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Modeling nutrient and water uptake responses to the environment by New Guinea Impatiens

Mankin, Kyle Ross, Ph.D.

The Ohio State University, 1994
MODELING NUTRIENT AND WATER UPTAKE RESPONSES
TO THE ENVIRONMENT BY NEW GUINEA IMPATIENS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy
in the Graduate School of The Ohio State University

by

Kyle R. Mankin, B.S., M.S.

* * * * *

The Ohio State University
1994

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Approved by

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Department of Agricultural Engineering
to my mother and father ...

the teachers
ACKNOWLEDGMENTS

The document which follows is the tangible product, the unfurled flower, which has resulted from years of care and cultivation by many individuals. Here, I wish to thank those people who contributed not only to the final blossom, but to my growth through every stage of my program's development.

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Life-long learning is the process where continual growth and development leads to perennial bloom. This dissertation is dedicated to those who have instilled in me my love for learning, my parents Diane and Walt, as well as my brothers, Kirby and Korey, and my special uncle, Gordon. I also wish to thank Rani Gustafson for our many years of thriving growth. Finally, I wish to thank Kris Boone for her unending love and support in mind, body, and soul which has helped allow this dissertation to flower, and will help bring my life to its full brilliance.
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Irrigation Systems
Finite Element Modeling

Microclimatology
Biosystem Modeling
Plant Nutrition
Plant Physiology
Structures and Environment
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<tr>
<td>A</td>
<td>m²</td>
<td>area</td>
</tr>
<tr>
<td>C, c</td>
<td>mol kg⁻¹ (or) mg L⁻¹</td>
<td>concentration</td>
</tr>
<tr>
<td>C_p</td>
<td>J kg⁻¹°C⁻¹</td>
<td>specific heat</td>
</tr>
<tr>
<td>CAI</td>
<td>m²_canopy m²_ground</td>
<td>canopy area index</td>
</tr>
<tr>
<td>D</td>
<td>m² s⁻¹</td>
<td>diffusion coefficient</td>
</tr>
<tr>
<td>d</td>
<td>kg_vapour m³_air</td>
<td>absolute humidity</td>
</tr>
<tr>
<td>DW</td>
<td>g</td>
<td>dry weight</td>
</tr>
<tr>
<td>E</td>
<td>kg m⁻² s⁻¹ (or) mol m⁻² s⁻¹</td>
<td>evaporation flux per unit area</td>
</tr>
<tr>
<td>EC</td>
<td>µhos cm⁻¹</td>
<td>electrical conductivity of a solution</td>
</tr>
<tr>
<td>ET</td>
<td>kg m⁻² s⁻¹</td>
<td>evapotranspiration per unit area</td>
</tr>
<tr>
<td>e</td>
<td>Pa</td>
<td>vapor pressure</td>
</tr>
<tr>
<td>F</td>
<td>J</td>
<td>free energy</td>
</tr>
<tr>
<td>g</td>
<td>mol m⁻² s⁻¹</td>
<td>conductance</td>
</tr>
<tr>
<td>J</td>
<td>mol m⁻² s⁻¹</td>
<td>diffusivity (diffusion flux density)</td>
</tr>
<tr>
<td>K_m</td>
<td>µmol m⁻² s⁻¹</td>
<td>Michaelis-Menten constant: concentration at half-maximal reaction rate (here referred to as a &quot;concentration&quot; of light flux)</td>
</tr>
<tr>
<td>L_period</td>
<td>h</td>
<td>photoperiod</td>
</tr>
<tr>
<td>L_vap</td>
<td>J kg⁻¹</td>
<td>latent heat of vaporization</td>
</tr>
<tr>
<td>LAI</td>
<td>m²_leaves m²_ground</td>
<td>leaf area index</td>
</tr>
<tr>
<td>N</td>
<td>unitless</td>
<td>number of plants</td>
</tr>
<tr>
<td>NAR</td>
<td>mg m⁻² h⁻¹</td>
<td>net assimilation rate</td>
</tr>
<tr>
<td>NUE</td>
<td>unitless</td>
<td>nutrient use efficiency</td>
</tr>
<tr>
<td>n</td>
<td>unitless</td>
<td>number of moles of substance</td>
</tr>
<tr>
<td>P</td>
<td>Pa</td>
<td>pressure</td>
</tr>
<tr>
<td>p</td>
<td>Pa</td>
<td>total atmospheric pressure</td>
</tr>
<tr>
<td>PPFD</td>
<td>µmol m⁻² s⁻¹</td>
<td>photosynthetic photon flux density</td>
</tr>
<tr>
<td>P_n</td>
<td>mol m⁻² s⁻¹</td>
<td>net CO₂ depletion by leaf photosynthesis</td>
</tr>
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<td>Q</td>
<td>W m⁻²</td>
<td>energy flux density</td>
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<tr>
<td>R</td>
<td>J mol⁻¹ K⁻¹</td>
<td>gas constant (8.314)</td>
</tr>
<tr>
<td>r</td>
<td>s m⁻¹</td>
<td>resistance to diffusion</td>
</tr>
<tr>
<td>r_f</td>
<td>unitless</td>
<td>resistance adjustment factor</td>
</tr>
<tr>
<td>S</td>
<td>mg m⁻² h⁻¹</td>
<td>rate of nutrient replenishment (or supply)</td>
</tr>
<tr>
<td>Symbol</td>
<td>Description</td>
<td>Units</td>
</tr>
<tr>
<td>--------</td>
<td>-------------</td>
<td>-------</td>
</tr>
<tr>
<td>T</td>
<td>temperature</td>
<td>K, °C</td>
</tr>
<tr>
<td>u</td>
<td>molar flow rate</td>
<td>mol s⁻¹</td>
</tr>
<tr>
<td>V</td>
<td>volume</td>
<td>L</td>
</tr>
<tr>
<td>V</td>
<td>rate of nutrient uptake</td>
<td>mg m⁻² h⁻¹</td>
</tr>
<tr>
<td>v</td>
<td>partial molar volume</td>
<td>m³ mol⁻¹</td>
</tr>
<tr>
<td>V_max</td>
<td>maximum (saturation) rate of nutrient uptake (in Michaelis-Menten relationship)</td>
<td>mg m⁻² h⁻¹</td>
</tr>
<tr>
<td>w</td>
<td>mole fraction of water vapor</td>
<td>mol_water mol_air⁻¹</td>
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- **α**: unitless absorptivity
- **γ**: Pa °C⁻¹ psychrometric constant
- **δ**: Pa °C⁻¹ slope of the curve relating saturation vapor pressure to temperature
- **ε**: unitless molar conversion from water to dry air
- **ε**: unitless emissivity
- **λ**: m wavelength
- **μ**: J kg⁻¹ chemical potential
- **ρ**: kg m⁻³ density
- **σ**: W m⁻² K⁻¹ Stefan-Boltzmann constant (5.67 x 10⁻⁸)
- **Ω**: m K Wien's displacement constant (2897 x 10⁻⁶)
- **ψ**: Pa water potential

**Subscripts**

- **a**: air
- **adj**: adjusted
- **canopy**: plant canopy
- **E**: latent heat
- **e**: entering (initial) condition
- **f**: exiting (final) condition
- **H**: sensible heat
- **i**: state of a substance
- **j**: species of substance
- **k**: location
- **leaf**: plant leaf
- **LW**: longwave radiation
- **M**: metabolism
- **m**: measured
- **max**: maximum response
- **n**: nutrient
- **o**: initial location
- **R**: radiation
ref reference
s saturation
s stomatal
S storage
SW shortwave radiation
t total
v vapor
w water
w' pure water
x coordinate in Cartesian x direction
z coordinate in Cartesian z direction
CHAPTER I
INTRODUCTION

1.1 Description of the Problem

Intelligent management of applied nutrients to plants could improve crop production by increasing growth rates, reducing the amount (and cost) of applied nutrients, and reducing the amounts of unused nutrients which accumulate in soil, groundwater, and surface water. Even where water is currently applied with great precision to plant root zones by sprinklers, drip emitters, and hydroponic systems, selection of nutrient application rates and recipes remains more art than science. Knowledge of plant nutrient use has not kept pace with knowledge of water use; and as a result, development of technologies to control nutrient application has been impeded.

Notwithstanding, individual nutrient injectors allow the creation of precise nutrient recipes by adding measured quantities of nutrients to irrigation water from a defined menu of stock solutions. At this writing, manually adjusted individual injectors are already in widespread use by commercial greenhouse growers, and computer-controlled injectors are under development (Fynn and Roberts, 1992;
Papadopoulos and Liburdi, 1989; Bauerle et al., 1988). Injector technology allows precise modification of both individual nutrient concentrations and element to element ratios. However, this technological advance has "placed the cart before the horse:" we have the technology to provide plants with their exact nutrient needs, but we still cannot define those needs. Models which predict near-future, individual nutrient requirements of plants are needed to make intelligent use of injector technology. Fynn et al. (1994, 1989) address this need using an expert systems approach, applying the experience of an expert greenhouse operator in selecting optimal nutrient recipes. This study, instead, takes a more mechanistic approach, applying the existing literature on nutrient uptake and plant responses to environment toward the development of a demand-based nutrient uptake model.

Growers of both field and greenhouse crops commonly add nutrients to plant root zones at levels much higher than those required for optimal growth. This practice is intended to ensure that the available nutrient supply meets or exceeds plant needs. However, the excess nutrients not used by the plants are leached away from the root zone by irrigation and/or rain water, and eventually enter the groundwater and/or surface water systems. Unless the leachate is physically captured, this increased nutrient load strains the assimilative capacity of local soil and aquatic ecosystems and can lead to hazardous soil, groundwater, and surface water contamination.

In the U.S. alone, agriculture used more than 12 million tons of nitrogen fertilizer in 1990, up six-fold from 1955. Greenhouse agriculture uses higher fertilizer concentrations than field production, and applications occur all year rather than only
seasonally. For example, poinsettia or chrysanthemum production using 600 ml of solution with 300 mg L⁻¹ nitrogen per 15 cm pot every three days results in fertilizer use of 2258 kg ha⁻¹ yr⁻¹ compared with 100 to 400 kg ha⁻¹ yr⁻¹ for agronomic and vegetable crops. It is estimated that commercial greenhouse nutrient application rates are typically 2 to 10 times more than required for optimal growth (Drees et al., 1990; Nelson, 1990). A Florida Department of Environmental Resources study found groundwater nitrate concentrations of 40 mg L⁻¹ near commercial greenhouse operations, far above the 10 mg L⁻¹ standard for drinking water. Morisot et al. (1978) found nitrate soil solution contents averaging 140 mg L⁻¹ and as high as 500 mg L⁻¹ from 1.0 to 1.6 m beneath 19 floriculture greenhouses in France. Clearly, there is a need to reduce nutrient effluent.

Concern for ground and surface water contamination caused by high intensity greenhouse agriculture is leading the global greenhouse industry to search for technologies to reduce chemical and nutrient effluent. Governmental regulation of greenhouse effluent, a topic of concern throughout America and the European Community, is already being implemented in Minnesota, The Netherlands, and Germany. The Ohio Environmental Protection Agency is pushing agricultural producers to reduce effluents through self-imposed management solutions rather than regulation (Wilson, personal communication). There are systems which could "solve" the effluent problem by capturing the leachate and runoff, and treating it before returning it to the environment. However, costs of such systems can be prohibitive. This has lead researchers to look toward source reductions in water and nutrient use by
intelligent management as the most promising method of reducing greenhouse effluent (Drees et al., 1990; Nelson, 1990; Fynn et al., 1989).

1.2 Modeling Nutrient Uptake

Knowledge of actual plant nutrient requirements is essential for reducing the adverse environmental impacts of agricultural management systems. Plant nutrient requirements and uptake are complex functions of external environment and the physical and physiological plant responses to that environment (Figure 1.1). The goal of nutrient uptake modeling, then, is to simulate these interactions for the purpose of predicting required nutrient uptake.

Models are generally either empirical or mechanistic (or some combination of the two). Empirical models reflect experimentally determined relationships, while mechanistic models are based on fundamental (physiological, physical, etc.) relationships. For nutrient uptake modeling, lack of detailed knowledge about the physiological plant responses involved in nutrient uptake has forced researchers to rely on purely empirical models, based upon the direct effect of single aspects of the environment (such as temperature, light level, etc.), rather than using knowledge of actual plant mechanisms to predict nutrient uptake. Regardless of the type used, the model must predict nutrient uptake based on easily measurable parameters, and ultimately must improve crop growth, quality, or production efficiency to be a practical plant production management tool. A basic question lies in determining the
Figure 1.1  Model relating plant nutrient requirements and uptake to external environment, and the physical and physiological plant responses to that environment. Directions of the "Primary" and "Feedback" effects were assumed in developing the nutrient uptake model.
important plant and environmental parameters, and how they interact to affect plant
nutrient demand.

This question is difficult to answer conclusively because plants do not respond
to single environmental parameters in isolation, but rather respond to a sum of all
incident environmental conditions simultaneously (Bloom et al., 1985). In engineering
terminology this can be referred to as "parallel processing," using an analogy of the
action of parallel resistances in a circuit. Plant responses are further influenced by a
sum of the plant's previous growth and development as reflected in its current physical
and physiological status. This can be considered another parallel influence on plant
response. It is because of parallel processing that it becomes difficult to generalize
from results which isolate a single environmental parameter, since the response to this
parameter depends on the level of all the remaining parameters presently and
historically through the life of the plant. Nonetheless, current limitations in
understanding, data processing capability, and research resources will force the
continuation of this method of studying plants and developing models.

1.3 Scope of the Study

The primary aim of this study was to improve the understanding of nutrient
uptake in relation to the plant environment. The specific objectives of this study were
to:
1) Develop a plant growing system capable of detecting short-term (hourly-scale) nutrient uptake by measuring nutrient depletion in the irrigation solution.

2) Determine the time response characteristics of nutrient uptake to changes in light level.

3) Evaluate the steady state nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) uptake responses to various combinations of light level, air temperature, and nutrient solution concentration.

4) Evaluate the steady state water uptake responses to various combinations of light level and air temperature.

5) Compare growth chamber results of water and nutrient uptake to those results found in a similar greenhouse experiment, and interpret these results in light of the environmental differences.

6) Synthesize the water and nutrient uptake results found in this study in order to provide recommendations to improve water and nutrient management in the commercial greenhouse industry.

The overriding goal of this dissertation was to provide a better understanding of the environmental factors which affect water and nutrient uptake. The early dissertation chapters are organized to help provide the background necessary to understand the important factors in this biosystem. The later chapters present the experimental details and results, and discuss the implications of this work toward the goal of improved water and nutrient management.
Chapter 1 provides the impetus for this study. Limitations with the current approach toward nutrient management are discussed, and biosystem modeling is presented as a framework for improving our understanding of this complex topic.

Chapter 2 presents the subject of plant lighting in considerable detail as the primary driving force for many plant physical and physiological functions. Chapter 3 reviews the current state of the literature on nutrient uptake studies. Nutrient uptake mechanisms and existing models are discussed and related to the concept of a nutrient demand model. Here, nutrient demand is proposed to determine the required rate of nutrient uptake. Chapter 4 develops the combination model of evapotranspiration and discusses this model in relation to plant responses and the growth chamber environment.

Chapter 5 describes the growth chamber used for this study. The detailed characterization includes light quality, spatial distributions of the important environmental parameters, and physical characteristics of the growth chamber itself.

Chapter 6 provides a characterization of the test plant used in this study: New Guinea Impatiens (Impatiens hawkeri) ‘Equinox’. A general discussion is followed by details of a photosynthetic response analysis.

Chapter 7 presents the experimental methods used to study the time response characteristics of nutrient uptake to changes in light level. The results are presented and discussed in terms of the implications for future nutrient uptake studies. Chapter 8 describes the factorial experiment used to study the effects of light, air temperature, and nutrient solution concentration on steady state water and nutrient uptake rates.
Five levels of light, three temperatures, and four nutrient concentration levels were studied. Statistical significance of the results are discussed in relation to both scientific theory and engineering practice.

Chapter 9 summarizes the major conclusions of this study, specifically with reference to the established objectives. This summary includes perspective and implications for nutrient and water management in the commercial greenhouse industry. Recommendations for future study are presented as a natural outgrowth of the results and conclusions of this work.
2.1 Introduction

Radiation from the sun is required for virtually all plant growth on earth. Technically, "light" refers to the portion of solar radiation which is detectable by the human eye, generally described by the spectrum of colors: violet, indigo, blue, green, yellow, orange, and red. These colors correspond to the wavelengths between 350 and 770 nm. The eye's sensitivity to light peaks at 555 nm and diminishes to near zero at 350 and 770 nm. Plants are sensitive to a similar but distinctively different range of the radiation spectrum. Photosynthetically active radiation (PAR) describes the waveband between 400 and 700 nm, corresponding to the range of the spectrum used for photosynthesis. Though PAR is the only portion of the spectrum used in photosynthesis, other portions of the spectrum also affect plant growth and development (Sager et al., 1982).

In terms of microclimate, an important differentiation is made between shortwave and longwave radiation. Shortwave, or solar, radiation refers to the portion of the electromagnetic spectrum that is within the sun's emission spectrum. Solar
emission is almost entirely between 300 and 3000 nm and corresponds to a black body radiator at 6000 K. Longwave, or terrestrial, radiation refers to the black body emission from the earth (at about 300 K), spectrally between 4000 and 100,000 nm. Conveniently for climatologists, these two spectra do not significantly overlap, which allows simple separation of the two effects in surface radiation balances. These radiation terms are important factors in plant growth and development, and critical variables in plant modeling.

The units used in reporting radiation are defined in ASAE (1986). The units important to this study will be summarized here. Radiant flux density (measured in W m⁻²) is the rate of energy flow per unit surface area, and as such is called an energy unit of light measurement. Irradiance refers to incident radiant flux density, while emittance refers to emitted radiant flux density. These are not to be confused with radiant intensity (measured in W steradian⁻¹), which defines the energy flux per unit solid angle. Photon flux density (PFD, measured in quanta m⁻² s⁻¹ or mol m⁻² s⁻¹) is the rate of flow of photons per unit surface area. PAR, as discussed above, is the total radiation in the photosynthetically active region, and can be referred to in energy (irradiance) units or quantum (PFD) units.

Sager et al. (1982) showed that PFD units are preferable to irradiance units, but that plant absorptance and utilization efficiency should also be considered, particularly when comparing artificial sources. In other words, if it were possible to design an ideal sensor, it would mimic the plant leaf's absorptance and utilization response characteristics in measuring PAR. Pearcy (1989) provides an interesting measure of
the degree to which the currently accepted units meet the requirements for this ideal sensor. He compared solar, high-intensity discharge, and fluorescent light sources using the ratio of photosynthetic rate to unit of light flux (using data adapted from McCree, 1972b) as a measure of the suitability of the light unit to measure PAR. Whereas an ideal sensor would produce the same ratio for every light source (since it is a perfect predictor of photosynthetic rate), he found an 8% variation in the ratio using quantum units to measure source output, 21% variation using energy units, and 49% variation using photometric units. Photometric units (footcandle and lux) are based on sensitivity of the human eye, and were (mis)used in early plant research. Conversion between these radiation units is a common problem in interpretation of plant research. Thimijan and Heins (1983) address this problem by providing methods for interconversion among radiation units for a number of common lamp types.

2.2 Artificial Light

Electric lighting sources, commonly referred to as artificial light in contrast to natural solar light, are used for supplemental lighting in greenhouses and as total light sources in some plant growth facilities. Three basic categories of electric lights exist: incandescent, fluorescent, and high-intensity discharge (HID). Incandescent lights use a metal filament, often tungsten, within a glass globe. When current is passed through the element, it heats and emits radiation in a continuous spectrum according to the Stefan-Boltzmann law,
\[ Q_{LW} = \varepsilon_{LW} \sigma T^4 \]

with a peak wavelength which can be determined using Wien's law,

\[ \lambda_{\text{max}} = \frac{\varphi}{T} \]

where:

- \( Q_{LW} \) = total energy emitted (W m\(^{-2}\))
- \( \varepsilon_{LW} \) = longwave emissivity (black body = 1.0)
- \( \sigma \) = Stefan-Boltzmann constant (5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4})
- \( T \) = temperature of the body (K)
- \( \lambda_{\text{max}} \) = wavelength of maximum output (m)
- \( \varphi \) = Wien's displacement constant (2.897 \times 10^{-3} \text{ m K})

Fluorescent lamps are glass tubes with phosphor coatings on the inside which absorb ultraviolet (UV) photons from a mercury arc and then emit photons of lower energy visible light. The resulting spectrum consists of mercury emission lines superimposed on a continuous spectrum from the phosphor, and is usually brightest in the blue region. HID lamps pass a current through hot vapor in an arc tube to produce a particular light emission spectrum. This spectrum consists of a series of emission lines according to the gas being used: sodium vapor emits mainly orange, mercury vapor mainly blue and green. Metal halide lamps combine the emission lines of several metal salts of halide elements, such as fluorine, chlorine, bromine, and/or iodine, to produce a relatively broad emission spectrum.
Sager et al. (1982) present the relative spectral distributions of 18 artificial light sources and solar radiation. These distributions graphically illustrate the spectral characteristics of and differences among the sources discussed in general terms above. The spectral differences are critical when measuring radiation. For instance, Sager et al. demonstrated that though a blue fluorescent lamp used in their study had over twice the irradiance of a red fluorescent lamp, it only had a 57% higher PFD. This is because blue light has a higher energy per quanta than red light. So for an equivalent amount of energy, red light has more photons than blue light. Thus, the units used in reporting comparisons of artificial lamps are critical.

2.3 Physiological Effects: Photosynthesis and Photomorphogenesis

Light energy is transformed into useable chemical energy in plants by the process of photosynthesis. Chlorophyll, the primary light-harvesting pigment, is found in large quantities in plants' light gathering surfaces, typically leaves (though stems may also be photosynthetically active in some plants). Photosynthesis uses light energy in discrete parcels (i.e. quanta of energy, or photons) to transform carbon dioxide (CO₂), water (H₂O), and mineral nutrients into stored chemical energy in the form of carbohydrates. The products of photosynthesis are used to make new plant materials, and are responsible for a large majority of plant dry matter production, or growth.
Definition of PAR has occurred relatively recently. McCree (1972a, 1972b) studied the photosynthetic and leaf absorptance characteristics of 22 plant species. He found that all of the plant leaves had nearly the same response characteristics, presumably due to the same photosynthetically active pigments (such as chlorophyll). Using these results, he defined a photosynthetic action spectrum, based on the photosynthetic rate (measured by CO₂ uptake rate) per unit of absorbed quanta, and a photosynthetic quantum yield spectrum, which adjusted the action spectrum by the spectral absorptance of the leaf (Figure 2.1). From this data, he defined PAR as the quantum energy in the wavelength range of 400 to 700 nm, measured as a

![Figure 2.1](image_url)  
Figure 2.1 Normalized relative photosynthetic action and relative quantum yield spectral responses (Sager et al., 1982).
photosynthetic photon flux density (PPFD). Though this definition of PAR does not include the photosynthetic absorptance characteristics of the plant, it is easily measurable. As a result, this definition has been widely accepted and has led to the adoption of quantum units (μmol m⁻² s⁻¹, rather than energy units) as the preferred units for reporting PPFD (ASAE, 1986).

A subsequent study found PPFD to be inferior to photosynthetic action PFD (APFD) or photosynthetic yield PFD (YPFD) as an indicator of photosynthetic utilization efficiency (Sager et al., 1982). Generally, light sources with higher proportions of red wavelengths were more efficient than those with more blue light due to the higher photosynthetic action of red light. Thus, metal halide, with its higher proportion of blue light, was less efficient than HPS lamps. By comparison, warm white and cool white fluorescents were higher than metal halide and lower than HPS in terms of APFD, but higher than both in terms of YPFD. This suggests that the spectra from the fluorescents was more efficient than metal halide and less efficient than HPS when considering photosynthetic absorption alone, but that the higher leaf absorptance characteristics of their light pushed the effective yield above both HID sources. However, photosynthetic characteristics of a lamp are not the only important factor in evaluating light quality.

Photomorphogenesis, the effects of light on plant development, covers the remaining physiological effects related to light (Salisbury and Ross, 1992, Chapter 20). Phytochrome is a pigment responsible for such photomorphogenic effects as photoperiodism, seed germination, stem elongation, and flowering. The ratio of red to
far-red light incident on the plant dictates which form of this reversible pigment predominates and in turn whether the mentioned photomorphogenic responses are promoted or suppressed. Other pigments certainly affect morphological development as well, but their actions have been quantified still less than phytochrome. Photomorphogenic effects may influence not only plant development, but also may alter the photosynthetic responses for a given PPFD. In addition, phytochrome and most photomorphogenic pigments require very low light energy to be activated. Due to the wide acting spectral sensitivities and wide range of plant responses, a single action spectrum of the type found for photosynthesis is not possible for photomorphogenesis (Sager et al., 1982).

