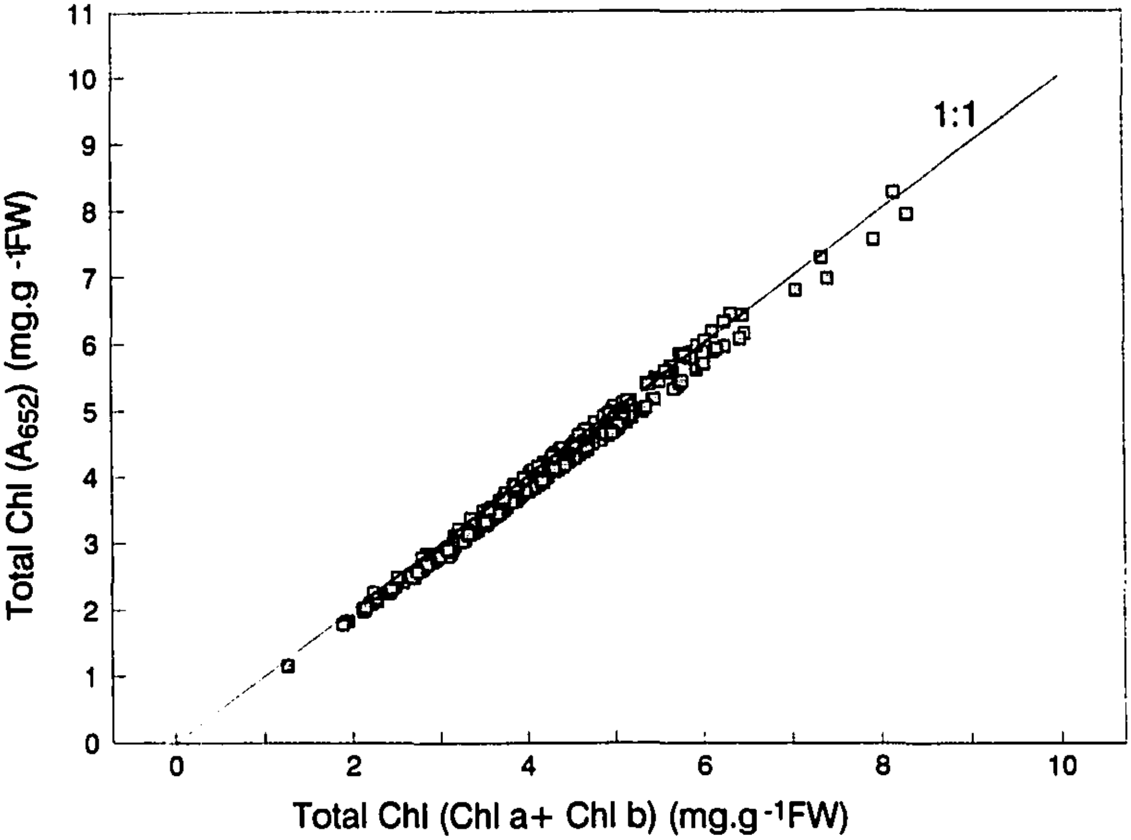
Spec (Milton-Roy Spectronic 1001 Plus with bandwidth resolution at 1 nm) is blanked with DMSO. Absorption taken at 645 nm, 652 nm and 663 nm. It is best to keep absorption for 645 nm between 0.4 and 0.8. Dilute extract if necessary.
Extracts can be stored in fridge but since DMSO freezes at 18°C, it will take about 2 hours to thaw (based on 5 ml samples).

Chlorophyll content can be calculated from formulas given below (Arnon 1949, Bruinsma 1963, Šesták et al 1971).

$C_a=12.7(A_{663})-2.7(A_{645})$
$C_b=22.9(A_{645})-4.7(A_{663})$
$C_{a+b}=20.2(A_{645})+8(A_{663})=27.8(A_{652})$

Comparing total chlorophyll derived from Chl a+b using 645 nm and 663 nm and chl a+b estimated from 652 nm; large deviations from the 1:1 relationship indicate chlorophyll degradation during the extraction process (Figure 1). Total chlorophyll levels given in the thesis were Chl a+b from 645 nm and 663 nm.

Figure 1. Total chlorophyll level derived from the sum of Chl a (A_{645}) and Chl b (A_{663}) is compared with that estimated from A_{652} (Arnon 1949, Bruinsma 1963). Pooling data for all plants used in this study (given in both Chapters 1 and 2), I found a strong agreement (r=0.995, N=321) between the two estimates indicate absence of chlorophyll degradation products. 1:1 line is shown.