2.4 Physical Effects: Thermal

Both short and long wave radiation affect the heat balance of a plant. Figure 2.2 shows the relative proportions of absorption, transmission, and reflection characteristic of a plant leaf. This varies with leaf species, age, and location in the canopy. Of the radiation absorbed by the leaf, only PAR is utilized for growth. Efficiency of PAR energy conversion to dry matter has been found to range from 6 to 24% in the laboratory, although plants in optimal agricultural production rarely exceed 2% PAR utilization efficiency over an entire growing season (Wassink, 1966). The rest is thermal load which either heats the leaf or is transferred from the leaf by convection, radiation, or evaporation.
Figure 2.2  Spectral absorptance, reflectance, and transmittance of green leaves of *Populus deltoides* (Gates, 1965).
Consider a basic energy balance of a leaf:

\[ Q_R + Q_E + Q_H + Q_M + Q_S = 0 \]  \hspace{1cm} (2.3)

where:

- \( Q_R \) = net radiation (W m\(^{-2}\)), irradiance > emittance (+)
- \( Q_E \) = latent heat transfer (W m\(^{-2}\)), evaporation (-), condensation (+)
- \( Q_H \) = sensible heat transfer (W m\(^{-2}\)), leaf temp > air temp (-)
- \( Q_M \) = chemical energy storage (metabolism and other plant factors, W m\(^{-2}\))
- \( Q_S \) = heat energy storage (W m\(^{-2}\))

Conservation of energy (the first law of thermodynamics) dictates that this balance must equal zero. However, the components may vary greatly in reaching this balance. Generally, the chemical storage (mainly by photosynthesis) is negligibly small for horticultural crops grown in the greenhouse. Thus, the leaf essentially must balance the incident radiation input with emitted radiation, convective sensible heat, and transpirational latent heat outputs, with heat storage reflecting the difference. This will be covered to some extent in Chapter 4. A basic outline of this process and equations used to calculate each term is provided by Salisbury and Ross (1992, Chapter 4), and a thorough discussion of the details of this energy balance are presented by Nobel (1974, Chapter 7) and Yang (1988). The primary concern in this study was how this energy balance affected plants grown in a growth chamber, and how this compared with plants grown in a greenhouse.
2.5 Plant Response to Light

2.5.1 Effect of light on leaf energy balance

The principal difference in plant energy balance between growth chambers and greenhouses is the difference in radiation environment. Though the growth chamber environment may be able to simulate greenhouse air temperature, humidity, or air movement over the canopy, it is unavoidable that the radiation environment is significantly different. For example, Thimijan and Heins (1983) report that HPS lamps have 64% of their total radiation output outside the PAR range, MH have 63%, and cool white fluorescents (CWF) have 61%, compared to 57% for daylight. But 38% of HPS, 47% of MH, and 58% of CWF radiation is in the thermal region above 2700 nm while almost no daylight is in this range. This is important in terms of heating surfaces like plant leaves or growth chamber walls, since these surfaces often have distinctly different absorption characteristics for short and long wave radiation. For instance, a white paint surface absorbs approximately 20% of shortwave radiation but more than 90% of longwave, while weathered galvanized sheet metal is almost the opposite, absorbing 80% and 28% (respectively), and concrete is between these two, absorbing 60% and 88% (Incropera and deWitt, 1985). A representative absorption spectrum of a plant leaf is shown in Figure 2.2. Gates (1965) reports that plant absorption averages about 60% for shortwave radiation and 97% for longwave. The type of barrier between the light source and the plant is also important. Acrylic transmits 93% of PAR and < 5% of thermal radiation, while glass transmits 88% and
3%, and polyethylene film transmits 85% and 50%, respectively (Aldrich and Bartok, 1986). Growth chambers tend to use more white paint in close quarters to the plants, while greenhouses have more of an open structure with the barrier occupying a significant portion of the plants' view factors. In general, the high thermal load from lamps in close proximity to the plants, the higher proportion of thermal spectral activity, the close proximity of thermally absorptive chamber walls, and the high thermal absorptance of plant leaves combine to provide plants in growth chambers with a higher thermal load than the same plants in a greenhouse under the same PAR irradiance. Referring back to the energy balance (Equation 2.3) reveals that a higher thermal radiation load and the same PAR level, air temperature and humidity, forces plant leaves to either: 1) increase temperature, and thus increase the driving temperature difference for all the heat transfer processes, 2) increase transpiration, thus removing the thermal load as latent heat, or 3) some combination of the two.

Leaf temperature is a measure of the net result of the leaf heat balance described by Equation 2.3. For instance, Mankin (1987) measured lettuce leaf temperature under air-cooled and water-cooled HPS lamps in a growth chamber at 24 °C with aluminized polyester curtain walls. The water-cooling apparatus was a glass test-tube over a HPS bulb with a 150 mm layer of water circulating between them. The water apparatus removed about 30% of the thermal radiation (3000 to 50,000 nm) and 60% of the near IR (800 to 3000 nm) portion of the HPS lamp output. This difference in thermal load resulted in leaf-air temperature differential (LTD, $T_{leaf} - T_{air}$) being consistently higher under the air-cooled lamp than the water-cooled lamp. LTD
under air-cooled ranged from 0.4 °C higher than under water-cooled at 80 μmol m\(^{-2}\) s\(^{-1}\) to 2 °C higher at 300 μmol m\(^{-2}\) s\(^{-1}\). As PAR increased within this range, LTD decreased slightly under water-cooled HPS (from -0.4 to -1.0 °C), while it increased under air-cooled HPS (from -0.1 to over +1.5 °C). These results demonstrated that thermal and near IR radiation loads may heat leaf surfaces beyond their capacity to be evaporatively cooled. Mellor et al. (1964) studied thermal responses of several plant species to wide ranges of environmental conditions in a growth chamber. They found LTD to be positive (leaf temperature higher than air temperature) for almost all air temperatures, irradiance levels, vapor pressure deficits, and air speeds they studied. The lamp and chamber thermal radiation was most effective in raising leaf temperature at low air temperatures. For example, LTD was +11 °C at 15 °C air temperature and 80% rh, but decreased to almost 0 °C at 35 °C and 40% rh with air velocities between 0.15 and 0.23 m s\(^{-1}\). They also found that visible light (up to 650 nm) increased LTD more effectively than visible plus IR (up to 1400 nm).

In the greenhouse under solar light, Yang (1988) found average canopy temperature of cucumber to be consistently lower than air temperature throughout the day. Fynn et al. (in review) found leaf temperature closely followed solar irradiance. Leaf temperature for both chrysanthemums and New Guinea Impatiens was higher than air temperature during the day and lower at night. Chrysanthemum was found to have a high transpiration capacity, with LTD following irradiance and rarely exceeding +2 °C during the day. By contrast, transpiration of New Guinea Impatiens peaked at ≈250 W m\(^{-2}\) causing LTD of exposed leaves to average +2 °C and peak as high as +7
\[ ^\circ C \text{ during the day. Fynn et al. also found large differences in LTD, as high as } 6 ^\circ C, \]
between exposed and shaded New Guinea Impatiens leaves at high irradiance levels.

2.5.2 Effect of light on stomatal function

Temperature regulation by leaves leads to the question of stomatal control, since stomates are the primary regulators of latent heat loss from leaves. Is stomatal aperture driven by transpirational demand or photosynthetic demand? If the stomates open primarily to release heat, then they should be controlled by the total incident energy, including short and long wave radiation. However, if the stomates open according to the demand for CO\textsubscript{2} by photosynthesis, then the stomates should be driven by PAR regardless of the additional thermal load.

Experimental evidence on stomatal function is not conclusive (Salisbury and Ross, 1992, Chapter 4). Stomatal response historically has been attributed to CO\textsubscript{2} concentration in the leaf. A high CO\textsubscript{2} gradient between the leaves and free air causes stomates to open. This gradient can be induced by decreasing the CO\textsubscript{2} concentration in the leaf or by increasing the concentration in the free air. This suggests that light affects stomatal opening only through its effect on photosynthesis and the resultant affect on intercellular CO\textsubscript{2}. For example, an increase in PPFD would decrease intercellular CO\textsubscript{2} (since photosynthesis would use more CO\textsubscript{2}) and cause stomates to open. Contradictory evidence was found in an experiment by Sharkey and Raschke (1981a). They found that cocklebur, cotton, common bean, Perilla frutescens, and
maize responded to increased irradiance with increased stomatal conductance, which
seems to support the model of stomatal control based on CO₂ gradient. However,
stomatal response in the first four species was only to a small extent related to
intercellular CO₂ concentration. They found intercellular CO₂ concentration could
actually increase as irradiance increased, contrary to what would be expected if
internal CO₂ drove stomatal opening. They also found that blue light (430 to 460 nm)
was almost 10 times as effective as red light (630 to 680 nm) in producing a given
stomatal opening (Sharkey and Raschke, 1981b). The red light effect was apparently
related to chlorophyll and photosynthesis, but the blue light effect was independent of
photosynthesis.

There is also evidence that stomates respond to atmospheric humidity or vapor
pressure deficit between the leaf and free air (Tibbits, 1979). Low water potential in
the leaf (water stress), high temperature (30 to 35 °C), and gentle breezes can all
induce stomatal closing (Salisbury and Ross, 1992, Chapter 4). These all seem to
indicate some level of control according to water status of the leaf. Indeed,
physiologists have elucidated two feedback loops which seem to control stomatal
opening and closing (Salisbury and Ross, 1992, Chapter 4). One loop allows K⁺ to
enter the guard cell when CO₂ decreases in guard cells, thus creating an osmotic
gradient for water to enter the guard cell, pressurize it, and open it. The other loop
calls for abscisic acid (ABA) when water stress develops. ABA mediates stomatal
closure. Thus the first loop specifically controls CO₂ for photosynthesis while the
second loop prevents excessive water loss.
CHAPTER III

NUTRIENT UPTAKE

3.1 Introduction

Plants may be thought of in a general sense as "flavored water," where each plant or plant product's "flavor" is determined by its composition of chemical elements. Water is indeed the dominant component in all living plants. In general, carbon (C), hydrogen (H), and oxygen (O) from water (H₂O) and carbon dioxide (CO₂) comprise more than 90% of a plant's dry weight and about 99% of a plant's fresh weight. This leaves only 1% of a plant's total mass to be divided among all the remaining mineral nutrients. This 1% is the focus for the entire field of nutrient uptake study.

Though they constitute only a small portion of plant tissue, these nutrients are absolutely essential to carry out the diverse processes which allow a plant to grow, mature, and reproduce. In nature, plants must compete for a limited store of available soil nutrients, and their ability to do so successfully may determine their survival. Agricultural crops are provided with artificially high levels of nutrient fertilizers which makes competition less important than productivity. Particularly in the controlled
greenhouse environment, where both productivity and fertilizer use far exceed even that of field agriculture, nutrient management is critical. However, at present only small, isolated pieces of the overall nutrient uptake puzzle are available to help growers make intelligent nutrient management decisions. This chapter aims to provide a synthesis of the current bounds of nutrient uptake knowledge.

3.2 Nutrient Uptake Mechanisms

Inorganic ions enter the plant primarily through their roots. These nutrients may diffuse readily into the outer "free space" of the root cortex. However, the impermeable Casparian strip on the outer endodermal wall forces both water and nutrients to cross the semi-permeable plasmalemma membrane into the cell cytoplasm in order to reach the xylem. Water freely crosses the plasmalemma by osmosis down an electrochemical gradient, though against considerable resistance. Nutrients must be transported across the outer plasmalemma, and do not simply pass from soil solution to transpiration stream along with water. Several mechanisms of transport, or uptake, have been proposed. Determination of the transport mechanisms has been an integral aspect of the study of nutrient uptake.

Active nutrient uptake requires energy to absorb a nutrient against an electrochemical gradient. It has been proposed that a pump uses energy directly from ATP to move nutrients across the cell plasma membrane in the root. With passive nutrient uptake, nutrients move down an electrochemical gradient -- basically, from
higher to lower ion concentrations and electrical gradients. This type of uptake uses no energy directly, though metabolic energy is required to establish the gradient in the first place. Facilitated diffusion is a third category of transport which uses channels or carriers to allow selected ions across the otherwise impermeable plasma membrane. A channel allows a specific nutrient to travel passively down an electrochemical gradient, while a carrier may allow its target nutrient to actively accumulate against a gradient. Nutrients are often classified generally as either active or passive, according to the type of uptake mechanism which is used to transport the ion from the external solution to the root cytoplasm (Salisbury and Ross, 1992; Sutherland, 1988; Gislerød and Adams, 1983; Mengel and Kirkby, 1987; Claassen and Barber, 1974; Maas, 1969; and Epstein et al., 1963). Review of this and other literature reveals many inconsistencies in classifications, demonstrating the difficulty in classifying a nutrient as strictly passive or active. In some cases both mechanisms appear to contribute depending on nutrient concentration.

In summary, current understanding indicates that all nutrients must be escorted across the plasmalemma into the cytoplasm through specific uptake sites. This suggests that uptake is selective to some extent. Overall plant uptake rate would then be influenced by the number of uptake sites, the rate of activity of these sites, and the rate of replenishment of new nutrients to these sites. The first two are plant factors which may allow control of uptake either by increasing the number of uptake sites or by increasing the activity of these existing sites. The latter factor is determined by the physical root-zone environment, and is influenced by the plant indirectly through the
gradient established by plant water and nutrient removal from the root-zone. Clarkson (1974) states, "the inherent properties of the transport systems are not the only factors controlling the rate at which roots absorb ions." It is likely that both plant and environment influence individual nutrient uptake rates.

3.3 Modeling Nutrient Uptake

Most recent research studying nutrient uptake rates has focused on the relationship between rate of uptake of an individual nutrient and its concentration within the root zone solution. This will be referred to as the "supply" approach to nutrient uptake modeling. In contrast, demand modeling is based on the assumption that some factor or factors in a plant control nutrient uptake by determining the plant's level of demand for each nutrient. Instead of treating plant roots like passive sponges, indiscriminately absorbing all nutrients they come in contact with, the demand model supposes that a plant establishes a particular demand for nutrients according to its physiological development, and then selectively absorbs only those nutrients which it requires from those available in the plant root zone. Though it is likely that both supply and demand contribute to the overall nutrient uptake, it may be instructive to begin by considering them separately.
3.3.1 Nutrient Uptake Supply Models

The relationship between root zone nutrient concentration, or nutrient supply, and nutrient uptake was an area of active research as early as 1952, when Epstein and Hagen began using the Michaelis-Menten concept to relate nutrient absorption by excised roots to external nutrient concentration. They borrowed the enzyme-kinetics concept of a carrier-ion complex to explain the unidirectional transport of ions through the root membrane. Michaelis-Menten kinetics accurately describes uptake in dilute nutrient solutions of less than 1 mM (Epstein, 1973). However, for higher nutrient concentrations the data may be more accurately described by a multiphasic mechanism (Nissen, 1991), graphically represented by a series of Michaelis-Menten hyperbolas with successively increasing plateaus. Multiphasic kinetics suggests that one transport structure displays both carrier- and channel-like properties depending on conformational changes in response to external solute concentrations (Nissen, 1991).

Nutrient supply models have both experimental and practical limitations. The use of nutrient-starved, excised root tissue immersed in a labelled nutrient solution to determine uptake rate may not reflect nutrient uptake in vivo. Characterization of the relationship between uptake and concentration is confounded further by nutrient depletions in the immediate root zone caused by the time-dependency of both nutrient uptake and replenishment. However, when external concentration and temperature change gradually, as is common in natural ecosystems, it has been suggested that a nearly constant supply of nutrients is maintained over a wide range of temperatures.
and external nutrient concentrations (Glass and Siddiqi, 1985). Several studies have demonstrated that for wide ranges of nutrient concentrations common in natural soil solutions, uptake is independent of concentration: for example, nitrate in dwarf bean in the range of 0.08 to 0.48 mM (i.e. 1 to 7 mg L⁻¹ of NO₃⁻-N) (Breteler and Nissen, 1982); K⁺, Cl⁻, and other ions in a variety of plants over the same range (e.g. 3 to 19 mg L⁻¹ of K) (Nissen, 1974); and K⁺, Rb⁺, Cl⁻, and many other ions between 0.2 and 1.0 mM (e.g. 8 to 39 mg L⁻¹ of K) (Epstein, 1973). Other researchers have demonstrated that the limiting nutrient in the external solution may be used almost entirely to depletion (Ingestad, 1982; Ingestad and Lund, 1986), and that dilute nutrient solutions, near the Kₘ value (the concentration of half-maximal uptake) found by traditional uptake studies, can sustain maximal growth (references in Clarkson, 1985; Clement et al., 1978, Ingestad, 1982). In any case, plants may naturally seek an equilibrium between feeding mechanism, nutrient uptake, and photosynthesis (Ingestad and Ågren, 1988). Thus, there is a large body of work that suggests that near equilibrium or within wide bands of nutrient concentrations, nutrient supply may be less important than nutrient demand.

### 3.3.2 Nutrient Uptake Demand Models

The "demand" approach to nutrient uptake modeling is based on the assumption that a plant's nutrient uptake is ultimately driven by its demand for nutrients. The assumption, supported by work on whole plant nutrition, is that "net ion absorption by
roots is closely regulated by the growth of the plant given that nutrients are not limiting (Clarkson, 1974). Plant biochemistry may naturally seek an equilibrium between nutrient uptake, nutrient supply, and nutrient demand. The demand model proposes that once at equilibrium, plant nutrient demand controls uptake by a feedback mechanism. A decreased nutrient status in the plant signals for increased uptake. The signal may either elicit root growth to increase the overall uptake area, or modify the transport system to increase uptake rate (Clement et al., 1978; Glass and Siddiqi, 1985; Ingestad and Ågren, 1988).

Plant nutrient demand is difficult to define. First, it is important to make a distinction between "required" nutrient uptake and actual nutrient uptake. We call nutrient requirement the amount of nutrients necessary for the elusive "optimal" plant growth under a given set of environmental and plant conditions. Nutrient uptake, on the other hand, refers to actual uptake and includes a nebulous component termed luxury consumption. Since luxury consumption of nutrients does not directly translate into plant growth, we do not consider it to be an immediate plant requirement. Plants often absorb more nutrients than necessary to meet current requirements, and store them for later use. Though the storage component of nutrient uptake may be required for plant ecological competitiveness and survival, these nutrients will only be used to meet a future need of the plant, and thus are not strictly a current requirement.

Nye and Tinker (1969) suggest that root demand, determined by plant growth and external concentration (diffusion gradient), must be the driving force for nutrient uptake. Scaife and Smith (1973) counter that since plants maintain nutrient status
within tight tolerances regardless of external concentration, nutrient concentration at the root surface only indirectly controls uptake. They suggest that plant nutrient status provides a more reliable indicator of how well nutrient supply is keeping pace with demand. A split-root study by Claassen and Barber (1977) demonstrated that maximal growth rate could be maintained with only 50% of the roots supplied with potassium, suggesting that plant demand had some self-regulating role in overcoming nutrient supply deficiencies. Similar results were reported by Drew and Nye (1969), where potassium uptake rate was substantially greater in a small section of root when the remaining root system was not supplied with potassium. This suggests that nutrient uptake in the roots relies on complex feed-back mechanisms from other parts of the plant, and emphasizes that uptake must be studied using whole, intact plants.

A demand nutrient uptake model has no inherent preference of active over passive influx, but does require that the plant be able to control uptake. All forms of facilitated transport, whether "passive" facilitated diffusion or active transport, selectively transport ions across the plasma membrane, which affords the plant a level of specificity in uptake of nutrients. Thus, as long as uptake is facilitated and not merely unrestricted passive influx, the proposed demand model approach remains applicable. As more work is done to elucidate the precise physiological mechanism(s) used to assimilate individual nutrients, truly mechanistic models may be attainable.
3.4 Development of a Nutrient Demand Model

The proposed demand model concept assumes that the uptake of individual nutrients is related to the demand for those nutrients established by the incident levels of specific microenvironmental parameters. The model which will be discussed in the remainder of this chapter suggests that demands for individual nutrients are dictated by incident levels of photosynthetic photon flux density (PPFD) (Figure 3.1). PPFD describes the light energy utilized for photosynthesis, which converts CO₂, H₂O, and mineral nutrients into the products necessary for plant growth. The rate of this process establishes a level of demand for many individual nutrients. Considerable physiological and empirical evidence exists supporting the important role of PPFD in determining nutrient uptake rates. Though nutrient uptake ultimately will be related empirically to an environmental parameter in this model, the compiled evidence presented herein provides a logical mechanistic framework upon which to build the model. The following sections provide qualitative support for the organization of the model presented in Figure 3.1, and suggest relationships between the elements of the model. These relationships ultimately lead to the final form of the uptake equation being proposed.
Figure 3.1 A simple model relating plant demand for individual nutrients to PPFD.
3.4.1 Relating PPFD to nutrient uptake

Many studies have shown a strong relationship between uptake of various nutrients and incident irradiance levels. The earliest work in this area studied the role of light in ion absorption using plants in which the same cells performed the functions of both photosynthesis and the primary acquisition of mineral nutrients (Epstein, 1972). The synthesis of carbohydrates and other respiratory substrates depends on the energy of light trapped in the process of photosynthesis. Epstein indicated that green algae's accumulation of both nitrate and phosphate depended upon light as a source of energy. Epstein also reported that the leaf tissue of corn accumulated potassium in the light at twice the rate it did in the dark. He concluded that the transport of inorganic ions by plant cells was affected by mechanisms dependant upon energy from cellular metabolism.

Magalhaes and Wilcox (1983a, 1983b) demonstrated that total uptake of N, P, K, Ca, and Mg increased with increasing irradiance for plants supplied with NO$_3^-$-N, but plants supplied with NH$_4^+$-N showed either no response or decreased uptake with irradiance. Other studies also showed a correlation between uptake of various nutrients and irradiance: K, Mg, and Ca by Chu and Toop (1975), N and K by Adams (1980) and Adams and Massey (1984). Tremblay et al. (1988) offer a word of caution which is particularly pertinent for studies using supplemental lighting: equal photosynthetic irradiance does not necessarily result in equivalent nutrient uptake since spectral quality influences several physiological processes related to uptake.
Diurnal variations were found to affect uptake of NH$_4^+$ and K$^+$ (Hatch et al., 1986). Statistical analysis of this data revealed that 5 and 6 hours lag times (respectively) gave the best correlations between uptake and irradiance. Similar results were obtained by Clement et al. (1978) who recorded peak rates of NO$_3^-$ uptake with a 5 to 6 hour lag behind solar radiation. This lag time was not reported by Gislerød and Adams (1983), who found that uptake of both water and K$^+$ increased in response to solar radiation, with the highest nutrient uptake rates occurring during the brightest part of the day. Nonetheless, these data suggest that diurnal variations in the uptake rate of NH$_4^+$, NO$_3^-$ and K$^+$ may result from "feedback mechanisms which regulate the demand for mineral nutrients through the photoperiodic supply of photosynthate" (Hatch et al., 1986). This sampling of literature demonstrates the strong relationship between light levels and nutrient uptake, and provides an indication that nutrient uptake may be directly related to growth, and perhaps regulated by photosynthesis.

3.4.2 Relating growth to nutrient uptake

Plant growth, in the most general sense, is a result of transforming raw materials into plant materials. The raw materials for plant growth are CO$_2$, H$_2$O, and mineral nutrients. Ingestad and Lund (1986) studied the effects of mineral nutrition on growth under steady-state internal nutrient concentrations and growth. Under these conditions, uptake rate of nutrients (per unit of nutrient in the plant) is directly related to relative growth rate (see also Salisbury and Ross, 1992, Chapter 7). Willits et al.
(1992) demonstrated that relative accumulation rates of 11 nutrients by chrysanthemum were linearly related to relative growth rate with high correlation (e.g. \( r^2 \) for N (0.96), P (0.90), K (0.95), Ca (0.89), and Mg (0.84)). Other researchers also show correlation between uptake and plant productivity (Landi and Fagioli, 1983; Cacco et al., 1980; Cacco et al., 1978; Frick and Bauman, 1979; Motto and Salamini, 1981). Raper et al. (1977a, 1977b) found nitrate uptake was directly related to the photosynthate supply from the leaves of tobacco, cotton, and soybean, and concluded that there is a balance between nitrate uptake, photosynthate supply, and plant growth functions. These results all indicate that growth rate is a driving factor in uptake of nutrients, and suggest that ultimately these factors relate to the rate of photosynthesis.

3.4.3 Relating photosynthesis to growth

Plant growth rate is commonly measured by the rate of increase in dry weight, which essentially reflects the rate of uptake of \( \text{CO}_2 \). Plants assimilate \( \text{CO}_2 \) through photosynthesis. Thus, growth rate is clearly a direct function of photosynthetic rate. McCree (1967) suggests that the relationship between photosynthetic rate and growth is linear. This has been a common assumption in dynamic crop modeling. For instance, Curry (1971) and Curry and Chen (1971) used this assumption in a simulation model of corn growth, and found a good correlation with field data for the first 45 of a 60 day simulation. Charles-Edwards and Acock (1977) also used the assumption that growth is a linear function of photosynthesis in their model of
chrysanthemum growth, and found good correlations with actual growth data for the entire 35 day simulation period. The same mechanistic assumptions were used in the proposed model.

3.4.4 Relating PPFD to Photosynthesis

Photosynthesis generally increases proportional to PPFD up to a level where light saturates the mechanism for a given plant-environment system. McCree (1972a, 1972b) found the relationship between photosynthetic rate ($P_n$) and irradiance ($I$) to be described by the rectangular hyperbola ($a$ and $b$ are constants)

$$ P_n = \frac{aI}{1 + bI} \quad (3.1) $$

or rearranging,

$$ P_n = \frac{a I}{1 + 1/b \cdot I} \quad (3.2) $$

This is the same form as the Michaelis-Menten equation with $(a/b)$ replacing $V_{\text{max}}$ and $(1/b)$ replacing $K_m$. Data can be described using a Michaelis-Menten hyperbola by determining the values of $V_{\text{max}}$ and $K_m$. These constants may be determined using established curve-fitting methods (Lineweaver and Burke, 1934; Persoff and Thomas, 1956).
3.5 A Nutrient Uptake Demand Model

3.5.1 Single-factor demand model: Uptake vs. PPFD

The proposed model relates individual nutrient uptake to PPFD by the Michaelis-Menten form of the rectangular hyperbola equation (Mankin and Fynn, 1992):

$$V = \frac{V_{\text{max}}[\text{PPFD}]}{K_m + [\text{PPFD}]}$$

(3.3)

where:

- $V$ = rate of nutrient uptake (mg m$^{-2}$ h$^{-1}$)
- $V_{\text{max}}$ = maximum rate of nutrient uptake (mg m$^{-2}$ h$^{-1}$)
- $K_m$ = Michaelis-Menten constant: the PPFD at 0.5 $V_{\text{max}}$ (µmol m$^{-2}$ s$^{-1}$)
- $[\text{PPFD}]$ = photosynthetic photon flux density (µmol m$^{-2}$ s$^{-1}$)

The model (Figure 3.2) predicts that at low PPFD, an increase in PPFD leads to a corresponding increase in nutrient uptake while further increases in PPFD beyond some saturation point have little effect on nutrient uptake. An increase in PPFD in the linear response range causes plants to photosynthesize faster and demand more of the
Figure 3.2 The relationship between individual nutrient uptake and PPFD by the proposed model -- a Michaelis-Menten form of the rectangular hyperbola equation.

nutrients involved in energy, plant material, and photosynthate production. This in turn effects an increase in the rate of nutrient uptake.

3.5.2 Multi-factor demand model: Uptake vs. PPFD, temperature, and CO₂

The demand concept may be expanded to include the influences of other microclimatic parameters to provide an interactive prediction of nutrient uptake. For instance, air temperature and aerial CO₂ level are known to influence plant growth rate. Idso and Baker (1967) and Chmora and Oya (1967) present empirical curves relating temperature to photosynthetic rate. Similarly, Moss (1965) presents curves
relating atmospheric CO₂ level to photosynthesis. Again with the assumption that
photosynthesis has a linear effect on nutrient uptake, three-dimensional graphic
surfaces can be created showing the combined effects of these parameters on nutrient
uptake (Figures 3.3 and 3.4).

3.5.3 Model assumptions

These types of graphs represent a first approximation and have many inherent
assumptions. A principal assumption is that the parameters do not interact with each
other to affect nutrient uptake. This allows the combined effect of the various
parameters to be simply the product of their separate effects. If interactions between
model elements are found to be significant, weighting factors could be determined and
incorporated into a combined model to account for such affects.

These models also assume that individual nutrients are taken up independently
within a plant's tolerance (or luxury consumption) range. In other words, uptake of
any given nutrient does not depend on the concentration of any other nutrient, thus
there is no competition between nutrients for uptake by the plant. This allows each
nutrient to be analyzed separately and independently of other nutrients, and greatly
simplifies the modeling process. But interactions do exist between nutrients (Mengel
and Kirkby, 1987). More work needs to be done to quantify nutrient supply
interactions with regard to uptake.
Figure 3.3 A multi-factor demand model relating individual nutrient uptake to PPFD and temperature.

Figure 3.4 A multi-factor demand model relating individual nutrient uptake to PPFD and CO₂.
The nutrient demand concept suggests that plant demand determines both the amounts and types of each individual nutrient required. Photosynthesis produces the chemical energy and carbohydrates necessary to produce and maintain plant materials. Wareing et al. (1968) demonstrated that demand for photosynthates has a positive effect on rate of photosynthesis, and that demand may be governed by higher light levels, higher levels of CO₂, or even partial defoliation, which affects the photosynthetic source/sink relationship. The strength and proximity of plant resource sinks have been found to be major determining factors for photosynthetic rate of photosynthetic tissue (Evans, 1991; Hilliard and West, 1970; Neales and Ingoll, 1968; Kazaryan et al., 1965). It follows that nutrient requirements must be dependent on the specific plant materials being produced at any given time and stage of growth. Sutherland (1988) demonstrated a distinct change in nutrient uptake as cucumber development moved between growth stages (vegetative → flowering → fruiting). In contrast, Willits et al. (1992) found that there was a gradual change from week to week in the relationship between relative assimilation rate and relative growth rate for chrysanthemum. This may indicate that the plant's nutrient demand characteristics continually change as the plant grows, and may not be assumed to remain constant throughout each stage of growth. In any case, separate demand models must be developed for each distinct stage of plant growth which distinguishes the changing relationships for each individual nutrient.
CHAPTER IV
WATER UPTAKE

4.1 Introduction

Water is the universal medium for life. It is an essential component of all living cells. Green plant material, for instance, is roughly 80 to 95% water. Though water comprises a large percentage of plant living tissue, the amount of water which a plant uses for this purpose is small compared to the total water which the plant absorbs. Only about 0.01% of the water taken up by plants is required for photosynthesis (Mengel and Kirkby, 1978), and only a small percentage of total water uptake is used to form plant tissues. The remaining water is held in the plant as free water and ultimately released from leaves in the process of evapotranspiration.

Evapotranspiration, generally defined, refers to the movement of water from the ground back to the atmosphere, including evaporation from both soil and plants. Transpiration refers only to the evaporation from plant leaves. In this dissertation, evapotranspiration and transpiration are often used synonymously to refer to evaporation from plant leaves, with the assumption that soil evaporation in many
experiments is minimized to negligible levels. Any necessary distinctions will be made explicitly.

Evapotranspiration from plants has been an area of active research for many years (Bowen, 1926; Penman, 1948; Monteith, 1963; Stanghellini, 1987; Yang, 1988; Fynn et al., in review). These studies have led to a form of the combination equation (so named because it combines energy balance and heat/vapor transfer equations in modeling evapotranspiration) which closely approximates evapotranspiration from plants in a greenhouse environment (Stanghellini, 1987; Yang, 1988; Al-shooshan, 1991, Pang et al., 1993, Fynn et al., in review). However, the radiative environments of growth chambers differ significantly from those of greenhouses, as discussed in Chapter 2. This may lead to significant differences in evapotranspiration rates. Because the relevant evapotranspiration models have been developed in reference to the greenhouse environment, their assumptions have been made consistent with the particular conditions which are a byproduct of the greenhouse radiative environment. Thus, the assumptions made during development of these evapotranspiration models must be reassessed before automatically being generalized to the growth chamber environment.

4.2 Evapotranspiration Model Development

The purpose of this section is to lay out a concise yet complete development of evapotranspiration in general, and the combination model in particular, as it pertains to
a growth chamber environment. In this way, the limitations of our current understanding of evapotranspiration will become evident, and the assumptions necessary for the practical use of the combination model will be better understood. The grounding provided in this section will be important during the discussion of the effects of the plant environment on evapotranspiration, and in the comparison of evapotranspiration within growth chamber and greenhouse environments.

4.2.1 Physical foundations of transpiration and evaporation

Evapotranspiration varies considerably with plant species and microclimate. Water is absorbed by roots and translocated though the plant in the direction of decreasing chemical potential gradient, driven from a high chemical potential in the soil solution to a low potential in the atmosphere. Chemical potential is derived from the concept of Gibbs free energy. The free energy of a substance is related to temperature and pressure. For example, at a constant temperature, the free energy of an ideal gas would change with pressure from state 1 to state 2 according to:

\[ F_2 - F_1 = nRT \ln \left( \frac{P_2}{P_1} \right) \]  

\[ (4.1) \]
Similarly for ideal solutions,

\[ F_2 - F_1 = nRT \ln \left( \frac{C_2}{C_1} \right) \]  

(4.2)

where:

\( F_i \) = free energy of substance in state \( i \) (J)

\( n \) = number of moles of substance

\( R \) = gas constant (8.314 J mol\(^{-1}\) K\(^{-1}\))

\( T \) = temperature (K)

\( P_i \) = pressure of a substance in state \( i \) (Pa)

\( C_i \) = concentration of a substance in state \( i \) (mol kg\(^{-1}\))

Chemical potential is free energy per mole of a substance. The chemical energy of a solution can be related to the vapor pressure above that solution using a form of Equation 4.1.

\[ (\mu_w - \mu_{w^*}) = RT \ln \left( \frac{\epsilon}{\epsilon_s} \right) \]  

(4.3)

where:

\( \mu_w \) = chemical potential of water in the system (J kg\(^{-1}\))

\( \mu_{w^*} \) = chemical potential of pure water at atmospheric pressure and at the same temperature as the system under consideration (J kg\(^{-1}\))

\( \epsilon \) = vapor pressure of water in the system (Pa)
\( e_s \) = saturation vapor pressure of water at the same temperature (Pa)

Plant physiologists commonly use water potential, with its more convenient and easily understood units of pressure, in place of chemical potential.

\[
\Psi = \frac{\mu_w - \mu_w^*}{\nu_w}
\]  \hspace{1cm} (4.4)

where:

\( \Psi \) = water potential (Pa)

\( \nu_w \) = partial molar volume of water (18 cm\(^3\) mol\(^{-1}\))

Generally, water moves from the soil solution (where \( \Psi \) is near 0) to the leaf (where solute concentration is higher and \( \Psi \) is negative) and finally to the air (where \( \Psi \) is even more negative). Water transported as such ultimately evaporates from the leaf according to the basic laws of mass transfer. Fick’s first law describes basic diffusion for a species j by the equation:

\[
J_j = -D_j \frac{\partial C_j}{\partial x}
\]  \hspace{1cm} (4.5)

where:

\( J_j \) = diffusion flux density (mol m\(^{-2}\) s\(^{-1}\))

\( D_j \) = diffusion coefficient (m\(^2\) s\(^{-1}\))

\( \partial C_j/\partial x \) = concentration gradient of species j in the x direction (mol m\(^{-3}\) m\(^{-1}\))
Integrating Equation 4.5 between locations 1 and 2, and defining resistance as the inverse of conductance (the diffusion coefficient divided by distance), results in:

\[ J_j = \frac{C_{j2} - C_{j1}}{r_j} \]  \hspace{1cm} (4.6)

where:

- \( C_{jk} \) = concentration of species \( j \) at location \( k \) (mol m\(^{-1}\) m\(^{-1}\))
- \( r_j \) = resistance to diffusion of species \( j \) in some medium (s m\(^{-1}\))

Evaporation is commonly expressed as a mass of water evaporated over a unit area and unit of time. The diffusive flux density term in Fick's law can be converted to these units by multiplying by the molecular weight of water (approximately 18 g mol\(^{-1}\)). The concentration gradient applicable to evaporation from the leaf is the difference in humidity between the location of water evaporation in the leaf and the outside air. Thus, Fick's law can be rewritten as

\[ E = \frac{d_{w0} - d_{wz}}{r_v} \]  \hspace{1cm} (4.7)

where:

- \( E \) = evaporation per unit area (kg m\(^{-2}\) s\(^{-1}\))
- \( d_{w0} \) = absolute humidity at leaf liquid/vapor phase transition (kg-vapor m\(^{-1}\)-air)
- \( d_{wz} \) = absolute humidity of surrounding air (kg-vapor m\(^{-1}\)-air)
- \( r_v \) = resistance to vapor diffusion (s m\(^{-1}\))
The evapotranspiration models used for plant canopies expand on this basic equation of vapor diffusion.

4.2.2 Derivation of the combination equation

It is simplest to model transpiration as applied to the basic energy balance of a plant leaf (similar to Equation 2.3).

\[ Q_E = Q_R - Q_H - Q_S \]  (4.8)

where:

\( Q_E \) = latent heat flux density (W m\(^{-2}\)-leaf)

\( Q_R \) = net radiative flux density (W m\(^{-2}\)-leaf)

\( Q_H \) = sensible heat flux density (W m\(^{-2}\)-leaf)

\( Q_S \) = heat storage density (W m\(^{-2}\)-leaf)

This equation basically restates the first law of thermodynamics. The heat which is lost through latent heat flux must offset the portion of the heat gain from net radiation which is not removed by convective sensible heat flux or stored in the canopy.

The latent heat flux is the energy used in evaporation, which can be determined from Equation 4.7.

\[ Q_E = L_v E = L_v \frac{d_{wo} - d_{vz}}{r_v} \]  (4.9)
where:

\[ L_v = \text{latent heat of vaporization (J kg}^{-1}) \]

This can be rewritten in terms of the more common humidity term, vapor pressure. Here, the leaf temperature is assumed to define the temperature at the interface between liquid and vapor within the leaf.

\[ Q_E = L_v \frac{\rho \varepsilon (e(T_{\text{leaf}}) - e(T_a))}{p r_v} \]  \hspace{1cm} (4.10)

where:

\[ \rho = \text{density of air (kg m}^{-3}) \]
\[ \varepsilon = \text{molar conversion from water to dry air ((kg mol}^{-1})_w (kg mol}^{-1})_{\text{dry}} \]
\[ p = \text{total atmospheric pressure (Pa)} \]
\[ e(T_{\text{leaf}}) = \text{saturation vapor pressure at the temperature of the leaf (Pa)} \]
\[ e(T_a) = \text{vapor pressure at the temperature of the air (Pa)} \]

The psychrometric constant is applied to consolidate some of the physical constants. The resistance to vapor diffusion in evapotranspiration can be separated into two distinct functional terms: one mass transfer term which describes the resistance offered by the air and one physiological term which describes the variable resistance offered by the leaf, mainly due to the stomatal opening. This yields the fundamental equation describing leaf evapotranspiration:
\[ Q_E = \frac{C_p \rho \ v_s(T_{leaf}) - \varepsilon(T_a)}{\gamma (r_w + r_s)} \]  

(4.11)

where:

\( \gamma = \) psychrometric constant \( ([C_p \rho / L_v] = 66 \text{ Pa } \text{°C}^{-1} \text{ at } T = 20 \text{ °C}, \rho = 100 \text{ kPa}) \)

\( C_p = \) specific heat of air \( (\text{J kg}^{-1} \text{°C}^{-1}) \)

\( r_w = \) resistance to vapor diffusion in the air around the leaf \( (\text{s m}^{-1}) \)

\( r_s = \) resistance to vapor diffusion due to the leaf, or stomates \( (\text{s m}^{-1}) \)

This equation is difficult to use directly since measurement of the leaf temperature term is problematic. The saturation vapor pressure at leaf temperature can be approximated using a basic relation between saturation vapor pressure deficit and a corresponding temperature difference.

\[ e_s(T_a) - e_s(T_{leaf}) = \delta(T_a - T_{leaf}) \]  

(4.12)

where:

\( \delta = \) slope of curve relating saturation vapor pressure to temperature \( (\text{Pa } \text{°C}^{-1}) \)

The slope of \( \delta \) is generally evaluated at \( T_a \) as a first approximation. This approximation becomes worse as the temperature difference between leaf and air increases, but is generally within 4% accuracy as long as the temperature difference is within 4 to 5 ºC (Fynn et al., 1994 citing Monteith and Unsworth, 1990). A better approach is to solve for \( T_{leaf} \) iteratively (with a known ET), with improving
approximations of $\delta$. Substituting $e_s(T_{leaf})$ from Equation 4.12 into Equation 4.11 results in:

$$Q_E = \frac{C_p \rho [e_s(T_a) - e(T_a)]}{\gamma_r + r_s} - \frac{C_p \rho \delta [T_a - T_{leaf}]}{\gamma_r + r_s}$$  \hspace{1cm} (4.13)

The sensible heat flux from a surface can be derived from Fick's law (Equation 4.5) in a similar manner to the latent heat flux, with temperature as the appropriate driving potential.

$$Q_H = C_p \rho \frac{(T_a - T_{leaf})}{r_H}$$  \hspace{1cm} (4.14)

where:

$r_H$ = resistance to heat diffusion in the air around the leaf (s m$^{-1}$)

This can be used to simplify the second term in Equation 4.13 and remove the problematic leaf temperature term.

$$Q_E = \frac{C_p \rho [e_s(T_a) - e(T_a)]}{\gamma_r + r_s} - \frac{\delta r_H Q_H}{\gamma_r + r_s}$$  \hspace{1cm} (4.15)

The sensible heat flux can be determined using Equation 4.8. Rearranging terms yields:

$$Q_E = \frac{C_p \rho [e_s(T_a) - e(T_a)] + \delta r_H(Q_K - Q_S)}{\gamma \left(1 + \frac{\delta r_H}{\gamma_r + r_s}\right)(r_w + r_s)}$$  \hspace{1cm} (4.16)
The denominator of Equation 4.16 can be simplified using an adjustment factor term

\[ r_f = 1 + \frac{r_z + \delta r_H}{r_w \gamma} \]  \hspace{1cm} (4.17)

where:

\[ r_f = \text{resistance adjustment factor (unitless)} \]

Note that the resistance adjustment factor is always greater than or equal to unity.

Equation 4.17 can be substituted into Equation 4.16 and expressed in evapotranspiration units.

\[ ET = \frac{Q_E}{L_v} = \frac{C_p \rho [e_s(T_a) - e(T_a)] + \delta r_H (Q_R - Q_0)}{L_v \gamma r_w r_f} \]  \hspace{1cm} (4.18)

where:

\[ ET = \text{evapotranspiration (kg m}^2 \text{s}^{-1}) \]

This is a basic form of the combination equation for a single leaf.

4.2.3 Application of the combination equation to a canopy

Equation 4.18 describes the evaporation from a single leaf on a purely physical basis. A plant canopy is comprised of many individual leaves, each having an individual energy balance based upon the mass and energy transfer characteristics unique to that leaf in that environment. This can be described as
The difficulty with using this equation directly is that the leaf internal resistance cannot be evaluated using physical relationships, but must be derived empirically. This is done in practice by measuring all environmental parameters as well as actual evaporation from a plant canopy and using these measurements in Equation 4.18 to derive the stomatal resistance for those particular canopy conditions.

There are several limitations to this approach. Resistance to vapor and heat fluxes in the boundary layer around the canopy are calculated based on approximations of the coefficients of heat and mass transfer in that boundary layer. The stomatal resistance term is dependent upon the accuracy of these assumptions. Any inaccuracies are inherently included in the evaluation of stomatal resistance. The stomatal resistance calculated this way may be used only under conditions of similar canopy structure and heat and mass transfer characteristics, and care must be taken to evaluate the heat and vapor resistance terms using the same methodology.

A multiple layer model would be preferable. This would group together leaves with similar environmental conditions and heat and mass transfer characteristics. Evaporation could then be evaluated for each homogeneous "layer" of leaves. However, a separate stomatal-resistance-type term would be required for each layer of leaves. This would require evaporation to be measured separately for each layer so that the stomatal resistance terms could be empirically derived. This would be difficult since few methods exist to measure evapotranspiration on a canopy unit smaller than a single plant, as will be discussed in Section 5.6.2.
The simplest, and most common, application of Equation 4.18 to the case of an entire canopy is to assume that the canopy acts like a "big leaf." The canopy is approximated using a single leaf with an area equal to the total area of the leaves in the canopy. Total leaf area per unit ground area is described by the term leaf area index (LAI). Equation 4.18 becomes:

\[
ET_{\text{canopy}} = LAI \left( \frac{C_p \rho [\varepsilon(T_\text{a}) - \varepsilon(T_\text{a})] + \delta \tau (Q_\text{H} - Q_\text{S})}{I \gamma r_s r_f} \right) \tag{4.20}
\]

where:

\[
LAI = \text{leaf area index (m}^2 \text{leaves m}^{-2} \text{ground})
\]

One problem with the natural extrapolation of Equation 4.18 to Equation 4.20 is that shortwave and longwave radiation do not strike all leaves in a canopy equally. A term which has been called canopy area index (CAI) can be used as a reduction factor to account for the portion of incident light which strikes the plant canopy (Pang, 1992). Net radiation can be estimated by:

\[
Q_r = \frac{CAI}{LAI} (\alpha_{SW} Q_{SW} + \alpha_{LW} Q_{LW} - \varepsilon_{LW} \sigma T^4_{\text{canopy}}) \tag{4.21}
\]

where:

\[
CAI = \text{canopy area index (m}^2 \text{canopy m}^{-2} \text{ground})
\]

\[
\alpha_{SW} = \text{canopy absorptivity to shortwave radiation (unitless)}
\]

\[
Q_{SW} = \text{incident shortwave radiation (W m}^{-2})
\]

\[
\alpha_{LW} = \text{canopy absorptivity to longwave radiation (unitless)}
\]
\( Q_{l,w} \) = incident longwave radiation (W m\(^2\))

\( \varepsilon_{l,w} \) = canopy longwave emissivity (unitless)

\( \sigma \) = Stefan-Boltzmann constant (5.67 x 10\(^{-8}\) W m\(^{-2}\) K\(^{-1}\))

\( T_{canopy} \) = canopy temperature (K)

Net radiation is divided by LAI to distribute the effect of radiation over the entire "big leaf" canopy area. The assumption made in the process is that the radiation which is absorbed differentially throughout the canopy can be applied uniformly to all layers in the canopy. This assumption only holds true if leaf evapotranspiration increases linearly with increasing radiative heat load. This is a primary limitation in the big leaf combination model. However, this allows canopy surface measurements of shortwave and longwave radiation to be used directly in the model.

4.3 Discussion of the Combination Equation

All the terms in the combination equation are well defined and can be calculated by measurable parameters, except for stomatal resistance. Thus, it has been suggested that the combination equation itself essentially provides a definition of stomatal resistance (Stanghellini, 1987). As such, discussion of the combination equation cannot proceed without a discussion of this term. Because definition of stomatal resistance depends on the boundary defined for external resistance, both will be addressed here.
4.3.1 Resistance to vapor flux

Movement of water between the leaf and the environment is governed by two resistance terms: one internal to the leaf and one external. The internal resistance regulates flow of water from the phase interface of liquid and vapor to the leaf surface, and the external resistance defines the movement of vapor from the leaf surface to the free air outside the leaf boundary layer. The external resistance is determined by the physical leaf surface and air flow characteristics, while the internal resistance is a function of the diffusivity of the leaf cuticle layer and the stomates. Both resistances are discussed in general by Monteith and Unsworth (1990), and in detail by Stanghellini (1987) and Yang (1988) for greenhouse environments.

External resistance can be estimated using standard heat and mass transfer terms for convection from a surface (refer to most any heat and mass transfer text, e.g. Incropera and deWitt, 1985). Convection, a process where heat diffuses into a moving medium, may be either forced convection, in which the movement is caused by some external device, or free convection, in which the movement is caused by buoyancy of the medium itself. In either case, the resistance is defined by the efficiency of the process to remove heat from the surface. It is clear that forced movement of air over a canopy by fans and free movement of air rising from a radiatively heated canopy both contribute to convective flux in a greenhouse or growth chamber environment. Stanghellini (1987) and Yang (1988) provide relations for calculating external resistance which consider both forced and free convection effects. However, both
Stanghellini and Yang studied plants with significantly different canopy structures (tomato and cucumber, respectively) than the floriculture crop used in this study (New Guinea \textit{Impatiens}). While external resistance can be rather clearly defined in relation to the movement of water vapor from a leaf surface to the free air, the extrapolation of external resistance from a leaf surface to a canopy surface may not be entirely straightforward. Canopy structure and leaf orientation dictate the environment applicable for the evaluation of external resistance for a canopy. For instance, leaves with greater surface area have higher resistances than smaller leaves. Orientation of a leaf with respect to the air stream also influences transfer processes. The canopy of New Guinea \textit{Impatiens} closes (the leaves grow closer together) at an early stage. This configuration produces a bi-level structure: a top layer of leaves which are radiatively and convectively active, and a confined, relatively inactive layer beneath which is effectively blocked from either of these exchanges with the outside environment.

Stanghellini (1987) assumed that the canopy acted as a "big leaf," where mean environmental parameters are applied to a theoretical leaf surface with an area equal to twice the LAI (to include both surfaces of the leaf). Yang (1988) approximated the plant stand as a continuum with rectangular cross section and multiple levels using a finite difference model. However, a single stomatal resistance was applied to all levels. Pang (1992) used a single layer big leaf model for New Guinea \textit{Impatiens} and was able to achieve a good correlation between predicted and measured ET ($r^2 = 0.85$); however, the model was never verified on an independent data set (i.e. data collected from an independent experiment). This high correlation is an interesting result.
because the bi-level structure of an *Impatiens* canopy appears to contraindicate use of a big leaf type model, for reasons discussed previously (Section 4.2.3). This may indicate that the precise definition of external resistance is only critical to the extent that it is consistent with the evaluation of internal (or stomatal) resistance. In other words, the only strict requirements for the definition of external resistance are that the canopy configuration must be consistent between model calibration and application conditions, and the sum of external and internal resistances must include all resistances between the phase interface in the leaf and the free air without overlap. Thus, external resistance can be approximated based on a standard set of conditions from heat and mass transfer equations. Then internal resistance, calculated deterministically from a rearranged combination equation, will automatically compensate for the difference between the actual and assumed external resistance. Again, this method derives an internal resistance which is only applicable for specific canopy configuration and a specific method of calculating external resistance.

Internal resistance is a measure of the resistance offered to mass flows between some internal location in the leaf and the leaf surface. Water vapor diffuses out of the leaf while CO₂ diffuses inward. Because stomatal resistance to these mass flows is considerably less than that of the leaf cuticle layer, and because the variable stomatal openings are the established point of control for mass flow into and out of the leaf, the internal leaf location is often assumed to be the stomatal cavity internal surface. This invites the use of the term stomatal resistance to describe the total resistance offered by the leaf. However, the stomatal cavity is generally not maintained at 100% relative
humidity, since that would require the unlikely condition of supersaturated evaporation into a saturated vapor environment, there needs to be a gradient for evaporation to occur. But the stomatal cavity's inadequacy in meeting the definition required for the location of the internal phase interface may be a problem only in theory. The derivation of the combination equation only specifies that there must be a location having saturation humidity which is at leaf temperature (see Equation 4.10), but it does not dictate that it must occur at a precise physical location.

This study was concerned with internal resistance (or stomatal resistance, \( r_s \)) terms which were empirically determined. This method used the combination equation itself to solve for \( r_s \) deterministically from known evaporation, environmental, and external resistance variables. The internal resistances thus defined were clearly species dependent. Care must be exercised in extrapolation of internal resistance terms found empirically, since these terms may include bias from theoretically determined heat and vapor flux resistance terms to the extent that the theory does not match reality.

4.3.2 Effects of radiation and vapor deficit

Evapotranspiration is driven by the leaf vapor pressure deficit (LVPD), the difference in vapor pressure between the leaf and the surrounding air. Water evaporates inside the leaf, moves out of the leaf by diffusion and mass flow, and is removed from the leaf surface by convection. LVPD is increased by increasing the difference between the saturation vapor pressure of the leaf and the vapor pressure of
the free air. Increasing leaf temperature increases the saturation vapor pressure of the leaf, while decreasing the moisture content of the free air decreases the vapor pressure of the free air. For example, the heat load from an increase in incident irradiance causes an increased LVPD by increasing leaf temperature. The heat load is a result of the net total radiation balance (both shortwave and longwave) on the leaf. Note that the decrease in air relative humidity that accompanies an increase in air temperature does not decrease the vapor pressure of the free air (because moisture content remains constant), and thus does not affect LVPD.