1:1
Total Chl (A_{652}) (mg.g $^{-1}$FW)
Total Chl (Chl a+ Chl b) (mg.g $^{-1}$FW)
0
1
2
3
4
5
6
7
8
9
10
11
0
2
4
6
8
10

APPENDIX 4

Information on archival data files

Part 1. Listing of raw data files in Lotus 123 (Version 2.2)

Chapter 1: **EX2ALL.WK1**

Traits included are:

Pre-experimental / Post-experimental size- VHT1/VHT2 (vertical plant height, cm); LHT1/LHT2 (linear plant height, cm); BDIA1/BDIA2 (stem basal diameter, mm); TL1/TL2 (total twig length, including main stem, cm); MOD1/MOD2 (number of growth points).

API (apical shoot length, 1990 growth, cm); LAT (sum of two uppermost lateral shoot lengths, cm); TAREA (total leaf area, cm^2); LFN (total leaf number); LFW (total leaf and petiole dry wt, g); TDW (twig dry wt, g); Wood density (g cm^{-3}); ABDW (total aboveground biomass, g dry wt); RDW (root dry wt, g). FRD (fine root density, number cm^{-1}); FRP (fine root production rate, number cm^{-1} day^{-1}). LDIL (leaf display index by twig length, TAREA/TL90, cm^2 cm^{-1}); LDIW (leaf display index by twig mass, TAREA/TDW, cm^2 g^{-1}).

SLM (specific leaf mass, g cm^{-2}); SDEN (stomatal density (number mm^{-2}); SDIA (stomatal pore diameter, μm); CHLA (chlorophyll a, mg g^{-1} FW); CHLB (chlorophyll b, mg g^{-1}); TOTCHLW (total chlorophyll, mg g^{-1}); LEAFNW (leaf nitrogen, % dry wt); LEAFNA (leaf nitrogen, g m^{-2}).

Photosynthetic rates (μmol m^{-2} s^{-1}) are given as steady-state in dim light (AD), steady-state in bright light (AMAX), and as transient rates after exposure to bright light for 0.5 min (A05) and 4.5 min (A45). Two sets of measurements were taken in June 26-July 2, 1990 (e.g., AD_1) and in July 23-30, 1990 (AD_2).

RGRVH (relative growth rate in vertical plant height, cm cm^{-1} yr^{-1}); RGRTL (relative growth rate in total twig length, including the main stem, cm cm^{-1} yr^{-1}); RGRBD (relative growth rate in stem basal diameter, mm mm^{-1} yr^{-1}).

Chapters 2-4: **EX1MORPH.WK1**

Traits included are the same as in EX2ALL.WK1 except for 1) the addition of TOTCHLA (total chlorophyll, mg m^{-2}), and 2) the omission of photosynthetic traits.

EX1PHYSI.WK1

This file contains gas exchange and chlorophyll fluorescence data:

> Photosynthetic rates (μmol m^{-2} s^{-1}) are given as steady-state in dim light (AD), steady-state in bright light (AMAX), and as transient rates after exposure to bright light for 0.5 min (A05) and 4.5 min (A45). Four sets of measurements were taken: June 15-25, 1990 (e.g., AD_1), July 16-20, 1990 (AD_2), August 6-16, 1990 (e.g., AD_3), and September 5-13, 1990 (e.g., AD_4). Stomatal conductance (mmol m^{-2} s^{-1}) corresponding to the photosynthetic rates are given as (C..) with the same subscript codes.
>
> Dark respiration (RD, μmol m^{-2} s^{-1}) was measured twice: August (RD1) and September, 1990 (RD2).
>
> Chlorophyll fluorescence parameters include: T12 (half time from F_o to F_m, s); F_o (constant flourescence); F_m (maximum fluorescenc), and F_f (quenched fluorescence). See Figure 3 in Chapter 2 for an explanation of these terms. Two censuses of fluorescence were taken: August (e.g., T12_1) and September 1990 (e.g., T12_2).

The archival data diskette is deposited with Dr. M.J. Lechowicz, to whom inquiries regarding data files should be sent. Mailing address: Dept. of Biology, McGill University, 1205 Ave. Docteur Penfield, Montreal, Quebec, H3A 1B1 Canada. Electronic mail: EH39@MUSICA.MCGILL.CA. FAX: (514) 398-5069.

Part 2. Input data set and procedures for path analysis

Data on plant traits (as species means) used in the path analysis are in Pathplot.wk1. Path model specification and execution commends are kept in Path.cmd.

Procedure for executing the path analysis- Import Pathplot.wk1 into Systat (Version 5.01). Run Spearman correlation in Systat, save output correlation matrix as a Systat data file <filename.sys>. Invoke EzPath (Version 1.0), run Path.cmd containing model specification and EzPath commands (Maximum Likelihood Method used). The computed path coefficients can be saved in a file.