Light also may have a physiological influence on evapotranspiration through its direct effects on stomatal aperture, as discussed in Section 2.5.2. Higher light levels (particularly in the blue region) may increase stomatal opening, which would increase vapor conductance with the atmosphere. This affects evapotranspiration predicted by the combination equation through the stomatal resistance term. However, stomatal resistance is also influenced by water status of the leaf, as discussed in Section 2.5.2. Water stress conditions may induce stomatal closure, reducing evaporative losses at the expense of reduced CO₂ influx for supporting photosynthesis.

A purely physical interpretation of a leaf dictates that evaporation from a leaf increases or decreases primarily in response to LVPD. This interpretation was espoused by Mellor et al. (1964), who concluded that leaf temperature and transpiration responses of plant leaves in a growth chamber environment could be explained based on purely physical reactions, without consideration of leaf physiology. Yang (1988) modeled cucumber evapotranspiration in a greenhouse using physical,
energy-based relationships and also found good correlation with measured evaporation. His model included an exponential regression of stomatal resistance with both total shortwave radiation ($r^2 = 0.65$) and PAR ($r^2 = 0.70$). Al-shooshan (1991) found a similar exponential relationship between stomatal resistance and shortwave radiation ($r^2 = 0.81$) for chrysanthemum in a greenhouse with coefficients which were surprisingly similar to Yang’s cucumber crop. Though the predictions of evapotranspiration resulting from use of the combination equation with this stomatal resistance were reasonably close during the day, they were erratic at night. This indicates that stomatal resistance is not exclusively controlled by a light-mediated stomatal response. Light level may be an overwhelming factor in predicting stomatal resistance during high light periods, but other contributing factors may be significant when shortwave radiation level is low.

4.3.4 Effects of soil moisture

Water lost by leaf transpiration must be replaced with water absorbed through the roots. Through this interconnection, deficiencies in root-zone moisture content can influence transpiration rates. Al-Ani and Biernhuizen (1971) found that daily transpiration rates of bean, cucumber, and tomato initially increased slightly as soil moisture decreased, followed by a steady, rapid reduction. Stomatal resistance increased exponentially with decreasing soil moisture. While transpiration began to decline significantly below 70, 80 and 100% soil moisture for tomato, cucumber, and
bean (respectively), leaf moisture content remained essentially unchanged until soil moisture fell below 50%. Thus, the reduction in transpiration response to increasing root-zone water deficit may not be reflected in leaf water content until the point of wilting, when an abrupt reduction in leaf moisture occurs. Abdel-Rahman et al. (1994) found that reductions of soil moisture decreased the vegetative production in tomato. This supports the observation that increasing soil moisture tension can reduce plant photosynthesis (Moss, 1965). Together, these results indicate that even though the plant can maintain an adequate leaf water content with increasing soil moisture deficit, a decrease in transpiration and subsequent decrease in productivity may result.
CHAPTER V

GROWTH CHAMBER AND EXPERIMENTAL MATERIALS:
DESCRIPTION AND CHARACTERIZATION

5.1 Introduction

Plants grow and develop in response to the cumulative effects of their environments over their lifetimes. Variability in environment means variability in plant growth and development. Plant research scientists often require that variability among plants in a study be minimal, and thus require a facility which can minimize environmental variation. Growth chambers have been developed to meet this need. Light, air temperature, water and nutrients were the factors being studied in these experiments, and as such, it was desired to minimize their variability over space and time. This study incorporated a walk-in sized growth chamber, or growth room, to allow the light and air temperature to be closely controlled and uniformly applied to the plant experimental units. In addition, an irrigation system was designed to control water and nutrient application, and maximize the sensitivity of their measurement.
5.2 Growth Chamber Description

The growth chamber used in this study was constructed in-house in the 1960's for use in agronomic crop modeling research (Figures 5.1, 5.2, and 5.3). The chamber internal dimensions were 2.4 x 3.6 x 2.4 m high. There was a 32 mm double acrylic barrier between the lamps and the growing area to reduce the lamp thermal load on the plants. The walls were 1 mm thick sheet steel, painted semi-gloss latex white, enclosing 0.15 m thickness of rigid polystyrene foam insulation. The floor was white vinyl sheet on a wooden plywood frame with a single drain.

The plants were grown on four 1 x 1.2 m ebb-flood benches (Midwest Trading, Model Grow Master) with drip irrigation to individual potted plants. Each bench used a 4.5 L tank with a small centrifugal pump (Little Giant Pump Co., Model NK-1) sealed within. Drip emitters rated at 0.5 L hr\(^{-1}\) supplied each pot with continuous irrigation. Rooted cuttings in a peat/perlite mix were removed from 96-cell packs and transplanted in grade H Haydite (Hydraulic Press Brick Company, Cleveland, Ohio) in 0.1 m diameter pots. Haydite is a combination of shale and clay, fused at high temperatures. Grade H is the horticultural grade with a quoted sieve analysis of: 0% by weight retained by % in. screen (9.5 mm sieve opening), 27.7% retained by No. 4 (4.75 mm sieve opening), 66.7% retained by No. 8 (2.36 mm sieve opening), 1.8% retained by No. 16 (1.1 mm sieve opening), and 3.8% retained by screens less than No. 16. The irrigation water was passed through each pot, captured on the ebb-flood
Figure 5.1 Biosystems Engineering Growth Chamber facility at the Department of Agricultural Engineering, Ohio Agricultural Research and Development Center, Wooster, Ohio. Side view.
Figure 5.2  Biosystems Engineering Growth Chamber. Front view.
Figure 5.3  Biosystems Engineering Growth Chamber. Top view. Approximate relative plant, lamp, and light characterization measurement locations are shown. Plant numbers are shown for reference.
bench, and returned to the pump tank. The total volume of the irrigation system for each bench was 6.5 ±0.2 L.

Eight 400 W high pressure sodium (HPS) and seven 400 W metal halide (MH) lamps were used on a 0.38 x 0.45 m spacing (Figure 5.3). The lamps were mounted above the acrylic barrier. The MH lamps were horizontally mounted 2.72 m from the chamber floor, while the HPS lamps were declined 15° from horizontal at 2.67 m from the floor (distance from center of lamp). A 370 W (0.5 hp), 0.61 m (24 in) diameter axial fan drew air in through two filtered air inlets above the acrylic panels, and across the lamps to remove a portion of the lamp thermal load. Lamp ballasts were mounted on the outside wall of the chamber.

The chamber was capable of ten irradiance levels using eight levels of shading plus full on and full off. Eight pieces of 2.3 x 3.0 m shade cloth were attached along their wide side to form a continuous roll. The shading system was designed to allow a single layer of shade cloth to lay flat on top of the acrylic panels with the remaining cloth in rolls flush against either side wall, so that neither roll interfered with air flow across the lamps (Figure 5.3). Shade cloth was woven black polypropylene fabric (pak unlimited, Inc.) with standard weave densities rated at 30, 47, 55, 63, 73, 80, 85, and 95% shade.

The recirculating air inlet was a slot which extended the entire width of one end wall at a height 0.2 m beneath the acrylic barrier. On the bottom corner of the opposite wall, the air outlet was a 0.5 x 0.5 m located 0.1 m from both the floor and the side wall. The air leaving the chamber passed a cool coil and a hot coil heat
exchanger successively before reentering the chamber in a closed system. The cool coil and hot coil heat exchangers in the recirculating air stream use water chilled and heated (respectively) by a 10.5 kW (3 ton) chilled water refrigeration unit (Model PC-300, Heat-X, Inc., Brewster, NY). Centrifugal fans mounted along the length of both side walls near the acrylic barrier could be turned on to increase air movement and turbulence over the plant canopy.

The growth chamber environment was controlled by a programmable PC-based greenhouse environmental control computer (GEM III, Q-Com, Inc., Santa Ana, CA). Temperature was controlled to a set point by programming the cool coil and hot coil pneumatic control valve settings. Pneumatic control valves were set to change stages as temperature deviated from the set point in 1 °F (0.6 °C) steps. Humidity was controlled secondary to temperature by programming the control valve stages to minimize dehumidification. Lights were turned on and off according to time.

5.3 Growth Chamber Instrumentation

The growth chamber had independent control and instrumentation systems. The instrumentation was based around a programmable datalogger (Kaye, Model Digistrip III). The growth chamber was instrumented to monitor up to 20 thermocouple channels and 15 mV instrument output channels within the chamber, and the CO₂ and anemometer channels which were by necessity located outside the chamber. CO₂ was measured using an infrared CO₂ gas analyzer (Mine Safety
Company, Model 202) with a 6.5 mm I.D. Tygon collection tube placed in the plant canopy. Air humidity was measured using an aspirated, matched set of dry bulb/wet bulb thermocouples (Priva, Inc.) located at canopy level above the air outlet from the chamber, and an infrared dew point hygrometer (EG&G Company, Model 911). The dew point sensor sampled the air in the tygon tubing prior to leaving the chamber on route to the CO₂ gas analyzer. A hot-wire anemometer probe (Thermo-Systems, Inc., Model 1201-60) was used to monitor wind speed at the top of the plant canopy continuously during the study. Current (mA) output from the sensor was converted into a mV signal using an anemometer monitor and power supply (Thermo-Systems, Inc., Model 1051-10). Four PAR quantum sensors (LiCor, Model LI-190) were used to measure light at canopy level and beneath canopy shading. Leaf temperature was measured using 0.013 mm (0.005 in) type T thermocouples (Omega Engineering Company, Model 5TC-TT-T-36-36) inserted into the abaxial leaf vein approximately 1 cm from the base of the leaf. Air, media, and solution temperatures were measured with extension grade type T thermocouples (Thermo Electric Company, Model PP20TX) sealed with shrink tubing.

A scale measuring from 0 to 151 kg with 1 g precision was used as a lysimeter for this study (Sartorius Company, Model F330S). This lysimeter could be used to measure weight changes due to evaporation for a single bench by placing the entire bench and irrigation system on the 0.6 x 0.8 m scale, or it could be used to measure the evaporative losses for all benches in the system by measuring the weight of the
water stock tank used to maintain the other benches at constant volume. Both methods were used during this study at different times (discussed in Section 5.6.2).

The irrigation solution was monitored continuously using in-line electrical conductivity (EC) and pH sensors. Three platinum-band EC sensors with a range of 0 to 10,000 µmhos cm\(^{-1}\) (Omega, Model CDCN-36 meter and CDCN-36-EP sensors) and one temperature-compensated titanium-electrode sensor with a 0 to 2800 µmhos cm\(^{-1}\) range (Signet, Model CDTX-80) were used. The pH was measured using a temperature-compensated double junction electrode (Signet, Model PHTX-80). Spot checks were made periodically using hand held pH (Omega, Model PHH-IX) and EC (Cole Parmer, Pocket-size with 100 to 19,900 µS cm\(^{-1}\) range) sensors.

5.4 Light Characterization

The radiative environment in a growth chamber can be determined by many factors: 1) the total energy of the light source(s), 2) the spectral distribution of the light source(s), 3) the location of the light source(s) with respect to the chamber, barrier(s), and receivers of the light (i.e. plants, light sensors, etc.), 4) the characteristics of the reflective surfaces between the light source(s) and the light receivers, 5) the characteristics of the barrier(s) through which the light passes, and 6) the temperature of the surfaces exposed to the radiation receivers. This environment is not constant with time for any growth chamber, though this is a common assumption. Factors such as degradation of lamp output, discoloration of the barrier and reflective surfaces...
surfaces, variations of the reflective and transmissive characteristics of the plant canopy, and chamber surface temperature can all affect radiative spectral quantity and quality. The interaction of all these factors causes the radiative environment to vary significantly between different growth chambers, spatially within a particular growth chamber, and even temporally between experiments carried out in the same growth chamber. This makes it necessary to characterize the specific conditions which exist over the growing surface during each growth chamber study.

The radiative environment in this study was characterized using four instruments. An Eppley Black and White Radiometer (Model 8-48, Pyranometer) was used to measure shortwave radiation between 285 and 2800 nm. Longwave radiation between 4000 and 50,000 nm was measured using an Eppley Infrared Radiometer (Model PIR, Pyrgeometer). A LiCor Quantum Sensor (Model LI-190) was used to measure photosynthetically active radiation between 400 and 700 nm. Finally, a LiCor Portable Spectroradiometer (Model LI-1800) was used to measure the spectral distribution between 300 and 1100 nm (or 300 and 850 nm) in 2 nm (or 1 nm) increments. Measurements were taken over a 1.0 x 2.0 m symmetrical half of the growth chamber growing surface area on a 0.25 m grid spacing at the beginning and end of the study. Figure 5.3 shows the measurement locations with respect to the chamber and the growing area.

The spatial distribution of several wavelength bands important to plant growth are shown in Figures 5.4 to 5.9. Both the PAR and total shortwave irradiance iso-line plots show a peak in the center of the growing area, and a gradual but symmetrical
Figure 5.4  Spatial distribution of PPFD (400 to 700 nm; μmol m⁻² s⁻¹) at 1.0 m height.

Figure 5.5  Spatial distribution of PPFD (400 to 700 nm; μmol m⁻² s⁻¹) at 1.85 m height.
Figure 5.6  Spatial distribution of shortwave radiation (285 to 2800 nm; W m\(^{-2}\)) at 1.0 m height.

Figure 5.7  Spatial distribution of shortwave radiation (285 to 2800 nm; W m\(^{-2}\)) at 1.85 m height.
Figure 5.8  Spatial distribution of longwave radiation (4000 to 50,000 nm; W m⁻²) at 1.0 m height and 20 °C air temperature.
Figure 5.9  Spatial distribution of longwave radiation (4000 to 50,000 nm; W m⁻²) at 1.85 m height and (a) 30 °C, (b) 25 °C, and (c) 20 °C air temperature.
decrease in irradiance toward the outer edge. The plot of total longwave radiation is less uniform, but still has a relative peak in the center and lower levels toward the edges. Longwave radiation measured by the sensor is a function of the temperature and surface emission characteristics within the sensor's hemispherical field of view. The degree of variation from symmetrical uniformity exhibited by the longwave plot was probably due to fluctuation of chamber temperature during the measurement period; air temperature was roughly 20 ±1 °C. For instance, the total emission from a black body surface at 21 °C is about 21.6 W m⁻² greater than from a surface at 20 °C (using the Stefan-Boltzmann Law, Equation 2.1).

The spectral combination of the HPS and MH lamps is shown in Figures 5.10 and 5.11. These figures show how the spacing of lamps in the chamber ceiling affected the net spectral distribution at the same location for the two canopy heights used in this study. Figures 5.12 to 5.15 show iso-line plots of specific wavelength bands as a proportion of total PPFD. The 436 nm monochromatic waveband is predominately from the MH lamps, while the 596 nm band is largely HPS light (based on figures in Sager et al., 1982). If the light from the two different types of lamps is not well mixed, then the relative proportion of PFD from these two wavebands would vary according to the spatial proximity of the measurement site to the source lamps. These plots show small spatial variations in relative spectral PFD of the two representative wavelengths presented. In addition, the variation that does exist appears to be influenced not only by lamp position in the ceiling, but by proximity to the reflective surfaces of the walls as well (e.g. see Figure 5.15). In general, however,
Figure 5.10  Spectral distribution (1 nm intervals) at 1.0 m height at 5 locations: Y = 2.0 m and X = 1.25, 1.0, 0.75, 0.5, and 0.25 m.
Figure 5.11 Spectral distribution (2 nm intervals) at 1.85 m height at 5 locations. Y = 2.0 m and X = 1.25, 1.0, 0.75, 0.5, and 0.25 m: (a) 300 to 1100 nm, and (b) 400 to 700 nm.
Figure 5.12 Spatial distribution of 436 nm monochromatic radiation as a percentage of PPFD (400 to 700 nm) at 1.0 m height.

Figure 5.13 Spatial distribution of 596 nm monochromatic radiation as a percentage of PPFD (400 to 700 nm) at 1.0 m height.
Figure 5.14  Spatial distribution of 436 nm monochromatic radiation as a percentage of PPFD (400 to 700 nm) at 1.85 m height.

Figure 5.15  Spatial distribution of 596 nm monochromatic radiation as a percentage of PPFD (400 to 700 nm) at 1.85 m height.
these data demonstrated that spectral quality at these two measurement levels was reasonably uniform, and the small deviations that did exist were symmetrical.

The effects of the shade cloth were measured in the center of the growing area. Table 5.1 shows the relative irradiance levels under each level of shading and compares the actual and rated levels of shading offered by each section of shade cloth. This data reveals that the rated shading levels differed by as much as 10% from actual levels. The spectral effects of shading are shown in Figures 5.16 and 5.17. Figure 5.16 shows the actual spectral distributions under each level of shading, and Figure 5.17 shows the spectral distributions expressed as a proportion of the total PFD from 300 to 850 nm. This ratio of spectral PFD to total PFD will be referred to as the S:T.

<table>
<thead>
<tr>
<th>Rated Shade Level (%)</th>
<th>Rated PPFD Level (%)</th>
<th>PPFD Measurement (µmol m⁻² s⁻¹)</th>
<th>Actual PPFD Level (% of max)</th>
<th>Actual vs. Rated Level (%) difference</th>
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Figure 5.16 Spectral distributions with 0, 30, 47, 55, 63, 73, 80, 85, and 95% shading at X = 1.25 m, Y = 2.0 m, and H = 1.0 m.

Figure 5.17 Spectral distributions with 0, 30, 47, 55, 63, 73, 80, 85, and 95% shading expressed as a percentage of total PFD at the measurement location (X = 1.25 m, Y = 2.0 m, and H = 1.0 m).
(spectral to total) ratio. These figures qualitatively demonstrate that shading had little effect on spectral quality. In fact, the variability of the S:T ratio at the different shading levels was too small to be resolved by Figure 5.17. Quantitatively, the small variation in spectral quality evident in Figure 5.17 can be analyzed using a ratio of the standard deviation among the 9 shade cloth S:T ratios at each wavelength to the means of the S:T ratios. If shading had no effect on spectral quality, the S:T ratio would be identical at each shading level; thus, the standard deviation of the S:T ratios among the nine shade levels expressed as a percentage of the mean S:T ratio at each wavelength would be 0%. In actuality, the standard deviation averaged 1.2% of the means over the 400 to 850 nm waveband (mean = 1.20%, sdev = 0.91%, range = 0.18%, 6.21%). (Note: the 300 to 400 nm waveband was omitted because spectral PFDs in this region were extremely small compared to instrument sensitivity, causing disproportionate relative standard deviations -- the same ratio was 0.78% when the 300 to 400 nm waveband was included due to several small negative values.) A 1.2% average and 6.2% maximum relative standard deviation supports the assumption that the shade cloth did not significantly affect spectral quality.

5.5 Air Velocity Characterization

Movement of air over the canopy is needed to remove evaporated water vapor from the leaf boundary layer, replenish depleted CO₂, convectively cool leaves, and generally promote healthy growth. This growth chamber provided air movement
horizontally over the plant canopy. The continuous slot air inlet opening was tapered (from 25 mm to 2 mm) to provide maximal uniformity of air velocity across the 2.2 m width of the chamber. An air velocity profile of the growth chamber was made using a portable uni-directional sensor (TSI, Model 1650). Air velocity was measured parallel to the general direction of flow to attain a maximum reading. Figure 5.18 shows the distribution found during the experiment discussed in Chapter 8. ASHRAE (1977) recommend that air speeds be maintained between 0.1 and 0.25 m s$^{-1}$ for optimal growth, and above 0.05 m s$^{-1}$ and below 2.2 m s$^{-1}$ to avoid inhibited growth in plant growth facilities. Figure 5.18 shows that average air velocity was between 0.1 and 1.4 m s$^{-1}$, well within an acceptable range for crop production. Air velocity was measured continually during each experiment at $X = 0.7$ m, $Y = 2.0$ m, and 2.0 m height.

Figure 5.18 Spatial distribution of air velocity (m s$^{-1}$) at 2.15 m height (55 cm above bench surface).
5.6 Fertigation System Description

Plants do not absorb nutrient solution like people drink water. When people drink, they swallow the water along with the dissolved minerals, carbohydrates, salts, dirt, and every other suspended substance. The plant uptake system is more discriminating, as was discussed in Chapter 3. Even if the environmental conditions induce the plant to absorb water (by the relations discussed in Chapter 4), the plant may not absorb all the dissolved substances that are supplied with the water (as discussed in Chapter 3). Assuming plants absorb water and nutrients selectively, by different pathways, and according to different demand schedules, then the irrigation system that supplies the water and nutrient fertilizer to the plants (the fertigation system) should be designed to meet these separate demands. In commercial applications, the fertigation system must also maximize the efficiency of plant growth and the cost effectiveness of the crop production system by allowing optimal timing to meet the plant demands (as they occur) with minimal waste. This section will discuss the interactions among the independent system constraints: nutrient demands, water demands, the physical fertigation system, and management strategies.

5.6.1 Separation of water and nutrients

It is important to conceptually separate the water and nutrient components of an irrigation system even though they are functionally integral. Though water and
nutrients are applied to the plant in a single irrigation solution, plants absorb water and nutrients by different pathways. The physical system dictates the use of concentration units to express the quantity of nutrients in solution. Parts per million (ppm), mg L⁻¹, and mol L⁻¹ (i.e. molar concentration or M, where M x molecular weight = g L⁻¹), all can be used to express the amount of an individual nutrient per unit solution volume. (Though this is not exactly true for ppm, which is a mass ratio, ppm are generally assumed to be equivalent to mg L⁻¹ with the assumption that water density is exactly 1000 g L⁻¹.) This study will generally use mg L⁻¹, because these units are readily understood by researchers and growers, and can be easily translated to elemental mass values.

Demand theory suggests that elemental mass values are the principle concern in nutrient uptake studies, while supply theory suggests that the driving consideration in nutrient uptake is the concentration of nutrients in solution. This study will separate water and nutrient uptake measurement in order to clarify the relative importance of demand and supply in plant nutrient uptake responses. The following sub-sections will outline the methods used for these measurements.

5.6.2 Water uptake measurement

The lysimeter method is perhaps the most conceptually direct method of the many methods available for measuring transpiration. An entire plant system, including soil, is placed on a scale. Changes in weight of the system are due to water being
added (+), plant growth (+), or evaporation (-). This method is easily applied to a greenhouse since plants are grown in containers which can be located on a scale without disturbing their growth. This study applied several adaptations of the lysimeter method.

**Volume Method.** The first application (used in Chapter 7) was based on the lysimeter method, but measured a change in volume rather than a change in weight. The irrigation system for each bench was in a closed loop with continuous drip irrigation to each pot (Figure 5.19). The irrigation solution was pumped from the pump tank to the pots, dripped onto the gravel, captured on an ebb-flood bench after passing through the gravel (and over the roots), returned to a 250 mL graduated cylinder attached to the pump tank, and finally passed through an EC sensor before returning to the pump tank. The 6.5 L volume of solution completed this cycle about every 15 minutes. The flow of solution into the graduated cylinder was adjusted to provide a steady rate of return. This assured minimal fluctuation (±2 mL) of the system volume as measured by the free surface of the solution in the graduated cylinder. The change of volume indicated by the graduated cylinder was essentially a direct measure of the change in volume of the entire system. This system required manual replacement of the water lost through water uptake. A measured amount of distilled/deionized water was added directly to the graduated cylinder as needed to replenish the system volume.
Figure 5.19  Schematic of water uptake measurement system using the Volume Method: discrete manual replacements of system volume depletion and measurement of uptake by volume differential.
System Weight Method. The second application (used on one peat-media bench in Chapter 7) placed the entire bench, its plants, the water supply and pump, and instrumentation on a scale (Figure 5.20). The inclusion of the water supply on the scale simplified the measurement of transpiration. If evaporation from bench and pot surfaces is minimized, then the only way for the system to lose weight would be through evaporation from leaves (i.e. transpiration), and the only way for the system to gain weight would be through CO₂ assimilation, or plant growth, which is negligible compared to evaporation. The scale measured up to 150 kg ±1 g on a 0.6 x 0.8 m base (see Section 5.3). A slightly different configuration was used in the return line to the pump tank to accommodate a different configuration EC sensor. A Water Level Apparatus was designed to maintain a constant irrigation system volume. A section of Tygon tubing was connected to the pump tank and oriented to extend arbitrarily several cm above the tank. Two hypodermic needles were inserted into the tubing above the tank and connected to a conductivity control board. When the resistance between the two needles exceeded 10,000 ohms (equivalent to 10 μmhos conductivity), the control board activated (opened) a solenoid valve which allowed water into the pump tank. Thus, when the water level fell below the level of the higher needle, the resistance between the two needles increased, causing the solenoid valve to open to refill the pump tank until the contact between needles was made once again. The water stock-tank fed the solenoid valve by gravity at a low head (< 1 m). Water level was maintained within ±1 mL variation.
Figure 5.20 Schematic of evapotranspiration measurement system using the System Weight Method: continuous automatic replacement of system volume depletion and measurement of evapotranspiration by lysimeter.
Stock-tank Weight Method. A third lysimeter application (used in Chapter 8) measured the weight change of a water stock-tank which replenished the water lost by water uptake from the benches which the tank supplied (Figure 5.21). Essentially, the water stock-tank was used to maintain a constant volume of each bench's continuously recirculating irrigation solution supply. The Water Level Apparatus described in the previous paragraph was use to refill each of the pump tanks separately from the single stock-tank.

The measurements made by each of the lysimeter methods described above fall into two categories: the first and third measured water uptake while the second method measured evapotranspiration. This distinction is critical. The Volume Method and the Stock-tank Weight Method both maintained a constant irrigation system volume by replacing lost water. The system boundary was defined by the irrigation solution. Water exited the system when it was absorbed by the plant roots. Water from the tank on the lysimeter, for example, was used to maintain the system volume at a constant level. Thus, the lysimeter measured water uptake by the plant. The System Weight Method placed the entire irrigation system, bench, and plants on the lysimeter. This system had a different boundary defined by the physical apparatus on the scale. Water left the system when it moved from the plant leaves to the atmosphere. Thus, the System Weight Method measured evapotranspiration. Water uptake rate and evapotranspiration rate are the same only during periods of constant plant water potential, a realistic condition when the plants can maintain full turgor.
Figure 5.21  Schematic of water uptake measurement system using the Stock-tank Weight Method: automatic replenishment of system volume depletion and measurement of uptake by lysimeter.
The stem-flow method offers another approach for transpiration measurement. Stem flow can be measured using several methods. Huber (1932) described a method by which a pulse of heat was applied to a discrete point on a stem, and xylem flow velocity was measured by the time required for the heat pulse to reach a downstream sensor. Flow rate (transpiration) was then calculated from velocity. More recently, Baker and van Bavel (1987) described a stem-flow gauge which was based on a heat balance approach. A constant heat flux was applied to the stem and a series of sensors measured the temperature gradient with distance away from the heater. This was used to calculate heat fluxes and ultimately the mass flow rate necessary to achieve those fluxes. The instrument used for this measurement was wrapped around the stem relatively unobtrusively and provided real-time transpiration monitoring. The stem-flow method was not used in this study, but will be referred to in discussion as appropriate at a later point in this dissertation.

5.6.3 Nutrient uptake measurement

Two methods were used to measure nutrient uptake. Both sampled the nutrient solution and assumed that any changes in nutrient content of the solution was due to net uptake by the plant. The Water Level Apparatus assured that concentration of nutrients in solution did not change because of evaporative water losses (assuming that pure water was evaporated), and the inert gravel media had negligible storage capacity.
and had a negligible contribution by leachate. By contrast, peat-based media contribute significantly to solution ion content, as discussed in Chapter 7.

**EC Method.** The first method used in-line EC sensors as a continuous measure of the total ionic strength of the nutrient solution, and thus the total nutrient content. The continuous flow of nutrient solution provided a constant supply of nutrients to the roots and constantly flushed nutrient-depleted solution out of the root zone and past the EC sensor. Pure water is an insulator, but ions in a water solution conduct electricity, higher ion concentrations cause higher solution conductivity. Changes in the conductivity of a solution indicate changes in the total nutrient content of the solution. Sutherland (1988) indicated that EC is a biased indicator of total nutrients in solution, citing Alt (1980) who found EC to be more correlated with K than N concentration. Nonetheless, EC remains the greenhouse industry standard method for measuring nutrient solution strength.

A 10 cm diameter pot filled with 420 g of Haydite H held about 40 mL of water at field capacity. This volume was included in the 6.5 L total system volume, but was not fully replenished with each full cycle of solution. This means that although the gravel provided a beneficial reduction in total system volume compared to other nutrient solution culture techniques, it also contributed a confounding lag to the time between actual plant uptake (in the root zone throughout the gravel) and measured uptake response (by the EC sensor at the pump tank). This effect will be discussed in more detail in Chapter 7.
**Individual Ion Method.** The second method measured specific individual nutrient uptake over a discrete period of time. Each pump tank was fitted with a septum disc through which a hypodermic needle could be used to sample the solution with minimal disturbance to the system. A 10 mL vacuum tube blood collection system (Vacutainer, Model B-D 6430) was used to collect solution samples. Two 10 mL samples could be taken from each of four pump tanks within a 30 s period using this system. The pump tank was assumed to be well mixed and representative of the current nutrient status of the system at any given time. Samples were taken from the nutrient solution at times representative of the beginning and end of a period of constant environmental conditions. The time response of nutrient uptake to changes in the environment must be considered to assure that the selected sampling period represented the period of environmental conditions being studied (as discussed in Chapter 7).

Samples were analyzed for individual nutrient concentrations. Two methods were used: 1) a compact individual ion electrode measured NO$_3^-$-N, and 2) inductively coupled plasma spectrophotometry measured P, K, Ca, Mg, Na, Fe, Mn, Zn, Cu, and B.

The compact individual ion electrode sensor (Horiba, Model Cardy NO$_3^-$), called a Cardy meter, measured NO$_3^-$-N. The Cardy meter measured specific ion concentrations in a small sample of solution (approximately 0.5 mL) placed on the sensor cell. The meter had 2-digit precision, and thus resolution was ±1 mg L$^{-1}$ (0 to 99 mg L$^{-1}$), ±10 (100 to 990 mg L$^{-1}$), and ±100 (1000 to 9,900 mg L$^{-1}$, full scale).
Although the quoted repeatability is ±20% of indication value, periodic calibrations with Research-Extension Analytical Laboratory (REAL) \( \text{NO}_3^- \cdot \text{N} \) evaluations (see below) were generally within 10%. Samples in this study greater than 100 mg L\(^{-1}\) were diluted with distilled/deionized water in accurate ratios (deviations less than ±1% by volume) of 1:1 (100 to 190 mg L\(^{-1}\)) or 2:1 (200 to 290 mg L\(^{-1}\)) in order to bring the measured concentration into the more sensitive 0 to 100 mg L\(^{-1}\) range. The resultant precision of ±2 or ±3 mg L\(^{-1}\) for the 1:1 and 2:1 dilutions, respectively, were improvements over the ±10 mg L\(^{-1}\) which would have been the case otherwise. The sensor was calibrated each day before measurements were taken as well as during the measurement period following each group of 8 measurements. Standard solutions of 500 and 20 mg L\(^{-1}\) \( \text{NO}_3^- \cdot \text{N} \) (in the form of NaNO\(_3\)) were used. The sensor was rinsed with distilled/deionized water following each measurement, which also provided a running check against a 0 mg L\(^{-1}\) \( \text{NO}_3^- \cdot \text{N} \) sample. At least 2 measurements were made of each nutrient solution sample. Nutrient solution samples were measured in groups of 8 during each measurement session, measuring from sample #1 to #8, then in reverse order from #8 back to #1. If successive measurements of the same sample were different by > 2 mg L\(^{-1}\), then 2 or more additional measurements were taken of that sample. Final data points were averaged over all measurements for each sample. It was found that the Cardy sensor should be used for no more than 8 successive samples. After 8 samples, or if instrument drift exceeded 4 ppm or the distilled/deionized water reading exceeded 1 mg L\(^{-1}\), the instrument was allowed to "rest" for at least 1 hr before continuing.
An analytical lab located on the Wooster campus (REAL) was used to analyze the solution samples for P, K, Ca, Mg, Na, Fe, Mn, Zn, Cu, and B. REAL analyzes nutrient solution samples by inductively coupled plasma spectrophotometry, where the cumulative spectral energy emitted from a heated solution sample was used to determine elemental concentrations in that sample.
CHAPTER VI
NEW GUINEA IMPATIENS CHARACTERIZATION

6.1 Introduction

One goal of this dissertation was to understand plant demand to determine if there is justification for relating nutrient uptake to demand. In Chapter 3 it was proposed that photosynthesis drives plant demand for nutrients. This chapter evaluates photosynthesis over the range of conditions surveyed in Chapters 7 and 8. In particular, a photosynthetic response curve is determined for the light and temperatures studied in the Chapter 8 factorial experiment. In addition to growth chamber conditions, photosynthetic response was evaluated under natural light greenhouse conditions to aid in interpreting comparisons of nutrient demand and uptake under artificial and natural light.

Nutrients or water are often limiting in the natural environment (Bloom et al., 1985). The ability to cope with the periodicity of nutrient or water availability may be a critical evolutionary adaptation for plant survival in nature. By contrast, an artificial condition can be established in agricultural and horticultural production systems where water and nutrients are managed to meet plant demands. In the greenhouse,
environment also can be managed to assure that the range of a plant's ability to cope with varied environments, its phenotypic plasticity, is not exceeded. Greenhouse growers must understand the inherent physiological characteristics of the plant which it has inherited in order to allow maximal productivity within the attainable range of greenhouse environments. For instance, plants must expend energy to store nutrients for later use (Chapin et al., 1990). This adaptation may not be necessary in the greenhouse, and may waste energy otherwise available for productive growth. In theory, energy utilization, and thus growth efficiency, may be improved if plants do not have to store nutrients, but rather absorb nutrients only as needed. A major assumption underlying the model presented in this dissertation relating plant nutrient demand to nutrient uptake is that there is either no storage or a constant level of storage in plant tissues. This would allow uptake to be directly related to demand at all times.

New Guinea Impatiens (Impatiens hawkeri) are indigenous to the Australian New Guinea subtropical highlands (Erwin et al., 1992). Impatiens spp. are annual or perennial succulent herbaceous plants with green stems. The Impatiens from New Guinea are adapted to full sunlight or partial shade, and inhabit moist mountainous and submontane forest climates. They typically grow in the damp margins of streams or runoff ditches, or amongst moist rocks (Quene and Strefeler, 1992). The variety used in these studies ('Equinox') have a dark green adaxial leaf surface and purple abaxial surface, which may serve to maximize the leaf's absorption of incident PAR, particularly in the blue region (Lee and Lowry, 1975). The purple lower surface
reflects light back through the leaf for increased light gathering effectiveness. This author found PAR transmittance for a single leaf layer to be less than 5%. These characteristics have led to New Guinea Impatiens' classification as a "low light" crop. Erwin et al. (1992) recommend a maximum PPFD of 500 to 600 μmol m⁻² s⁻¹. Pang (1992) found New Guinea Impatiens to have a limited transpirational capacity. He found stomatal resistance reached a minimum at 200 W m⁻², and possibly increased above 600 W m⁻² in a stress response. Fynn and Pang (unpublished) found a step change in light to 750 W m⁻² at 35 °C caused New Guinea Impatiens to wilt within 15 min, even though the root zone was well irrigated.

6.2 Experimental Description

Plants from the experiment described in Chapter 8 were used for this study. Data for the photosynthetic response curve at 30 °C in the growth chamber were taken on 26 August 1993, while response curves at 20 and 25 °C were determined from data taken on 2 October 1993. The actual air temperatures used in subsequent analyses were measured by the air entering the leaf chamber unit. Average actual temperatures for 20, 25 and 30 °C treatments were 20.2, 24.2 and 28.7 ±1 °C. Plants near the center of the chamber, in the zone of highest irradiance, were used in the same position in which they were grown during the factorial experiment of Chapter 8. Lighting in the growth chamber was a combination of high pressure sodium (HPS) and metal halide (MH) high intensity discharge (HID) lamps, as discussed in Chapter 5.
Different light levels were provided by the growth chamber shade cloth system described in Section 5.2.

The greenhouse response curve study was carried out on 2 October 1993. This study used plants from the same growth chamber bench zones as used in the above study. One plant from each bench was relocated to the south-facing select-a-shade experimental greenhouse (described by He et al., 1991). This greenhouse roof used the same double acrylic panels as the growth chamber. No polystyrene pellet shading was used in the acrylic panels. Different light levels were provided by 20 cm square panels of the same black polypropylene fabric used in the growth chamber shading system (6 levels: 100% (no shade cloth), 70% (30% shade cloth), 53% (47% shade cloth), 37% (63% shade cloth), 27% (73% shade cloth), and 15% (85% shade cloth)). A single shade cloth panel was placed directly on top of the leaf chamber analyzer (described below) during each set of readings. Readings were taken on each of the four plants at each light level from 100% to 15%. A new set of four plants was relocated from the growth chamber, one from each bench, and a second set of readings was taken from 15% to 100%. One data point was taken from each of eight different plants at each light level. Plant media was well irrigated during the tests. Average actual temperature of the air in the leaf chamber was 28.5 ±1 °C for all readings.

A portable leaf chamber analyzer (ADC, Model LCA-2) was used for the leaf photosynthesis and transpiration measurements. This unit passed air continuously through a small assimilation chamber which contained a portion of a leaf. The leaf removed CO₂ from the air stream and added water vapor. A measurement was taken
when the system reached steady-state between rates of photosynthesis, transpiration, and air flow. Air flow rate through the chamber was maintained at 300 mL min⁻¹. The sample leaf area was 6.25 cm² as determined by the configuration of the unit.

The quantum sensor on the ADC unit was calibrated against one of the LiCor quantum sensors used to monitor light levels in the growth chamber studies. PPFD readings were adjusted by the calibration factor and plotted against net CO₂ assimilation rate, \( P_n \), to determine the photosynthetic response. Michaelis-Menten parameters for describing a rectangular hyperbola were determined using the Eadie-Hofstee transformation, where \( V_{max} \) is the y-intercept and \( K_m \) is the negative of the slope of \( P_n \) plotted against \( P_n/PAR \). The CO₂ depletion data from the ADC unit was converted into CO₂ assimilation units using the standard formula (Field et al., 1989):

\[
P_n = \frac{u_c c_e - u_f c_f}{A_{leaf}}
\]  

(6.1)

For simplicity, total molar flow rates entering and leaving the leaf chamber were assumed to be equal (i.e. \( u_e - u_f \)). The rate of transpiration can be calculated from the rate of accumulation of vapor in the air stream according to the formula (with adjustment for the addition of water vapor from the leaf, Pearcy et al., 1989)

\[
E_{leaf} = \frac{u_f w_f - u_e w_e}{A_{leaf}} = \frac{u_e \left( \frac{1 - w_e}{1 - w_f} \right) w_f - u_e w_e}{A_{leaf}} = \frac{u_e (w_f - w_e)}{A_{leaf} (1 - w_f)}
\]

(6.2)
where:

\[ P_a = \text{net CO}_2 \text{ depletion by leaf photosynthesis (mol m}^{-2} \text{ s}^{-1}) \]

\[ E_{\text{leaf}} = \text{water vapor addition by leaf evaporation (mol m}^{-2} \text{ s}^{-1}) \]

\[ u_e = \text{total molar flow rate entering the leaf chamber (mol s}^{-1}) \]

\[ u_f = \text{total molar flow rate leaving the leaf chamber (mol s}^{-1}) \]

\[ c_e = \text{CO}_2 \text{ concentration entering the leaf chamber (mol mol}_{\text{air}}^{-1}) \]

\[ c_f = \text{CO}_2 \text{ concentration leaving the leaf chamber (mol mol}_{\text{air}}^{-1}) \]

\[ w_e = \text{mole fraction of water vapor entering the leaf chamber (mol mol}_{\text{air}}^{-1}) \]

\[ w_f = \text{mole fraction of water vapor leaving the leaf chamber (mol mol}_{\text{air}}^{-1}) \]

\[ A_{\text{leaf}} = \text{leaf area (m}^2) \]

The size of the chamber dictated that only fully expanded New Guinea *Impatiens* leaves could be used, since only the largest leaves completely filled the chamber area. Leaves which were exposed to light (sun leaves) were preferentially selected, since they represent the most active leaves for photosynthesis and thus the most pertinent for plant nutrient demand, according to the model presented in Chapter 3.

Leaf evapotranspiration values can be used to calculate a leaf conductance, the inverse of resistance discussed in Chapter 3. Some prefer to use conductance since it is proportional to transpiration flux rather than inversely proportional. Pearcy et al. (1989) derived an equation based on Fick's law which includes both leaf internal and leaf boundary effects on transpiration (Equation 6.3).
This equation includes the transpiration caused by both diffusion and mass flow through the stomatal pore. The mass flow correction is considered to be on the order of 2 to 3.5%. The leaf intercellular spaces are assumed to be at saturation humidity, which is said to be a good assumption for well-watered plants (Pearcy et al., 1989). They state that even with a leaf at a water potential of -2 MPa (i.e. turgor pressure near 0 MPa: wilting condition) and a leaf temperature of 25 °C, relative humidity approaches 98.5% in the intercellular spaces.

### 6.3 Photosynthetic Response

Photosynthetic rate of New Guinea *Impatiens* in the growth chamber (GC) increased significantly with PPFD, but was not significantly related to temperature (Figure 6.1). Idso and Baker (1967) and Chmora and Oya (1967) studied the effect of temperature on photosynthetic rate. They showed photosynthetic rate increased with temperature up to a peak between 35 and 45 °C. Data from this study did not provide
Fig. 6.1 Mean ±1 standard deviation of photosynthetic response (Pn) to light level (PPFD) at 3 temperatures in the growth chamber (20.2, 24.2, 28.7 °C), and 1 similar temperature in the greenhouse (28.5 °C).

statistically significant support for this reported trend in photosynthetic rate, though within the overlapping confidence bands the lower temperatures generally showed lower photosynthetic rates than the higher temperatures.

Also included on Fig. 6.1 is the photosynthetic response curve found under natural light greenhouse (GH) conditions. The mean GH response curve at 28.5 °C was slightly higher than would have been predicted by the GC curves, though this difference was insignificant. This may indicate a higher photosynthetic rate under natural light conditions for the same temperature.
Higher rates of photosynthesis under solar light relative to HID light was contrary to the relationship suggested by Pearcy (1989) using normalized values adapted from McCree (1972b). He showed that for an equal value of PPFD the spectral characteristics of HPS light effectively allow it to induce 6% greater photosynthetic rates than sun and sky light. MH light is effectively the same as natural light by this measure, because its ratio of actual photosynthetic rate to measured PPFD is the same as that for sun and sky light. Sager et al. (1982) demonstrated that HPS and MH sources have 39 and 22% higher APFD, and 34 and 25% higher YPFD than solar light, also contrary to the results of this study.

However, the radiant transmissivity of the acrylic roof panels must be considered. The same type of panel was between the light source and plants in both the GC and GH (described in Sections 5.2). A single sheet of acrylic has 93% transmission in the PAR waveband (400 to 700 nm), about 92% in the near IR band (700 to 2700 nm), and only 5% in the thermal band (> 2700 nm) (Aldrich and Bartok, 1986). This results in an effective transmission of 85% for solar radiation, 60% for HPS, and 45% for MH (using spectral distributions from Thimijan and Heins, 1983). The general distribution of PAR relative to IR radiation is not significantly changed for solar light, since its output is almost entirely within the range having 92 to 93% transmission. However, the HPS and MH light becomes a much more "pure" source of PAR after passing through acrylic, since only 5% of their thermal IR radiation is transmitted. The ratio of PAR to total radiation after acrylic filtering becomes 47% for solar light, 57% for HPS, and 71% for MH. Thus, the artificial lights should have
a lower heat load for the same photosynthetic response since a lower portion of their
energy is outside the PAR waveband. Similarly, solar light would have a higher heat
load, which would potentially cause larger stomatal openings for the same PPFD if
stomatal response is primarily a function of heat load rather than PPFD. Larger
stomatal openings would increase both evaporative cooling and CO₂ exchange rates,
which would explain the higher photosynthetic rates measured in the greenhouse.

6.4 Transpiration Response

Transpiration rate of New Guinea *Impatiens* in the GC was found to increase
with temperature, but did not show a significant response to PPFD (Figure 6.2). The
combination equation, discussed in Chapter 4, predicts an increase in transpiration with
both air temperature (through its effects on leaf temperature) and radiation level.
However, within the range of data in this study, radiation level as measured by PPFD
was not significantly related to transpiration. Also included on this figure is the
transpiration response curve found under natural light GH conditions. Transpiration
under GH conditions was slightly higher than that at a similar temperature under GC
conditions, though like with photosynthetic rate, this difference was insignificant. Any
increase could be explained by increased stomatal response to the higher heat load
relative to PPFD under the GH conditions in this study.
6.5 Leaf Resistance

The total resistance to evaporation from the leaf can be calculated by the inverse of Equation 6.3. Total resistance was plotted against two principle variables in the combination equation, $Q_R$ and VPD (Figure 6.3). Because these data were at a constant temperature (constant longwave radiation balance) and because data were recorded in PPFD, PPFD was an acceptable substitute for $Q_R$. Resistance generally decreased as radiation level increased, though this response was not significant. However, Figure 6.4 shows that resistance showed a more consistent increase with VPD.
Figure 6.3 Response of total leaf resistance ($r_{\text{total}}$) to radiation level, as measured by PPFD at 24.2 °C in the growth chamber.

Figure 6.4 Response of total leaf resistance ($r_{\text{total}}$) to vapor pressure deficit (VPD) at 24.2 °C in the growth chamber.
6.6 Discussion

Based on these data, New Guinea *Impatiens* leaves apparently have counter­acting responses to the two driving forces for transpiration: total radiation and VPD. From these relationships, it is not clear how the leaf would respond to changes in the ultimate evapotranspiration (ET) driving force: leaf vapor pressure deficit (LVPD). An increase in LVPD accompanies an increase in total radiation and would cause a predicted increase in ET, but increasing LVPD also accompanies an increase in VPD which would lead to a predicted decrease in ET.

The data did not clearly support or refute a single mode of stomatal control for both transpiration and photosynthesis. Photosynthesis increased with PPFD while transpiration generally increased with temperature. In addition, the shapes of their response curves were different and did not suggest a clear relationship between their responses. Further study would be necessary to determine if photosynthesis and transpiration are affected by the differences in spectral quality (in relation to overall radiation load) found within greenhouse and growth chamber environments.

The rectangular hyperbola relationship between PPFD and CO₂ assimilation was consistent with the general saturation model of photosynthesis. This supported the use of a Michaelis-Menten relationship between PPFD and plant growth, and ultimately nutrient demand as discussed in Chapter 3.
CHAPTER VII

NUTRIENT UPTAKE TIME RESPONSE CHARACTERISTICS

7.1 Introduction

Nutrient uptake is proposed in this dissertation to be related to the level of nutrient demand. A primary factor influencing nutrient demand is photosynthetic photon flux density (PPFD). Should a relationship exist between uptake and PPFD, two fundamental questions must be answered: 1) what is the magnitude of the response, or what is the steady-state rate of nutrient uptake induced by a particular PPFD; and 2) how fast does nutrient uptake respond to a change in PPFD, or how quickly does nutrient uptake reach its new steady-state rate after light is changed to a new level. From a researcher's standpoint, the second question must be answered before the first. This is because the magnitude of the nutrient uptake response must be measured during a steady-state condition, and only after addressing question 2 will it be known when that steady-state is reached. The following experiment was designed to evaluate the time response characteristics of nutrient uptake to changes in light level.
7.2 Experimental Design

The growth chamber described in Chapter 5 was used for this study. Four 1 x 1.2 m ebb-flood benches were arranged in the growth chamber to receive symmetrical lighting. For this experiment, the benches were sloped from 0.85 m high at the center-line of the chamber to 0.88 m at the edges. This resulted in bench level being 1.87 to 1.84 m beneath the center of the MH lamps. Thirty-six New Guinea Impatiens (Impatiens hawkeri) 'Equinox' were grown on each bench (Figure 5.3). Plants were received as rooted cuttings in 96-cell seedling trays on 27 January 1993 (courtesy of Mikkelsens Inc., Ashtabula, Ohio). Cuttings were transplanted with a portion of the peat/perlite seedling mix into 10 cm pots filled with either peat/rock wool, peat/perlite, or Haydite media (described below). Plants were grown for 36 days in a double poly greenhouse at 24/18 °C day/night set points with drip irrigation for the plants grown in Haydite and ebb-flood irrigation for the plants in peat-based media. Final relocation to the growth chamber occurred on 5 March 1993.

A hydroponic growing system was specifically designed for use in this study. The system was designed to provide for suitable plant growth while minimizing the system volume per plant. One type of media was selected based on the work of Laurie and Kiplinger (1940) who found that an inert gravel media, Haydite, supported excellent plant growth and had minimal impact on solution nutrient content and pH. Haydite H was an improvement over the coarser construction grade Haydite used by Laurie and Kiplinger, since finer gravel produced a more uniform distribution of roots
throughout the media. The use of Haydite in 10 cm (4 in) pots minimized the volume needed to keep the plant roots continuously bathed in the nutrient solution. Two benches used Haydite media and two benches used peat-moss-based mixtures, one with 50% rock wool (Pargro division of Partek Inc., Peatwool medium grade) and the other with 33% perlite (Custom mix from Justin Moratta, proprietor of Possum Run Greenhouses, Belleville, Ohio). Each bench had a separate, individual irrigation system (discussed in Section 5.2). Each pot was irrigated with a single drip emitter rated at 50 mL min⁻¹ capacity; however, due to the low pump pressure, actual flow rate averaged about 20 mL min⁻¹. A balanced nutrient recipe was used: 8.5 g (NH₄)₂PO₄, 23.4 g KNO₃, 26.0 g Ca(NO₃)₂, and 30 mL 85% H₃PO₄ in 114 L tap H₂O (8.4 pH, 700 µmhos cm⁻¹ EC, 3 mg L⁻¹ NO₃-N, 0.4 mg L⁻¹ P, 1.8 mg L⁻¹ K, 96 mg L⁻¹ Ca, 35 mg L⁻¹ Mg) yielding total elemental concentrations of 79 mg L⁻¹ N (20% as NH₄), 39 mg L⁻¹ P, 82 mg L⁻¹ K, 142 mg L⁻¹ Ca, and 35 mg L⁻¹ Mg.

Air temperature was maintained at 24 °C day and 19 °C night. Three light levels were used: 100% (no shade cloth), 37% (63% shade cloth), and 0% (lights off). Light level was changed abruptly between levels in various sequences and the effect on nutrient solution electrical conductivity (EC) was monitored. The period between light level changes was no less than 3 hours, based on preliminary data that showed that the rate of change in EC seemed to equilibrate within the first hour, leaving a substantial period for the new rate to be established.

The instrumentation discussed in Section 5.3 was used to monitor the environment continually and log data on either 10 or 1 minute intervals during the
experimental periods. EC was measured in the line returning from the bench before reentering the pump tank. Bench I (with peat media) was instrumented with the lysimeter and the in-line pH sensor. Environmental parameters measured continually during experimental periods were: air temperature (dry bulb and wet bulb), dew point temperature, solution temperature, media temperature, wind speed, and canopy CO₂.

Each bench was covered with black plastic to reduce evaporation from surfaces other than the plant shoots. The plastic sheet covered the gravel media surface as well, and allowed plant shoots to extend through slots cut in the plastic at each pot location. Water lost through evaporation was measured by a decrease in level of the 250 mL graduated cylinder free water surface using the Volume Method discussed in Section 5.6.2. The water level was replenished with distilled/deionized H₂O in increments of up to 250 mL at one time. Typical daytime transpiration rates for this crop under the conditions of this experiment were about 250 mL hr⁻¹ bench⁻¹.

Measured EC was affected by a change in system volume. Water loss was interpolated over the period between water replenishments, and adjusted the EC linearly by the percent change in system volume:

\[
EC_{adj} = EC_m - \left( \frac{V_{ref} - V_m}{V_{total}} \right) EC_m
\]  

(7.1)

where:

\[EC_{adj} = \text{EC adjusted for constant system volume (μmhos cm}^{-1})\]

\[EC_m = \text{EC measured by sensor (μmhos cm}^{-1})\]

\[V_{ref} = \text{reference volume level in graduated cylinder (L)}\]
\[ V_m = \text{measured volume in graduated cylinder (L)} \]

\[ V_{\text{total}} = \text{total system volume (L)} \]

All remaining graphs and analyses in this chapter are based on \( EC_{\text{adj}} \). For simplicity, the subscript \( \text{adj} \) will be dropped. Thus, \( EC \) will refer to the adjusted or "actual" solution \( EC \).

The following analysis outlines the mixing dynamics of the irrigation system. Water was added to the graduated cylinder at a rate of about 100 mL min\(^{-1}\) and system circulation rate was about 400 mL min\(^{-1}\) (or 6.5 L per 15 min). For instance, 250 mL of water would be evenly mixed with 1000 mL of solution as it was added to the system over a 2.5 min period. The well mixed solution would constitute about 20\% of the total system volume, and would contain a combination of about 4\% pure water and 16\% solution. The well mixed solution would move from the graduated cylinder through the EC sensor into the pump tank, which contained about 4.5 L of the entire 6.5 L system volume (about 70\%). Here, more mixing occurred as the pump emptied 400 mL min\(^{-1}\) from the pump tank (almost 10\% of its volume per min) and replaced it with return solution from the bench. Though a completely "well mixed" state surely never would arise, the graphs appear to indicate that the effects of the added water disappeared soon after the initial 5 min period.
7.3 Results

7.3.1 Haydite vs. peat-based media

Nutrient uptake by plants removes ions from the nutrient solution while root nutrient efflux adds ions. A basic assumption in using EC as a measure of overall net nutrient uptake in a recirculating irrigation system is that there should be no sources or sinks of ions other than the plant. As such, solution EC should decline with nutrient uptake. This was generally the case for the Haydite media treatments, but was not true for peat media treatments. The soluble salt content of peat moss is known to be significant and extremely variable according to its source. McCoy and Hudson (1993) report ECs ranging from 33 mmhos cm$^{-1}$ for light sphagnum peat to 195 mmhos cm$^{-1}$ for Dakota reed sedge peat. Pang (1992) found that New Guinea *Impatiens* grown in a 50% peat: 50% rockwool mixture consistently had higher leaf tissue nutrient levels than plants grown in 100% rockwool even though dry mass was similar.

Figure 7.1 shows results from a preliminary test comparing the solution EC for both Haydite and peat media benches. The EC for the Haydite benches decreased at a steady rate during each light level while the peat bench EC showed a steady increase through the same time period. This indicated that salts were being leached from the peat media. This violated a basic assumption of using EC as an indication of nutrient uptake: there must be no other sources/sinks of ions to/from the nutrient solution than the plant. This property of peat dictates that peat-based medias are not suitable for
Figure 7.1 Solution conductivity (EC), normalized to a constant system volume, vs. time for peat (bench 3) and Haydite H (benches 2 and 4) media. Arrows indicate times of water addition.

nutrient uptake studies particularly in recirculating solutions. Peat media was not used in any of the subsequent experiments or analyses.

7.3.2 Nutrient uptake time response

The preliminary test shown in Figure 7.1 provided support for proceeding with a detailed experiment studying the time response of nutrient uptake to changes in light level. The data points prior to the 12:30 p.m. change in light level, though not tested, were interpreted as having a steeper slope than the points following the light change.
The steeper slope also coincided with the higher light level, indicating that perhaps higher light levels induced greater rates of nutrient depletion in the solution. Further tests never conclusively or consistently supported these preliminary indications.

Data were taken during 13 separate days in the growth chamber between 3 and 22 June 1993. A general summary of the experimental treatments is shown in Table 7.1. Data logging period was decreased from 10 min to 1 min to insure that smaller scale fluctuations in EC were not being masked by the longer sampling period, and to improve the precision of short term averages in EC change rates.

Plots of EC vs. time provide general information about nutrient uptake from the solution. Figures 7.2 and 7.3 show data from two separate days in this experiment (cases GC1-10 and GC1-12, respectively). The slope indicates the rate of change of the EC, and thus the rate of overall nutrient uptake. The scatter of data points about this line reveals system variability. This variability was generally due to incomplete mixing of solution in the system, whether due to nonuniform mixing of the pure water additions, variable rates of nutrient-depleted solution movement from the gravel into the solution stream, or variable rates of nutrient uptake itself. The times at which water was added to the system to replace evaporation losses can be seen as peaks above the data point cluster which gradually return to the cluster within about 5 min. This does not mean that the added water had become well-mixed with the entire solution volume within 5 min, only that the added water had completely passed the EC sensor by this time.
Table 7.1 Summary of light levels cases studied in the nutrient uptake time response experiment, Growth Chamber experiment #1 (GC1).

<table>
<thead>
<tr>
<th>Case No.</th>
<th>Date</th>
<th>Light Level</th>
<th>Data Logging Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>GC1-01</td>
<td>3 June</td>
<td>0% no data</td>
<td>no data 10 min</td>
</tr>
<tr>
<td>GC1-02</td>
<td>4 June</td>
<td>0% 0% 100%</td>
<td>no data 10 min</td>
</tr>
<tr>
<td>GC1-03</td>
<td>6 June</td>
<td>0% 0% 100%</td>
<td>37% no data 10 min</td>
</tr>
<tr>
<td>GC1-04</td>
<td>7 June</td>
<td>37% 37% 100%</td>
<td>0% no data 10 min</td>
</tr>
<tr>
<td>GC1-05</td>
<td>8 June</td>
<td>0% 0% 100%</td>
<td>37% no data 10 min</td>
</tr>
<tr>
<td>GC1-06</td>
<td>9 June</td>
<td>0% 0% 100%</td>
<td>37% no data 10 min</td>
</tr>
<tr>
<td>GC1-07</td>
<td>11 June</td>
<td>0% 0% 100%</td>
<td>37% no data 1 min</td>
</tr>
<tr>
<td>GC1-08</td>
<td>14 June</td>
<td>0% 0% 100%</td>
<td>37% no data 1 min</td>
</tr>
<tr>
<td>GC1-09</td>
<td>15 June</td>
<td>37% 37% 0%</td>
<td>100% no data 1 min</td>
</tr>
<tr>
<td>GC1-10</td>
<td>16 June</td>
<td>0% 0% 37%</td>
<td>100% no data 1 min</td>
</tr>
<tr>
<td>GC1-11</td>
<td>17 June</td>
<td>0% 0% 37%</td>
<td>100% no data 1 min</td>
</tr>
<tr>
<td>GC1-12</td>
<td>18 June</td>
<td>0% 0% 100%</td>
<td>37% 0% 1 min</td>
</tr>
<tr>
<td>GC1-13</td>
<td>22 June</td>
<td>0% 0% 100%</td>
<td>37% 0% 1 min</td>
</tr>
</tbody>
</table>

A more direct representation of nutrient uptake as measured by EC can be graphed as the change in EC (or d(EC)) vs. time. Figures 7.4 and 7.5 show this relationship for bench 4 during cases GC1-10 and GC1-12, respectively (the same days shown in Figures 7.2 and 7.3). A 20 minute running average of d(EC) was used to help minimize short term fluctuations in the measurements and improve measurement precision. It should be noted that the resolution of the EC sensor was 1 μmhos cm⁻¹, while most of the data points fall between +1 and -2 μmhos cm⁻¹ min⁻¹ (those falling outside this band are not shown). A constant rate of uptake on this graph was shown.
Figure 7.2  Solution conductivity (EC), normalized to a constant system volume, vs. time from case GC1-10. Arrows indicate time of a step change in light level.

Figure 7.3  Solution conductivity (EC), normalized to a constant system volume, vs. time from case GC1-12. Arrows indicate time of a step change in light level.
Figure 7.4 Change in conductivity, d(EC), vs. time for bench 4 during case GC1-10. Each point is averaged over the previous 20 minutes. Arrows delineate light periods.

Figure 7.5 Change in conductivity, d(EC), vs. time for bench 4 during case GC1-12. Each point is averaged over the previous 20 minutes. Arrows delineate light periods.
by a straight line with no slope. The most important conclusion from these graphs is that the rates of change of EC appear small compared with the system variability.

Table 7.2 summarizes the $d(\text{EC})$ graphs for cases GC1-08 through -12. Ideally, the $d(\text{EC})$ values should have been the same at each light level for the two benches in the growth chamber for the same test. The values should also have been the same in each column as long as there was no pretreatment effect of previous light conditions on current nutrient uptake rate. Finally, the values should have increased from left to right if there was a direct relationship between PAR, nutrient demand, and nutrient uptake. Close inspection of Table 7.2 reveals about half of the bench pairs had reasonably similar $d(\text{EC})$ values under the same conditions, but an equal number can be found which were clearly dissimilar. Similarly, the means show that $d(\text{EC})$ was generally greater under 100% light level than under 37%, and 37% was greater than 0% (though less convincingly so). But the standard deviations also indicate that none of these differences, even between 100% and 0%, were significant. In addition, the standard deviations of treatment averages were on the order of 50% of the means for each light level. Again, though this analysis reveals trends in some cases, no conclusive assertions can be made.

A final analysis was made to determine if a lag existed between the PAR step change and nutrient uptake response. The basic analysis discussed to this point calculated $d(\text{EC})$ from EC data taken during the same period as the light level under which it was collected; i.e., if light level was 37% from 12:00 to 3:00 p.m., then EC values between 12:00 and 3:00 p.m. were used. Shifts of 10, 20, 30, 40, 50, and 60
Table 7.2  Average rate of change of EC for cases GC1-08 through GC1-12 during each light period, presented according to light period level. No time shift was applied.

<table>
<thead>
<tr>
<th>Case No.</th>
<th>0% Light Level</th>
<th>37% Light Level</th>
<th>100% Light Level</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bench 2</td>
<td>Bench 4</td>
<td>Bench 2</td>
</tr>
<tr>
<td>GC1-08</td>
<td>-0.233</td>
<td>-0.186</td>
<td>-0.282</td>
</tr>
<tr>
<td>GC1-09</td>
<td>-0.234</td>
<td>-0.228</td>
<td>-0.282</td>
</tr>
<tr>
<td>GC1-10</td>
<td>-0.357</td>
<td>-0.355</td>
<td>-0.153</td>
</tr>
<tr>
<td>GC1-11</td>
<td>-0.287</td>
<td>-0.133</td>
<td>-0.812</td>
</tr>
<tr>
<td>GC1-12</td>
<td>-0.163</td>
<td>-0.129</td>
<td>-0.451</td>
</tr>
<tr>
<td>Mean</td>
<td>-0.230</td>
<td>-0.236</td>
<td>-0.403</td>
</tr>
<tr>
<td>(Std. Dev.)</td>
<td>(0.082)</td>
<td>(0.103)</td>
<td>(0.208)</td>
</tr>
</tbody>
</table>

min were made between the light period and the EC data, and d(EC) was calculated for these shifted periods; i.e., if light level was 37% from 12:00 to 3:00 p.m., then EC values between 12:20 and 3:20 p.m. were used for the 20 min shift. An example of these results is shown for cases GC1-10 and GC1-12 in Table 7.3. There was no shift which clearly improved the relationship between light level and d(EC).

Cases GC1-10 and GC1-12 have been used as examples throughout much of this discussion since they demonstrated extremes in the obtained results. Table 7.4 allows direct comparison of these two cases, along with cases GC1-09 and GC1-11 for comparison, for data with 0 shift. Case GC1-12 apparently provided relatively clear support for the proposed relationship between PAR, nutrient demand, and nutrient
Table 7.3 Comparison of EC response analyzed using time shifts up to 1 hour between the light period and the period of EC response used for the average.

<table>
<thead>
<tr>
<th>Light Level</th>
<th>d(EC)_{avg} (µmhos cm^{-1} min^{-1})</th>
<th>shift period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 min</td>
<td>10 min</td>
</tr>
<tr>
<td>GCI-10 Bench 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0%</td>
<td>-0.357</td>
<td>-0.338</td>
</tr>
<tr>
<td>37%</td>
<td>-0.198</td>
<td>-0.232</td>
</tr>
<tr>
<td>100%</td>
<td>-0.204</td>
<td>-0.202</td>
</tr>
<tr>
<td>GCI-10 Bench 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0%</td>
<td>-0.355</td>
<td>-0.381</td>
</tr>
<tr>
<td>37%</td>
<td>-0.240</td>
<td>-0.253</td>
</tr>
<tr>
<td>100%</td>
<td>-0.231</td>
<td>-0.208</td>
</tr>
<tr>
<td>GCI-12 Bench 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0%</td>
<td>-0.163</td>
<td>-0.193</td>
</tr>
<tr>
<td>100%</td>
<td>-0.383</td>
<td>-0.435</td>
</tr>
<tr>
<td>37%</td>
<td>-0.055</td>
<td>-0.054</td>
</tr>
<tr>
<td>0%</td>
<td>-0.168</td>
<td>-0.108</td>
</tr>
<tr>
<td>GCI-12 Bench 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0%</td>
<td>-0.129</td>
<td>-0.205</td>
</tr>
<tr>
<td>100%</td>
<td>-0.429</td>
<td>-0.491</td>
</tr>
<tr>
<td>37%</td>
<td>-0.144</td>
<td>-0.138</td>
</tr>
<tr>
<td>0%</td>
<td>-0.127</td>
<td>-0.066</td>
</tr>
</tbody>
</table>
Table 7.4  Average rate of change of EC for cases GC1-09 through GC1-12 during each light period, presented in the order light period was applied. No time shift was applied.

| Light Level | GC1-09 | | | GC1-10 | | |
|---|---|---|---|---|---|
| | d(EC) avg (μmhos cm⁻¹ min⁻¹) | | | d(EC) avg (μmhos cm⁻¹ min⁻¹) | | |
| | Bench 2 | Bench 4 | | Bench 2 | Bench 4 | |
| 37% | -0.153 | -0.141 | 0% | -0.357 | -0.355 |
| 0% | -0.234 | -0.228 | 37% | -0.202 | -0.243 |
| 100% | -0.679 | -0.146 | 100% | -0.204 | -0.231 |

Uptake. The d(EC) uptake rates were related to light level, and the d(EC) values obtained by the different benches were similar (except 37% on bench 2). Furthermore, the 0% value at the end of the day was remarkably similar to the 0% at the beginning of the day on both benches, indicating a lack of pretreatment effect. Increasing the period shift worsened all these relationships (Table 7.3). On the other hand, case GC1-10 showed almost the opposite relationship between light level and d(EC), where the greatest rates of change in EC occurred under 0% light. Increasing the shift for this
case had no considerable effect on this relationship. Careful analysis of Table 7.4 reveals many contradictions.

7.4 Discussion

This experiment did not support the hypothesis that a lag time existed between a change in light level and a change in nutrient uptake rate. This result may be explained by one of several hypotheses.

1) Uptake was independent of light level. This hypothesis is not consistent with the literature presented in Chapter 3.

2) Uptake responded to light level in interaction with a set of other variables. Temperature, CO₂, light quality, and wind velocity were all controlled and monitored throughout this experiment to minimize the variability of these known influences on photosynthesis and plant function. Of course, plant response may have been sensitive to relative levels of certain single parameters or combinations of parameters. Such is the case with plant elongation, for example, which may respond to DIF (difference between day and night temperature) rather than to absolute magnitude of temperature.
3) The response lag time exceeded 1 hour. This experiment was designed to detect short term response characteristics and was unable to detect time response lags longer than several hours. A plant with great integrative capacity in responding to longer term environmental conditions would not require short response times or large magnitude response shifts. If New Guinea Impatiens is such a plant, then this type of experiment would not be capable of detecting such a long term, small magnitude response shift.

4) Uptake was related to light level and there was no lag time. This would simplify nutrient uptake modeling since elaborate response characterizations, such as determination of a time constant for plant nutrient uptake response to a step change in light level, would not be expected to improve model predictions. Future nutrient uptake experiments could be designed with this in consideration.

A general trend was found between light level and d(EC), though the relationship was not statistically significant. This serves as caution that more resolution or precision would be necessary to conclusively demonstrate this relationship in future experiments.

The periodic water replenishment system used in this study was less than ideal for measuring nutrient uptake by solution nutrient depletion because EC measurement was sensitive to changes in total system volume. One bench in this study used an
automatic refilling apparatus to maintain system volume at virtually constant levels. This system was used by Pang (1992) and Fynn (1988), and was described in Section 5.6.2 as well as their dissertations. Future experiments studying nutrient uptake by measuring the solution nutrient depletion, like the one in Chapter 8, must use this type of device for each irrigation system in order to remove the confounding effects of variable solution volume.

Plant media which use peat moss were found to be unacceptable for nutrient uptake studies using recirculating irrigation systems. Only inert media can be used.
CHAPTER VIII
NUTRIENT AND WATER UPTAKE CHARACTERIZATION

8.1 Introduction

Nutrient uptake was proposed in this dissertation to be related to the level of nutrient demand. Two environmental factors shown in Chapter 3 to have primary influences on nutrient demand were photosynthetically active radiation (PAR) level (or PPFD) and air temperature. Nutrient supply was also shown to affect nutrient uptake. The following experiment was designed to study the effects of each of these factors and their interactions on nutrient uptake of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg). In addition, water uptake was measured and related to environmental factors. The water and nutrient uptake information was combined to provide working recommendations for fertigation management.

8.2 Experimental Design

The growth chamber described in Chapter 5 was used for this study. Four 1 x 1.2 m ebb-flood benches were arranged in the growth chamber to receive symmetrical
lighting. For this experiment, the benches were sloped from 1.58 m high along the growth chamber center-line to 1.62 m at the edges. This resulted in the bench surface being 1.14 to 1.10 m beneath the center of the MH lamps. Thirty-six New Guinea Impatiens (Impatiens hawkeri) 'Equinox' were grown on each bench (Figure 5.3). Plants were received as rooted cuttings in 96-cell seedling trays (courtesy of Mikkelsens Inc, Ashtabula, Ohio) on 23 June 1993. Cuttings were transplanted with a minimum of the peat/perlite seedling medium into 10 cm pots filled with Haydite H on 30 June 1993. Plants were grown for 31 days in a double poly greenhouse at 24/18 °C day/night temperature set points with drip irrigation before being relocated to the growth chamber on 24 July 1993.

The hydroponic growing system discussed in Chapter 7 was also used in this study, with several modifications. Only Haydite H media was used. Water lost by evapotranspiration was replaced continually and measured with a lysimeter using the Stock-tank Weight Method described in Section 5.6.2. The nutrient recipe used in this study was designed to provide only NO₃-N, since only that form of N would be measured. Only distilled/deionized water was used. The baseline (1x) nutrient recipe was based on generally accepted concentrations and ratios, and the other recipes were fractions or multiples of this basic recipe (Table 8.1).

Different light levels were achieved using the shade cloth system described in Chapter 5. This experiment used five discrete light levels (levels of shading): 100% (no shade cloth), 70% (30% shade cloth), 53% (47% shade cloth), 37% (63% shade cloth), and 20% (80% shade cloth). Shading had little effect on spectral quality
### Table 8.1 Recipes for 2x, 1x, ½x, and ¼x nutrient solutions. All recipes are shown for 30 L distilled/deionized H₂O.

<table>
<thead>
<tr>
<th>Nutrient Recipes (for 30 L D/D H₂O)</th>
<th>2x</th>
<th>1x</th>
<th>½x</th>
<th>¼x</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Formula</strong></td>
<td><strong>Name</strong></td>
<td>(g)</td>
<td>(g)</td>
<td>(g)</td>
</tr>
<tr>
<td>Ca(NO₃)₂</td>
<td>Calcium Nitrate</td>
<td>30</td>
<td>15</td>
<td>7.5</td>
</tr>
<tr>
<td>KNO₃</td>
<td>Potassium Nitrate</td>
<td>3.7</td>
<td>1.9</td>
<td>0.9</td>
</tr>
<tr>
<td>MgNO₃</td>
<td>Magnesium Nitrate</td>
<td>118</td>
<td>5.9</td>
<td>3.0</td>
</tr>
<tr>
<td>K₂HPO₄</td>
<td>Mono Potassium Phosphate</td>
<td>10.2</td>
<td>5.1</td>
<td>2.6</td>
</tr>
<tr>
<td>MgSO₄</td>
<td>Magnesium Sulfate</td>
<td>7.0</td>
<td>3.5</td>
<td>1.7</td>
</tr>
<tr>
<td>&quot;Compound 111&quot;</td>
<td>Micronutrients</td>
<td>0.2</td>
<td>0.2</td>
<td>0.2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Element</th>
<th>Name</th>
<th>(mg L⁻¹)</th>
<th>(mg L⁻¹)</th>
<th>(mg L⁻¹)</th>
<th>(mg L⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NO₃⁻N</td>
<td>Nitrate-Nitrogen</td>
<td>200</td>
<td>100</td>
<td>50</td>
<td>25</td>
</tr>
<tr>
<td>P</td>
<td>Phosphorus</td>
<td>60</td>
<td>30</td>
<td>15</td>
<td>7.5</td>
</tr>
<tr>
<td>K</td>
<td>Potassium</td>
<td>200</td>
<td>100</td>
<td>50</td>
<td>25</td>
</tr>
<tr>
<td>Ca</td>
<td>Calcium</td>
<td>200</td>
<td>100</td>
<td>50</td>
<td>25</td>
</tr>
<tr>
<td>Mg</td>
<td>Magnesium</td>
<td>60</td>
<td>30</td>
<td>15</td>
<td>7.5</td>
</tr>
<tr>
<td>S</td>
<td>Sulfur</td>
<td>30</td>
<td>15</td>
<td>7.5</td>
<td>3.8</td>
</tr>
</tbody>
</table>
(Chapter 5) and was assumed to affect spatial distribution uniformly across each bench. The spatial distribution of PPFD at bench level for each level of shading can be extrapolated from data presented in Chapter 5. Figure 5.6 shows the distribution of PPFD at bench level in this experiment, and Figure 5.14 shows measured PPFD at one location under each shade level. These data can be combined to create predicted spatial distributions under each shade level. Table 8.2 summarizes the area distributions of PPFD levels on each bench. It is important to note the degree of overlap in PPFD levels among the light treatments in this growth chamber. For example, 45\% of each bench under the 53\% light level treatment and 76\% of the 37\% treatment were in the range between 100 and 200 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), while none of the 100\% or 20\% light level treatments were within this range. Due to this overlap, the five light level treatments were not completely independent.

The experiment was designed to isolate the daily nutrient uptake responses to planned combinations of light, temperature, and nutrient concentration, while minimizing the error contributions by continuous plant growth and spatial variations in the growth chamber environment. Five light level treatments were used: 100\%, 70\%, 53\%, 37\%, and 20\%. Three day temperature set-points were used: 30, 25, and 20 °C. Night temperature set-point was 20 °C for the duration of the experiment. One combination of light and temperature conditions was run each day of the experiment for an entire day. A different nutrient recipe was used on each of the 4 benches in the growth chamber. Thus, 15 days were needed for one replication of each complete set of light levels and temperatures. The 4 nutrient concentrations, 5 light levels, and 3
Table 8.2  Spatial distribution of PPFD at bench level.

<table>
<thead>
<tr>
<th>Spatial Distribution of PPFD at Bench Level (% of total bench area)</th>
<th>Light Level</th>
</tr>
</thead>
<tbody>
<tr>
<td>PPFD Range</td>
<td>100%</td>
</tr>
<tr>
<td>650 - 700</td>
<td>5</td>
</tr>
<tr>
<td>600 - 650</td>
<td>11</td>
</tr>
<tr>
<td>550 - 600</td>
<td>10</td>
</tr>
<tr>
<td>500 - 550</td>
<td>14</td>
</tr>
<tr>
<td>450 - 500</td>
<td>16</td>
</tr>
<tr>
<td>400 - 450</td>
<td>13</td>
</tr>
<tr>
<td>350 - 400</td>
<td>10</td>
</tr>
<tr>
<td>300 - 350</td>
<td>13</td>
</tr>
<tr>
<td>250 - 300</td>
<td>7</td>
</tr>
<tr>
<td>200 - 250</td>
<td>1</td>
</tr>
<tr>
<td>150 - 200</td>
<td>9</td>
</tr>
<tr>
<td>100 - 150</td>
<td>16</td>
</tr>
<tr>
<td>50 - 100</td>
<td>25</td>
</tr>
<tr>
<td>0 - 50</td>
<td>19</td>
</tr>
</tbody>
</table>

PPFD at Bench Level (µmol m⁻² s⁻¹)

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>446</th>
<th>288</th>
<th>200</th>
<th>122</th>
<th>65</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Standard Deviation</td>
<td>133</td>
<td>86</td>
<td>60</td>
<td>36</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>633</td>
<td>444</td>
<td>302</td>
<td>189</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>Minimum</td>
<td>236</td>
<td>152</td>
<td>106</td>
<td>65</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>397</td>
<td>292</td>
<td>196</td>
<td>124</td>
<td>66</td>
</tr>
</tbody>
</table>
temperatures were arranged in a split plot/split block experimental design with three replications. Temperature was the main plot treatment and was randomized over each block of 3 weeks (5 days of experiment per week). Nutrient recipe and light level were the split plot treatments and were arranged in a split block. Nutrient recipe was randomized among the 4 benches and remained unchanged for each week. Light level was randomized over the 5 days of each week. The complete randomization is summarized in Table 8.3. Tests were not run for two days between experimental weeks to allow the system time to reach equilibrium with the new nutrient levels.

The instrumentation discussed in Chapter 5 was used to monitor the environment. Data were logged on 15 minute intervals during the entire 9-week period. Environmental parameters measured were: air temperature (dry bulb and wet bulb), dew point temperature, solution temperature, media temperature, wind speed, canopy CO₂, leaf temperature, solution EC and pH, and water refill tank weight. Table 8.4 summarizes the environmental conditions measured.

Nutrient uptake was measured by the amount of nutrient depletion during a 9 hour period of the day, from 9:00 a.m. to 6:00 p.m., using the Individual Ion Method described in Section 5.6.3. Due to minor equipment problems, less than the full 9 hour period was used for bench 2 on day 236 (4 hours, 2:30 p.m. to 6:30 p.m.), and the sampling times for all benches were altered on day 267 (10:00 a.m. to 7:00 p.m.) and day 270 (11:00 a.m. to 8:00 p.m.). The measured concentration values were converted into uptake rates for a unit canopy area by adjusting for the 6.5 L system volume, 9 h sample period, 1.22 m² bench area, and the ratio of canopy area to bench
Table 8.3 Randomization of experimental treatments.

<table>
<thead>
<tr>
<th>Week</th>
<th>Nutrient Recipe</th>
<th>Bench</th>
<th>Temperature (°C)</th>
<th>Light Level (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>1</td>
<td>½x</td>
<td>2x</td>
<td>¼x</td>
<td>1x</td>
</tr>
<tr>
<td>2</td>
<td>½x</td>
<td>2x</td>
<td>1x</td>
<td>¼x</td>
</tr>
<tr>
<td>3</td>
<td>¼x</td>
<td>¾x</td>
<td>1x</td>
<td>2x</td>
</tr>
<tr>
<td>4</td>
<td>1x</td>
<td>¼x</td>
<td>2x</td>
<td>¾x</td>
</tr>
<tr>
<td>5</td>
<td>¼x</td>
<td>1x</td>
<td>2x</td>
<td>¾x</td>
</tr>
<tr>
<td>6</td>
<td>1x</td>
<td>2x</td>
<td>¼x</td>
<td>¾x</td>
</tr>
<tr>
<td>7</td>
<td>¼x</td>
<td>1x</td>
<td>2x</td>
<td>¾x</td>
</tr>
<tr>
<td>8</td>
<td>½x</td>
<td>2x</td>
<td>1x</td>
<td>¼x</td>
</tr>
<tr>
<td>9</td>
<td>1x</td>
<td>¼x</td>
<td>½x</td>
<td>2x</td>
</tr>
</tbody>
</table>

area (CAI) using Equation 8.1.

\[
V_{\text{canopy}} = C_n \left( \frac{6.5L}{\text{system}} \frac{1}{9h} \frac{1}{1.22 \text{m}^2} \frac{1}{\text{CAI}} \right) \tag{8.1}
\]

where:

\( V_{\text{canopy}} = \) rate of nutrient uptake by the canopy (mg m\(^{-2}\) h\(^{-1}\))

\( C_n = \) nutrient concentration (mg L\(^{-1}\))
Table 8.4  Measured environmental conditions. Each reported value is a mean ± 1 standard deviation of 15 daily averages.

<table>
<thead>
<tr>
<th>Environmental Conditions (Mean ±1 Std dev)</th>
<th>Treatment - Temperature Set Point</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>20 °C</td>
</tr>
<tr>
<td>T (boundary layer air - dry bulb), °C</td>
<td>20.4 ±0.5</td>
</tr>
<tr>
<td>T (canopy air - dry bulb), °C</td>
<td>19.6 ±1.0</td>
</tr>
<tr>
<td>T (canopy air - dew point), °C</td>
<td>15.2 ±0.9</td>
</tr>
<tr>
<td>rh (canopy air), %</td>
<td>76 ±3</td>
</tr>
<tr>
<td>CO₂ (canopy air), ppm</td>
<td>367 ±13</td>
</tr>
<tr>
<td>wind speed (@ X=0.7 m, Y=2.0 m, H=2.0 m), m s⁻¹</td>
<td>0.66 ±0.18</td>
</tr>
<tr>
<td>T (nutrient solution), °C</td>
<td>24.0 ±1.4</td>
</tr>
<tr>
<td>T (media), °C</td>
<td>20.8 ±0.8</td>
</tr>
<tr>
<td>T (leaf), °C</td>
<td>19.6 ±1.0</td>
</tr>
<tr>
<td>LTD (leaf - boundary layer db), °C</td>
<td>-0.8 ±0.7</td>
</tr>
<tr>
<td>LTD (leaf - canopy db), °C</td>
<td>-0.06 ±0.12</td>
</tr>
<tr>
<td>VPD (canopy air), kPa</td>
<td>0.58 ±0.09</td>
</tr>
<tr>
<td>LVPD (leaf - canopy air), kPa</td>
<td>0.47 ±0.16</td>
</tr>
</tbody>
</table>
Uptake per unit canopy area will be referred to simply as "uptake" in all subsequent discussion.

Intended nutrient solution concentrations were difficult to maintain on each bench during the experiment. The experimental design intended that each bench would begin each day with each nutrient at the desired solution concentration: 2x, 1x, \(\frac{1}{2}x\), or \(\frac{1}{4}x\). The nutrients absorbed each day needed to be replaced before the start of the next day. Management was complicated because the individual nutrients were not necessarily absorbed in the same proportions. In addition, the requirement of maintaining a well-mixed nutrient solution during the experimental period forced the nutrients to be added at the end of the previous day's sampling period. The amounts of nutrient additions to each bench were estimated based on the most recent \(\text{NO}_3\)-N measurement available (from that morning) and/or the current EC along with an estimate of the further nutrient depletion to occur before the next morning. This estimation procedure improved with experience during the experiment. The basic problem was that the needed information (the rate of uptake of each individual nutrient as a function of the environmental conditions) was the parameter that was being evaluated in this experiment.

Analysis rectified this situation by consolidating data from the four "intended" nutrient solution treatments into three "grouped" treatments: high (H), medium (M), and low (L) nutrient concentrations. Each individual nutrient was grouped separately for analysis. The medians of the grouped treatments for N, P, Ca, and Mg were selected to be geometrically related (H = 2M = 4L) with ranges of approximately
±35% above and below each median, while the grouped medians for K were related by $H = 3M = 9L$ with a range of approximately ±50% (Table 8.5). The grouped treatment medians and ranges were selected based on the distribution of actual concentrations for each individual nutrient, along with the requirement that each combination of light and temperature have exactly 3 replications. Ideally, each treatment (one specific combination of light and temperature) would have one value within the desired concentration range from each of the 3 blocks. However, a number of data points were "forced" into treatments, being either outside the desired treatment range or from a different experimental block. The overall result of the consolidation was a better separation of nutrient concentrations at a cost of decreased statistical sensitivity (i.e. reducing the degrees of freedom for nutrient concentration from 3 (n=4) to 2 (n=3)).

Water uptake was measured by the lysimeter for the sum total of all four benches. Differences in weight were recorded at 15 min intervals. It is important to understand that water uptake, and not evapotranspiration, was being measured in this study (see discussion in Section 5.6.2). Evapotranspiration was calculated using the combination equation (discussed in more detail below). One stomatal resistance used in analyzing the data was determined using total shortwave radiation in a regression relation for New Guinea Impatiens found by Pang (1992). This dictated that the same methods used by Pang for calculating resistances to heat and vapor fluxes must also be used (see discussion in Section 4.3.1). Stomatal resistance was also estimated independently from data in this study using two forms of the combination equation.
Table 8.5 Specification of the individual nutrient solution concentration median and range for each "grouped" nutrient level treatment.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Nutrient Level</th>
<th>High (H) (mg L⁻¹)</th>
<th>Medium (M) (mg L⁻¹)</th>
<th>Low (L) (mg L⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>Median</td>
<td>160</td>
<td>80</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>(230 - 110)</td>
<td>(110 - 50)</td>
<td>(50 - 20)</td>
</tr>
<tr>
<td>P</td>
<td>Median</td>
<td>90</td>
<td>45</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>(122 - 61)</td>
<td>(61 - 30)</td>
<td>(30 - 14)</td>
</tr>
<tr>
<td>K</td>
<td>Median</td>
<td>90</td>
<td>30</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>(135 - 45)</td>
<td>(45 - 15)</td>
<td>(15 - 1)</td>
</tr>
<tr>
<td>Ca</td>
<td>Median</td>
<td>190</td>
<td>95</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>(256 - 125)</td>
<td>(95 - 60)</td>
<td>(60 - 25)</td>
</tr>
<tr>
<td>Mg</td>
<td>Median</td>
<td>60</td>
<td>30</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>(81 - 45)</td>
<td>(45 - 22)</td>
<td>(22 - 8)</td>
</tr>
</tbody>
</table>

Net shortwave plus longwave radiation was used for the net radiation term, $Q_R$, since longwave can be a significant contributor to plant physical responses in the growth chamber.

Leaf area index (LAI) was calculated using data of the average total number of leaves per plant (3 plants from each of 4 benches on 2 separate days, day numbers 239 and 255). A rectangular hyperbola was used to model the increase in the number of leaves with time from plant day 0 through day 114 (the end of the study). The relationship between number of leaves and total leaf area was assumed to be constant, and was determined by unpublished data from Pang (1992) for the same variety of
New Guinea *Impatiens* as used in this study (‘Equinox’). LAI for the duration of the study was calculated for each day using the product of these terms along with 36 plants per bench and a bench area of 1.2 m$^2$ (Figure 8.1).

Canopy area index (CAI) was defined as the percentage of bench area covered by the canopy. The primary purpose of this index was to translate irradiance values from W of energy flux per m$^2$ of bench area to W per m$^2$ of canopy area. Thus, a crop with a CAI of 0.5 would intercept half the radiation intercepted by a crop with CAI of 1.0. This index cannot exceed 1.0. Plan view photographs were taken of portions of each bench on 5 different days during the study (day numbers 224, 230, 237, 244, and 251). Each overhead shot included one central plant and portions of 8

![Figure 8.1 Leaf area index (LAI) during experiment GC2.](image-url)
surrounding plants within the view. White paper was placed beneath the plants to improve contrast between the leaves and the background. High contrast black and white 18 x 25 cm enlargements were made and analyzed using a digital image analyzer. The imaging system included a personal computer (Apple IIe) with imaging software (Imageplus+, Scientific Microprograms), a television camera (Newvicon Model WV 1550, Panasonic Industrial Co.), and a television lens (Cosmicar, 16 mm, 1:1.4) with adapter (Tiffin, 40.5 F 6). Each photograph was digitized into a 194 (vertical) by 254 (horizontal) pixel image with 64 grey levels. The system then categorized each pixel as either dark or light, depending on whether the grey was within or without a selected grey scale cutoff range. Grey level discriminators were set manually for each photograph using upper and lower discriminator potentiometers. Photographs were retouched with white paper correction fluid (background) and black marker pen (leaves) to improve image discrimination. The percentage of dark in the frame was a direct measure of CAI. Figure 8.2 shows a canopy image with a CAI of 0.5, and Figure 8.3 shows a CAI of 0.9. Table 8.6 shows discriminator settings and raw canopy area data. A series of 3 linear curves were fitted to the data of CAI vs. plant age and used to estimate CAI for the duration of the study (Figure 8.4).
Table 8.6  Digital image analysis of canopy area from black and white photographs of portions of each bench.

<table>
<thead>
<tr>
<th>Date (Day No.)</th>
<th>Bench</th>
<th>Discriminator Settings</th>
<th>% leaf area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>8-12-93 (224)</td>
<td>1</td>
<td>0</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0</td>
<td>55</td>
</tr>
<tr>
<td>average</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8-18-93 (230)</td>
<td>1</td>
<td>0</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0</td>
<td>50</td>
</tr>
<tr>
<td>average</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8-25-93 (237)</td>
<td>1</td>
<td>0</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0</td>
<td>45</td>
</tr>
<tr>
<td>average</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9-1-93 (244)</td>
<td>1</td>
<td>0</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0</td>
<td>60</td>
</tr>
<tr>
<td>average</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9-8-93 (251)</td>
<td>1</td>
<td>0</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>average</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 8.2 Example of a canopy area index (CAI) of 0.5.

Figure 8.3 Example of a canopy area index (CAI) of 0.9.
8.3 Nutrient Uptake Results

Uptake of N, Ca, and Mg were not significantly related to daytime air temperature (T), nutrient concentration (C), or light level (L), or any interactive effects of these parameters. Uptake of P was significantly related only to the interaction of light, concentration and temperature (LxCxT, at a significance level of 0.90). Uptake of K was significantly related to concentration (0.99) and the interaction of LxCxT(0.95). Tables 8.7 through 8.11 summarize these results in analysis of variance (ANOVA) tables. The F statistic is a measure of the amount of variance in the data.
Table 8.7  ANOVA table for factorial of 3 temperature levels (T), 5 light levels (L), 3 "grouped" N concentration treatment levels (C), and 3 replications (B).

<table>
<thead>
<tr>
<th>Source</th>
<th>n</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F-calc.</th>
<th>F-tab. (0.1)</th>
<th>F-tab. (0.05)</th>
<th>F-tab. (0.01)</th>
<th>Signif</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blocks</td>
<td>3</td>
<td>2</td>
<td>22.2</td>
<td>11.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temp.</td>
<td>3</td>
<td>2</td>
<td>16.4</td>
<td>8.2</td>
<td>0.08</td>
<td>4.32</td>
<td>6.94</td>
<td>18</td>
<td>N.S</td>
</tr>
<tr>
<td>BxT</td>
<td>4</td>
<td>4</td>
<td>419.4</td>
<td>104.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conc.</td>
<td>3</td>
<td>2</td>
<td>597.5</td>
<td>298.7</td>
<td>1.51</td>
<td>2.81</td>
<td>3.89</td>
<td>6.93</td>
<td>N.S</td>
</tr>
<tr>
<td>CxT</td>
<td>4</td>
<td>4</td>
<td>133.0</td>
<td>33.2</td>
<td>0.17</td>
<td>2.48</td>
<td>3.26</td>
<td>5.41</td>
<td>N.S</td>
</tr>
<tr>
<td>error (C)</td>
<td>12</td>
<td></td>
<td>2372</td>
<td>197.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Light</td>
<td>5</td>
<td>4</td>
<td>71.8</td>
<td>18.0</td>
<td>0.24</td>
<td>2.19</td>
<td>2.78</td>
<td>4.22</td>
<td>N.S</td>
</tr>
<tr>
<td>LxT</td>
<td>8</td>
<td>4</td>
<td>489.3</td>
<td>61.2</td>
<td>0.81</td>
<td>1.94</td>
<td>2.36</td>
<td>3.36</td>
<td>N.S</td>
</tr>
<tr>
<td>error (L)</td>
<td>24</td>
<td></td>
<td>1811</td>
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which is due to differences in designed treatment means relative to the amount which is due to undesigned sources. The non-significant F tests in this study do not provide support for the hypothesis that there exists a relationship among these variables.

The relationships between variables for each individual nutrient are graphically presented in Figures 8.5 through 8.9. Uptake is related to the stated treatment variables singly in two-dimensions. All data were averaged over all levels of the remaining variables not represented in the graph.

A general trend evident from Figures 8.5 through 8.9 is that uptake increased with increasing nutrient concentration for all nutrients. The F statistic was significant
Figure 8.5 Mean ±1 standard deviation of hourly nitrogen (N) uptake rate vs. (a) air temperature, (b) light level, and (c) N solution concentration.
Figure 8.6  Mean ±1 standard deviation of hourly phosphorus (P) uptake rate vs. (a) air temperature, (b) light level, and (c) P solution concentration.
Figure 8.7    Mean ±1 standard deviation of hourly potassium (K) uptake rate vs. (a) air temperature, (b) light level, and (c) K solution concentration.
Figure 8.8 Mean ±1 standard deviation of hourly calcium (Ca) uptake rate vs. (a) air temperature, (b) light level, and (c) Ca solution concentration.
Figure 8.9  Mean ±1 standard deviation of hourly magnesium (Mg) uptake rate vs. (a) air temperature, (b) light level, and (c) Mg solution concentration.
Table 8.8 ANOVA table for factorial of 3 temperature levels (T), 5 light levels (L), 3 "grouped" P concentration treatment levels (C), and 3 replications (B).

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</tr>
</tbody>
</table>

Only for K, but showed a positive, if not statistically significant, relationship for N and P. Ca and Mg also showed positive, though less convincing, trends between concentration and uptake. Though K showed a significant increase in uptake as a function of concentration, it should be noted that K also had the largest separation between median grouped concentrations: a factor of 9 from lowest to highest as opposed to a factor of 4 for the other individual nutrients.

Light level showed a general positive trend, inducing higher nutrient uptake at the higher irradiance levels than at the lower levels. The factor of light level was confounded by a significant overlap between levels, as shown in Table 8.2. However, Table 8.2 does indicate that several treatment comparisons exist which have no PPFD
Table 8.9 ANOVA table for factorial of 3 temperature levels (T), 5 light levels (L), 3 "grouped" K concentration treatment levels (C), and 3 replications (B).

<table>
<thead>
<tr>
<th>Source</th>
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<td>17.2</td>
<td>1.47</td>
<td>4.32</td>
<td>6.94</td>
<td>18</td>
<td>N.S.</td>
</tr>
<tr>
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<td>2.48</td>
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</tbody>
</table>

Overlap (as discussed in Section 8.2). Yet even between these treatments, the relationship between uptake and light level does not show a significant relationship.

This supports the conclusion made based on the F-tests: that there existed no overarching relationship between uptake of these individual nutrients and the light levels studied, even in consideration of the experimental lighting conditions.

Temperature showed no consistent influence on nutrient uptake. It is important to note that unlike the spatial variation in light level, the variation in air temperature within each bench was small compared to the difference among experimental temperature treatments.
Table 8.10 ANOVA table for factorial of 3 temperature levels (T), 5 light levels (L), 3 "grouped" Ca concentration treatment levels (C), and 3 replications (B).

<table>
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<td>84.5</td>
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<td>2.81</td>
<td>3.89</td>
<td>6.93</td>
<td>N.S.</td>
</tr>
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<td>11.3</td>
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<td>3.26</td>
<td>5.41</td>
<td>N.S.</td>
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<tr>
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<td>0.35</td>
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<td>N.S.</td>
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</tr>
<tr>
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</table>

Tissue concentrations of each nutrient were measured at the end of the experiment (at plant age = 114 days). Results of this analysis are shown in Table 8.12. Nutrient concentrations were averaged over 12 plants: 3 each from the 4 benches. Standard deviations were less than 10% of the means for each nutrient.

Concentration was translated to net assimilation rate (NAR) by the following equation:

\[
NAR = \frac{C_n \cdot DW \cdot N}{A_{bench} \cdot age \cdot I_{period}}
\]  

where:

\(NAR\) = net assimilation rate of an individual nutrient (mg m\(^{-2}\) h\(^{-1}\))
Table 8.11  ANOVA table for factorial of 3 temperature levels (T), 5 light levels (L), 3 "grouped" Mg concentration treatment levels (C), and 3 replications (B).

<table>
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<tr>
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<td>4.6</td>
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<td>6.94</td>
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<td>3.6</td>
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<td>4</td>
<td>29.8</td>
<td>7.5</td>
<td>1.85</td>
<td>2.19</td>
<td>2.78</td>
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<td>1.84</td>
<td>2.35</td>
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<tr>
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</tr>
</tbody>
</table>

\[ C_w = \text{plant nutrient concentration (mg g}^{-1} \text{dry wt.)} \]

\[ DW = \text{plant dry weight (g)} \]

\[ N = \text{number of plants per bench (36)} \]

\[ A_{\text{bench}} = \text{bench area (m}^2 \text{)} \]

\[ \text{age} = \text{plant age (114 days)} \]

\[ L_{\text{period}} = \text{photoperiod (12 hrs)} \]

Using this formula, nutrient assimilation rates compare favorably with measured nutrient uptake rates. Measured N uptake was within 3% of the NAR predicted by
Table 8.12  Comparison of individual nutrient uptake rates predicted by measured tissue nutrient concentrations (NAR) and measured nutrient uptake rates.

<table>
<thead>
<tr>
<th>Nutrient Concentration</th>
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<th>Ca</th>
<th>Mg</th>
</tr>
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<tbody>
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<tr>
<td>(mg m⁻² h⁻¹)</td>
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</tr>
<tr>
<td>(mg m⁻² h⁻¹)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Difference (%)</td>
<td>+3%</td>
<td>-44%</td>
<td>+35%</td>
<td>-12%</td>
<td>-12%</td>
</tr>
<tr>
<td>Relative tissue</td>
<td>5.1</td>
<td>1.0</td>
<td>4.5</td>
<td>3.9</td>
<td>1.3</td>
</tr>
<tr>
<td>concentrations</td>
<td>(normalized to P = 1.0)</td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

measured tissue concentrations. This exceptional correlation provides strong support for the linkage of nutrient uptake with light. In this case, N uptake appeared to occur at the measured average rate over a duration equivalent to the 12 hour photoperiod. This may suggest that although N uptake is not sensitive to daily variations in light level, over the life of the plant it must absorb N according to the demand established by light.

The NAR of P was 44% less than the measured uptake rate, while the NAR for K was 35% greater than the measured uptake rate, and the NARs for Ca and Mg were both 12% less than the measured uptake rate. These nutrients did not appear to be as strongly linked to photoperiod as N.
8.4 Water Uptake Results

Water uptake was plotted against temperature (Figure 8.10a) and light level (Figure 8.10b) in a manner similar to the nutrient uptake figures of the previous section, for general comparative purposes. (A comparable figure of water uptake against nutrient concentration was not possible because a single water uptake measurement was made for the sum of the 4 benches without differentiation for the different nutrient concentrations.) However, Chapter 4 showed that temperature and light level are not the ultimate driving forces of evapotranspiration (ET). Rather, leaf vapor pressure differential (LVPD; $e_I(T_{leaf}) - e(T_J)$) drives ET (Equation 4.10). The relationship between water uptake and LVPD is shown in Figure 8.11. Water uptake increased as the driving vapor pressure gradient increased by the relation ($r^2 = 0.61$):

$$W_{wp} = 20.6 + 332.7 \text{ LVPD} - 74.6 \text{ LVPD}^2$$

(8.3)

where:

$W_{wp} =$ water uptake (g m$^{-2}$ h$^{-1}$)

$LVPD =$ leaf vapor pressure deficit (kPa)

A critical factor in the combination equation is the leaf resistance term, comprised of both an internal and an external resistance. The method of determination of these resistances is critical, as discussed in Section 4.3. Several methods were employed in the following analysis and compared.
Figure 8.10  Mean ±1 standard deviation of hourly water uptake rate vs. (a) air temperature and (b) light level.
Water uptake vs. several environmental parameters. (a) leaf VPD (LVPD), (b) vapor pressure deficit (VPD), and (c) total radiation ($Q_{\text{total}}$).

For LVPD:

$$ W_{up} = 143.5 + 225.0 \text{ LVPD} $$

$ r^2 = 0.36$

For VPD:

$$ W_{up} = 120.2 + 147.3 \text{ VPD} $$

$ r^2 = 0.59$

For total radiation ($Q_{\text{total}}$):

$$ W_{up} = 165.5 + 0.579 \text{ } Q_{\text{total}} $$

$ r^2 = 0.16$
First, a canopy analog of Equation 4.11 was used, where all terms referred to canopy characteristics rather than leaf characteristics.

\[
ET_{canopy} = \frac{C_p \Delta LAI [v(T_{canopy}) - v(T_u)]}{L_v \gamma (r_u + r_s)}
\]  

(8.4)

This equation uses leaf temperature directly to determine the LVPD driving potential of ET. Leaf vapor pressure was determined using an average of 8 leaf temperatures from the top layer of leaves in the canopy. All terms in Equation 8.4 can be found directly from measured values except the stomatal resistance term. Stomatal resistance was calculated using the actual LVPD along with actual LAI and ET (in this case, water uptake) values from this experiment.

Second, the big leaf combination equation was used (Equation 4.20). However, the resistance term in the denominator of Equation 4.20 was not the same as Equation 8.4. This is because the resistance term in Equation 4.20 included the terms introduced into the combination equation to replace the leaf saturation vapor pressure term (see Section 4.2.2). This becomes clear when LVPD is written in expanded form, using Equations 8.4 and 4.20 (in the expanded form of Equation 4.16):

\[
LVPD = \frac{[v(T_a) - v(T_u)] + \frac{CAI \Delta r_{II} Q_R}{LAIC_p \Delta}}{\left[1 + \frac{\Delta r_{II}}{\gamma (r_s + r_u)}\right]}
\]  

(8.5)

The denominator of Equation 4.20 must be converted to total resistance, the sum of the internal and external resistance \((r_s + r_u)\), in order to allow direct comparison with...
Equation 8.4. Substitution of Equation 8.5 into 8.4 (compared to the denominator of Equation 4.20) reveals the following relationship, which was used to determine total resistance from Equation 4.20:

\[
r_{\text{w}} + r_{s} = \frac{r_{f}r_{s}}{1 + \frac{\delta r_{H}}{\gamma (r_{w} + r_{s})}} \tag{8.6}
\]

This equation solves for total resistance using the VPD and total radiation terms as estimates of the driving potential of ET, as described in Chapter 4. Again, all values in Equation 8.5 can be determined directly from measured values except the stomatal resistance term.

Third, the results from these models were compared with results from a model developed by Pang (1992, Equation 5.5) for New Guinea Impatiens. Pang developed a regression equation for stomatal resistance based on solar radiation \(r^{2} = 0.86\):

\[
r_{s} = 1123.1 - 6.486 Q + 0.02243 Q^{2} - 3.40 \times 10^{-4} Q^{3} + 1.938 \times 10^{-6} Q^{4} \tag{8.7}
\]

where:

\[Q = \text{solar (short wave) radiation (W m}^{2})\]

This regression estimate of stomatal resistance was compared with empirical estimates of resistance from this experiment calculated using the two different methods outlined above. The same method was used to estimate external resistance \((r_{w})\) in all three methods. It is important to note that Pang's model of stomatal resistance was based on measurement of evapotranspiration, while the models from this experiment were based
on measurements of water uptake. In addition, use of a regression equation to
calculate $r_s$ (using the third (c) method: Pang's model) greatly reduced the apparent
scatter in Figures 8.12 through 8.14 compared with $r_s$ values calculated from raw data
(using the first (a) and second (b) methods).

Figure 8.12 shows the relationship between resistance and LVPD using the
three different methods of calculation described above: (a) using Equation 8.4, (b)
using Equation 4.20, and (c) using Pang's model (essentially Equation 8.7 along with
Equation 4.20). The total and stomatal resistances increased with increasing LVPD in
Figures 8.12(a) and 8.12(b), but decreased with LVPD in Figure 8.12(c).

Figure 8.13 shows the relationship between resistance and air VPD using the
same three methods as above. None of the figures show a clear relationship with
VPD. Figure 8.14 shows resistance versus total (shortwave and longwave) net
radiation, again using the same three methods as above. Figures 8.14(a) and 8.14(b)
both show a general trend of increasing resistance with increasing net irradiance, while
Figure 8.14(c) shows a decreasing relationship.

The stomatal resistance values determined using water uptake (methods (a) and
(b)), were within the same range as those determined using evapotranspiration (method
(c)). However, there was an important difference between the resistances calculated
using water uptake and evapotranspiration. Stomatal (internal) resistance increased
with LVPD (Figure 8.12) and total radiation (Figure 8.14) when determined using
water uptake (methods (a) and (b)), but decreased with LVPD and total radiation when
determined using evapotranspiration (method (c)). The data presented in Chapter 6
Figure 8.12  Calculated resistance vs. leaf vapor pressure deficit (LVPD) using three models: (a) Equation 8.4, (b) Equation 4.20, and (c) Equations 8.7 & 4.20.
Figure 8.13  Calculated resistance vs. air vapor pressure deficit (VPD) using three models: (a) Equation 8.4, (b) Equation 4.20, and (c) Equations 8.7 & 4.20.
Figure 8.14  Calculated resistance vs. total radiation ($Q_{\text{total}}$) using three models: (a) Equation 8.4, (b) Equation 4.20, and (c) Equations 8.7 & 4.20.
demonstrated that New Guinea *Impatiens* total leaf resistance decreased with both VPD and LVPD over the range of conditions used in this experiment. In addition, this trend was seen under both growth chamber and greenhouse conditions, which rules out spectral quality as a contributing factor to the differences noted above. However, several other factors may have contributed to this trend.

First, we may look at the results of measured leaf temperature difference (LTD; $T_{\text{leaf}} - T_{\text{air}}$), which is a direct result of a leaf energy balance. A negative LTD may indicate, for example, that transpiration is evaporatively cooling the leaf at a faster rate than it is being radiatively heated. Figure 8.15 shows the change in measured LTD with (a) light level and (b) air temperature, and Figure 8.16 shows LTD plotted against (a) LVPD, (b) VPD, and (c) total radiation. Figure 8.16 graphically demonstrates that LTD decreased (became more negative) with increasing transpiration load, as measured by LVPD. LTD also decreased with increasing VPD but did not respond to differences in total radiation load. At low LVPD and VPD (0.4 to 0.6 kPa), the LTD was very nearly zero, indicating a balance between heat load and evaporative cooling. While the model expressed by Equation 8.7 would predict that stomatal resistance would decrease with increasing radiation load with an accompanying increase in transpiration, no such increase in water uptake was seen in this experiment. This indicates that resistance estimated based on ET (by Equation 8.6) would increasingly under-estimate the resistance based on water uptake as radiation increased. Figure 8.14 supports this conclusion. It shows that as radiation increased, the prediction of
Figure 8.15  Mean ±1 standard deviation of leaf temperature difference (LTD) vs. (a) air temperature and (b) light level.
Leaf temperature difference (LTD) vs several parameters: (a) leaf VPD (LVPD), (b) vapor pressure deficit (VPD), and (c) total radiation ($Q_{\text{total}}$).

**Figure 8.16**
resistance by Equation 8.7 decreased (Figure 8.14(c)) while the resistance estimated by
results from this experiment increased (Figure 8.14 (a) and (b)). The decrease in LTD
with LVPD (Figure 8.16(a)) and VPD (Figure 8.16 (b)) indicates that ET increased at
a relatively faster rate than leaf heat load. This would indicate that ET increased
despite the increase in resistance shown in Figures 8.12 and 8.13 (a) and (b). This
suggests that resistance increased at a slow enough rate relative to the transpiration
driving force to allow a net increase in transpiration. However, this does not entirely
elucidate the differences between methods (a) and (b) and method (c) because it can
be shown by this argument that ET could either increase or decrease with either
increasing or decreasing resistance depending on the relative increase or decrease in
LVPD.

A second factor may also help explain the difference between water uptake-
determined and ET-determined resistances. Though Figures 8.12(a) and (b) show that
resistance increased with LVPD, Figure 8.11(a) showed that water uptake increased as
well. Recall the relationship between LVPD and water uptake with these simple
examples: if resistance was held constant and LVPD increased, water uptake would
increase; if resistance increased and LVPD was held constant, water uptake would
decrease. However, Figures 8.12(a) and (b) together with Figure 8.11(a) show that
both water uptake and resistance increased with increasing LVPD. This can only
occur, as stated above, if the increase in LVPD was larger in proportion to the
accompanying increase in resistance; i.e. the driving force increased at a faster rate
than the resisting force. In this case, the greater relative increase in LVPD would out-
pace the increase in resistance to cause a net increase in water uptake.

The difference in resistance trends between methods (a) and (b) and method (c) from Figures 8.12 through 8.14 is also evident in a plot of the ratio of actual water uptake to estimated ET, where ET was estimated in two ways: (a) by Equation 8.4 (based upon LVPD) and (b) by Equation 4.20 (based upon $Q_r$ and VPD), both using Pang's stomatal resistance estimate (Equation 8.7). Figure 8.17 shows these calculations in the form of the ratio of measured water uptake to ET plotted against light level. Each data point was the average of measured water uptake to calculated ET for 7 days of data. Water uptake was found to be greater than predicted ET at the lowest light level and less than predicted ET at the highest light level. More important than the actual values of the ratio was the overall trend: as light level increased, the ability of water uptake to keep up with the demand of ET decreased.

This data suggested that New Guinea *Impatiens*, colloquially called a "low-
light" crop, had a low transpiration capacity and may not have had the ability to uptake water at a rate fast enough to keep pace with evaporation from the crop's leaves under all conditions. Water uptake could be less than ET under conditions of higher evaporation potential, such as the increase in leaf temperature that accompanies higher radiation levels.

For this explanation to make physical sense, the plant must have adequate storage capacity for water in order to permit extended periods of water uptake deficit (water uptake lower than ET). In a small experiment to determine the water holding
Figure 8.17  Measured water uptake: evapotranspiration (ET) predicted by (a) Equation 8.4 and (b) Equation 4.20 vs. light level. Each point averaged 7 days of data.
capacity of New Guinea *Impatiens*, 12 plant shoots were measured at full turgor and
12 plant shoots measured in the range between temporary wilting and permanent
wilting. At full turgor, the plants were found to hold approximately 90.9% water by
weight (within the range of 80 to 95% typical range for plants: Chapter 4) and 10.0
$g_{\text{water}} \frac{g}{g_{\text{dry mass}}}$. This translates into 106 g of water per plant (excluding roots), with the
actual average measured shoot dry weight of 10.6 g (at the end of the GC2
experiment), and 3180 g m$^{-2}$ (using 30 plants m$^{-2}$ in this experiment). The data also
showed New Guinea *Impatiens* held an average of 3.4% less water at wilting point
than at saturation. From this, it can be estimated that the available storage capacity at
the end of the GC2 experiment was approximately 110 g m$^{-2}$. By comparison, the
water deficit experienced by the plants at 100% light level (the worst case scenario
from this study) would require approximately 400 to 1500 g m$^{-2}$ (from Figure 8.17(a)
and (b), respectively) of available water storage capacity during a 12 hour period ($ET - \text{water uptake} \approx (a) 367 - 0.91(367) = 33 g m^2 h^{-1}$ and (b) $367 - 0.66(367) = 125 g m^2 h^{-1}$). This calculation is quite rough, but shows that the storage volume of New
Guinea *Impatiens* may be adequate to support short periods of water uptake deficit.

If ET out-paces water uptake during the day, then in order for the plant to
remain reasonably turgid, water uptake must increase in the succeeding night period.
Figure 8.18 shows that even though LVPD from the previous day had no effect on
LVPD of the succeeding night (8.18(a)), water uptake increased (8.18(b)) and
accordingly LTD decreased (8.18(c)) during nights following days of higher LVPD.
This demonstrates that New Guinea *Impatiens* actively rehydrate during nights.
Figure 8.18 Effects of leaf vapor pressure deficit (LVPD) from previous day on night: (a) LVPD, (b) water uptake ($W_{up}$), and (c) leaf temperature deficit (LTD).
following days with large transpiration loads, irrespective of the nighttime environment.

Third, LVPD was estimated from the measurement of 8 leaf temperatures on the top layer of the canopy. Fynn et al. (in review) reported that the leaf temperature of the top layer of leaves in New Guinea *Impatiens* was higher than the lower layers, particularly during the day, when solar radiation load acted preferentially on the top layer of leaves. If this condition held true with the canopy of plants in this experiment, then the LVPD applicable to the whole canopy would have been overestimated by using only the leaf temperatures from the top layer to estimate LVPD (because leaf temperature would have been overestimated, and higher leaf temperature translates into higher leaf vapor pressure and higher LVPD). This would cause an overestimation of the driving force for ET. Since we used this LVPD along with the measured water uptake to calculate resistance (refer to Equation 8.3), we see that the calculated resistance term would have been overestimated in order to compensate for the artificially high LVPD. This potential deficiency in using a single layer leaf model to estimate transpiration responses of a whole plant was not evident in these analyses, stomatal resistances calculated by each of the 3 methods all averaged within the reasonably similar range of 600 to 800 s m⁻¹.

In conclusion, results from this data imply the existence of an additional "whole plant" resistance to transpiration which becomes significant when the rate of transpiration through the plant increases. This resistance prevents the water uptake from keeping pace with transpiration during the day. Failure to include such a factor
in an ET model may cause plant water uptake to be overestimated during high light periods, where uptake can not keep pace with demand, and underestimated during the low light recovery periods following the high light periods, during which the plant rehydrates. Data from this study was not of adequate precision to quantify such a resistance.

8.5 Discussion

Water and nutrients are generally applied and/or transported to the plant root zone together. If nutrients are also transported into the plant with water, referred to as passive uptake, then nutrient uptake can be predicted based on measured water uptake. Figures 8.19(a) and (b) show the rate of nutrient uptake predicted by a passive, mass-flow uptake of nutrients along with water uptake. Estimates were calculated from measured water uptake rate ($L \cdot m^{-2} \cdot h^{-1}$) multiplied by nutrient concentration (mg $L^{-1}$) to determine nutrient uptake rate (mg $m^{-2} \cdot h^{-1}$). Higher concentrations of nutrients in solution and higher water uptake rates resulted in higher passive nutrient uptake rates. Figures 8.20(a) and (b) compare measured uptake rates of each nutrient with the passive uptake predicted at an individual nutrient concentration of 100 mg $L^{-1}$. All nutrients were absorbed at rates considerably less than that predicted by passive uptake. This indicates that the plant in this study was able to selectively exclude nutrients from being absorbed.
Figure 8.19  Nutrient uptake rate predicted if nutrients were absorbed by the plant at the same rate as water uptake (i.e. by mass flow) vs. (a) air temperature and (b) light level.
Figure 8.20  Actual nutrient uptake rate and predicted uptake by mass flow (w/ H2O) for 100 mg L⁻¹ concentration vs. (a) air temperature and (b) light level.
Figure 8.21 plots individual nutrient uptake against concentration along with uptake predicted by mass flow with water. Again, nutrient uptake was always less than that predicted by passive flow of nutrients into the plant. Also, the difference between passive flux and actual uptake increased with concentration.

Nutrients clearly were not transported into the plant with water flow. However, movement of water into the plant draws new solution by mass flow to the plant root zone and into the root free space. Thus, higher nutrient concentrations and higher water uptake rates induce higher nutrient replenishment rates to the sites of active nutrient uptake in the roots. Assuming that nutrients were supplied to the roots at the
rate dictated by mass solution flow, a nutrient use efficiency (NUE) was calculated as the ratio of nutrient uptake to nutrient replenishment.

$$NUE = \frac{V_n}{S_n}$$

(8.6)

where:

$NUE = \text{nutrient use efficiency (unitless)}$

$V_n = \text{rate of nutrient uptake (mg m}^{-2}\text{ h}^{-1})$

$S_n = \text{rate of nutrient supply or replenishment (mg m}^{-2}\text{ h}^{-1})$

Data from Figure 8.21 was reexpressed in terms of NUE (Figure 8.22). NUE for N, P, Ca, and Mg generally increased as concentration of each nutrient decreased. K demonstrated a peak efficiency near 45 mg L$^{-1}$ before decreasing at lower concentrations. P appeared to be approaching a maximum efficiency at 20 mg L$^{-1}$.

NUE provides a simplistic indication of the plant's ability to absorb nutrients from the available solution. This approach was clearly limited since it did not take into account the nutrient accumulation that occurred when nutrient uptake was less than the net passive supply rate, or the influence of diffusion as nutrient concentration gradients changed. In addition, a high NUE did not necessarily indicate high growth efficiency or high quality production, which are two measures with more practical significance than efficiency of nutrient use.

Data from this study was used to predict the minimum nutrient solution concentrations necessary to replenish absorbed nutrients. For example, let us assume
that a crop of New Guinea *Impatiens* had a P uptake rate of 5 mg m\(^{-2}\) h\(^{-1}\) and a water uptake rate of 0.5 L m\(^{-2}\) h\(^{-1}\) under some set of environmental conditions. We can make a first approximation that the necessary concentration of P in solution would be 5 mg m\(^{-2}\) h\(^{-1}\) + 0.5 L m\(^{-2}\) h\(^{-1}\) = 10 mg L\(^{-1}\) in order to exactly replenish the nutrients absorbed by the plants. Figure 8.22 shows that the NUE for P at 10 mg L\(^{-1}\) was about 0.24; in other words, only 24% of the available nutrients would be absorbed at 10 mg L\(^{-1}\). This suggests that only 2.4 mg L\(^{-1}\) would be absorbed with a solution concentration of 10 mg L\(^{-1}\). Thus, the concentration must increase to account for NUE. A second approximation would be: 10 + 0.24 = 42 mg L\(^{-1}\). At this concentration the NUE decreased to 0.22; thus, the next iteration would generate a P solution concentration
requirement of: $10 + 0.22 = 45 \text{ mg L}^{-1}$. The solution stabilized at this iteration for this case, meaning that $45 \text{ mg L}^{-1}$ of P should be applied to meet the P requirements for those environmental conditions. Each nutrient concentration must be solved independently. Other nutrients with a greater NUE curve slope may require more than 3 iterations.

Figure 8.23 displays the results found using this technique to estimate the desired solution concentration of each nutrient for a range of possible water uptake rates. For instance, if water uptake during a certain period were to average $0.5 \text{ L m}^{-2} \text{ h}^{-1}$ (a moderately high water uptake rate for the plants in this study), we should apply a nutrient solution of $30 \text{ mg L}^{-1}$ N, $13 \text{ P}$, $25 \text{ K}$, $24 \text{ Ca}$, and $7 \text{ Mg}$ in order to meet the predicted uptake requirements for this period. By contrast, at a lower water uptake rate of $0.15 \text{ L m}^{-2} \text{ h}^{-1}$, we should apply a nutrient solution of $210 \text{ mg L}^{-1}$ N, $47 \text{ P}$, $180 \text{ K}$, $270 \text{ Ca}$, and $29 \text{ Mg}$. This compares with the common recommendation of $100 \text{ mg L}^{-1}$ N, $30 \text{ P}$, $100 \text{ K}$, $100 \text{ Ca}$, and $30 \text{ Mg}$ typical for New Guinea Impatiens production.

By this analysis it is evident that the standard nutrient recipe (i.e. the 1x recipe described earlier with $100 \text{ mg L}^{-1}$ N, etc.) would over-fertilize these plants under high transpiration periods and under-fertilize during low transpiration periods.

Based on the results of the nutrient uptake analysis from Section 8.3, nutrient uptake was assumed to be unaffected by light or temperature in these calculations. This greatly simplifies the calculations, though the procedure would be equally valid using an environmentally-based nutrient demand model instead of constant values.
Figure 8.23 Predicted solution concentrations of each nutrient to provide adequate nutrient supply to meet demand over a range of water uptake rates.
CHAPTER IX
CONCLUSION

9.1 Summary and Conclusions

The primary purpose of this dissertation was to improve the understanding of water and nutrient uptake in relation to the environment in order to help develop recommendations for effective use of greenhouse fertigation systems. Objectives 1 through 5 (Section 1.3) are concerned with achieving this goal, and will be addressed in this section.

Objective 1. A plant growing system was developed which was capable of detecting short-term changes in nutrient uptake. Peat moss media was found to be inappropriate for systems which measure nutrient uptake by changes in solution concentration in a steady-state, recirculating irrigation system. This was primarily due to the contribution of soluble salts contained in the media. An inert gravel media, Haydite (a sorted, expanded shale media), provided an adequate media for plant growth consistent with the requirements for studying nutrient uptake.

Objective 2. The experimental materials and methods used in this study did not have sufficient resolution to identify characteristic time responses of nutrient
uptake to changes in environmental conditions. Plant nutrient uptake did not have consistent time responses to changes in light levels, and ultimately were found to not respond to changes in light and temperature. It is likely that plant nutrient uptake response to short-term changes in environmental conditions was muted by nutrient storage. In other words, storage may allow plants to integrate short-term variations in nutrient demand.

**Objective 3.** Nutrient uptake of N, P, Ca, and Mg was not significantly related to daytime air temperature, light level, or nutrient concentration. Uptake of K was significantly related to K concentration (though the wider range of K concentration treatments contributed to this) but not temperature or light level. Although not statistically significant, general trends in the data were identified: uptake increased with increasing nutrient concentrations for all nutrients, and uptake showed a slight increase with increasing light level. This data did not provide clear statistical support for the hypothesis that nutrient demand influenced short term (less than daily) variations in nutrient uptake. This experiment was not designed to study the longer-term (greater than daily) effects the environment or demand may have had on nutrient uptake.

**Objectives 4 and 5.** This study distinctly separated water uptake by plant roots and transpiration from plant leaves. Water uptake increased with vapor pressure deficit (VPD) and leaf VPD (LVPD), but was not affected by total radiation ($Q_{\text{total}}$). In contrast, individual leaf transpiration response was found to increase with photosynthetic photon flux density (PPFD) under both greenhouse and growth chamber
environments. The leaf transpiration result was supported by Pang (1992), who showed a close relationship between canopy transpiration and solar radiation ($Q_{\text{solar}}$) for New Guinea *Impatiens* in the greenhouse. These results indicate that while transpiration rate was determined, at least in part, by irradiance, water uptake rate was independent of irradiance within the range of irradiance levels in this study. The differences between water uptake and predicted transpiration based on a model developed by Pang (1992) using New Guinea *Impatiens* in the greenhouse was at least in part due to the difference in canopy structure and plant density between the two studies.

Stomatal (internal) resistance was calculated using three different methods: (a) the combination equation using LVPD (Equation 8.4), based on measured water uptake in the growth chamber, (b) the combination equation using VPD and $Q_{\text{total}}$ (Equation 4.20), based on measured water uptake in the growth chamber; and (c) a model developed by Pang (1992) using VPD and $Q_{\text{total}}$ (essentially Equation 8.7 along with Equation 4.20), based on measured evapotranspiration in the greenhouse. Traditional curves of stomatal resistance plotted against the driving factors of transpiration (LVPD, VPD, and $Q_{\text{total}}$) resulted in poor regression correlations. The poor correlations reflected a poor correspondence between water uptake and transpiration, which was proposed to be due to an additional whole-plant resistance not accounted for in the combination equation model of evapotranspiration.

In general, the calculated stomatal resistances increased with increasing LVPD, VPD, and $Q_{\text{total}}$ using methods (a) and (b), but decreased with LVPD, VPD and $Q_{\text{total}}$.
using method (c). The difference in trends was proposed to be partly a result of changes in plant water status, where plant water stores were used to make up the difference between transpiration demand and water uptake supply. Again, the difference between water uptake and transpiration may imply the existence of an additional resistance to the transpiration process which has not been explicitly included in evapotranspiration models. A whole plant resistance, independent of stomatal resistance, was proposed to contribute to the difference between water uptake and transpiration. This resistance limits the rate of plant rehydration, which in turn influences the relative hydration of the plant, and ultimately impacts the ability of the plant to meet transpiration requirements.

Direct comparisons between the study by Pang (1992) and this study were complicated by the difference in canopy structure between the two studies. The leaf area index (LAI) in this study ranged from 4.5 to 8.0 while the LAI in the study by Pang only reached 4.5 at the end of that study period. The higher LAI in this study decreased the relative portion of the canopy's leaves which were in direct contact with the incident radiation and boundary layer aerial environment, and influenced the energy and mass flows between each leaf and those radiative and aerial environments. Thus, the model of stomatal resistance developed under the set of LAI conditions in the study by Pang may not be appropriately applied to the different canopy structure found in this study, even though the same crop was used.

Nighttime water and nutrient uptake were significant. Nighttime water uptake increased following days with high transpiration potential, as measured by LVPD.
This demonstrated New Guinea *Impatiens'* capacity for recovering from periods of water deficit during periods of lower water demand. In addition, nutrient uptake was found to occur at night, indicating that not all nutrient uptake was directly related to feedback mechanisms induced by environmental or growth factors.

### 9.2 Implications for Commercial Industry

Objective 6 (Section 1.3) was to develop water and nutrient management recommendations from the results of this study. The following section addresses this objective.

**Objective 6.** The conclusion that nutrient uptake was not affected by short term (daily) changes in the environment is significant for the greenhouse industry. If this result is shown to be generalizable to a wide range of plant types, growers would not need to be concerned with fine-tuning nutrient recipes according to short term swings in environment. In addition, developers of new computer fertilizer control systems will not need to focus their effort toward describing short term fluctuations in plant uptake, or developing software or hardware to accommodate such fluctuations.

The difference between water uptake and transpiration is a practical concern for growers who irrigate according to the combination equation prediction of transpiration, a practice which has begun to be incorporated in modern computer control systems. Model estimates of transpiration will exceed actual water uptake to the extent that whole plant resistance reduces water movement from the root zone to the site of leaf
evaporation. As such, ignoring whole plant resistance may cause growers to over-irrigate during periods of predicted high transpiration rate (e.g. midday) and under-irrigate during periods of low predicted transpiration rate during which the plant may require rehydration (e.g. night).

Nutrient recipes were calculated for a range of water uptake rates assuming constant nutrient demand. Though nutrient uptake was independent of environmental conditions, water uptake varied considerably with changes in the environment. In addition, nutrient use was found to be more effective (in terms of nutrient use efficiency, NUE) at lower nutrient concentrations. These results suggested that nutrient concentrations must be managed together with water supply rates to prevent excessive quantities of nutrients from reaching the root zone. It was concluded that the mass of applied nutrients must be maintained at a constant rate. Thus, resultant nutrient concentrations in the supply irrigation solution will decrease with increasing water supply rates.

9.3 Recommendation for Further Study

This study focussed on a single crop, New Guinea Impatiens, with specific physiological characteristics. Low transpirational capacity and high capacity for water storage both had significant effects on the results and conclusions of both water and nutrient aspects of this experiment. Crops with a range of water transpiring and storing characteristics should be studied before generalizations to other crops are made.
In addition, *Impatiens* begin flowering at a very early stage of growth; other crops with more determinate transitions between growth stages may demonstrate significantly different patterns of nutrient uptake.

Efforts should be made to develop growth chambers with spatially as well as spectrally uniform irradiance distributions over the growing surface. Such a growth chamber would more closely resemble the uniformity of light conditions achieved in the diffusive radiative environment of naturally-lit greenhouses. This would allow larger blocks of plants to be grown under specific irradiance conditions, permit more extensive replication of research results, and facilitate direct comparisons of water and nutrient uptake responses under artificial and natural light conditions. Data from such experiments would enable more appropriate generalizations from growth chamber to commercial greenhouse conditions.

Further work must evaluate the longer term effects of environment on nutrient uptake and demand. Growth chamber work allows great flexibility in applying consistent conditions for periods of time as long as an entire growing season, and could be used to help determine weekly or monthly relationships between environmental conditions and resultant nutrient uptake rates. For crops that are grown year-round, it may be important to determine seasonal difference in nutrient demand determined by seasonal differences in growing conditions as well as crop maturity. Technologically straightforward shading and temperature control studies could elucidate more complex relationships between nutrient uptake and the environment as well as test hypotheses from growth chamber studies, both within the context of
seasonal, diurnal, and transitory variations of the radiative environment inherent to commercial greenhouse systems.

The apparent difference between transpiration and water uptake found in this study is an important issue for automated irrigation control. An experiment in which both transpiration and water uptake were measured simultaneously would conclusively determine any such differences. This could be done using a combination of the System Weight and Stock-tank Weight methods outlined in Section 5.6.2. One lysimeter would measure plant canopy evapotranspiration by monitoring weight loss by an entire bench system, while a second lysimeter would measure water uptake by monitoring weight loss from the same system’s stock-tank alone. This would provide a real-time tracking of how well water uptake was able to keep pace with evapotranspiration.

A major limitation in the combination equation model of evapotranspiration is its inherent requirement that a canopy be modeled as a single layer of leaves which are influenced by a homogenous radiative and aerial environment. Future work should: 1) determine more appropriate methods of assigning environmental conditions to defined layers of leaves within the canopy of various plant structures, and incorporate these methods in a combination equation-like model; 2) develop theoretical simulation models to describe the transfer of energy and mass within canopies of various structures; and 3) develop methods and instrumentation to separately evaluate transpiration from different layers in the canopy and use these to test simulation results.
REFERENCES


ASAE (1986). ASAE Engineering Practice: EP411.1; Guidelines for measuring and reporting environmental parameters for plant experiments in growth chambers. ASAE, St. Josephs, MI.


