Comparative study of temperature and light on vegetative growth of Epipremnum and Fatshedera.

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Prologue

And he gave it for his opinion, that whoever could make two ears of corn, or two blades of grass grow upon a spot of ground where only one grew before, would deserve better of mankind, and do more essential service to his country than the whole race of politicians put together.

Gulliver's Travels, part II. Chapter VII.
A voyage to Brobdingnag.
Jonathan Swift, 1726.

Abstract

The relationship between temperature and light on vegetative growth of *Epipremnum aureum* (Linden and Andre) Bunt. and X *Fatshedera lizei* (Guillaum) plants was investigated in controlled environment study during the exponential growth phase. Normal and inverted day/night temperature treatments with means between 10 and 30 C were used. Maximum growth and development in *Epipremnum aureum* and X *Fatshedera lizei* occurred in constant temperature treatments at 28 ± 2 C and 22 ± 2 C, respectively. At less than 20 C relative growth rate and leaf area expansion rates for X *Fatshedera lizei* were usually higher than *Epipremnum aureum.* The difference between the two species decreased as the growth rate of *Epipremnum aureum* increased and X *Fatshedera lizei* decreased as the temperature was increased above 20 C. In both species growth in leaf area and rate of new leaf appearance were closely related to growth temperature and were less dependent on PFD. Leaf development was generally related to the sum of the rates at each temperature in the temperature regime. Growth and leaf development rates were similar in inverted and normal day/night temperature regimes. Leaf Chlorophyll was lower in high/low temperature (night/day) treatments.

Epipremnum aureum was more chilling-sensitive than X *Fatshedera lizei*, exposure to 10 C for 4 hr decreased photosynthetic competence and plant growth.

In constant day temperature (30 C) and normal night, split-night and sliding night temperatures with mean of 15 or 20 C growth of either species was similar at the same mean temperature. Growth of *Epipremnum aureum* was more acutely inhibited by the lower night temperatures than X *Fatshedera lizei.* Within each species equivalent growth and development occurred in treatments with the same mean temperature.

Epipremnum aureum and X *Fatshedera lizei* were grown at in a controlled environment at 20 and 30 C. Intact leaves were exposed to a PFD of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at leaf temperatures between 15 and 30 C and photoinhibition of photosynthesis was followed by measuring the time courses of light-saturated net

photosynthetic CO_2 uptake, photon yield of oxygen evolution and chlorophyll fluorescence kinetics at 77 K and 692 nm. Recovery of intact leaves from each growth temperature after photoinhibition for 300 min. at PFD of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 20 C was followed for 450 min. at 10, 20 or 30 C at PFD of 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Both species were similar in their sensitivity to photoinhibition manifested as a temperature-dependent quenching of chlorophyll fluorescence (Fv/Fm) at 77 K, coupled with concomitant parallel reduction in light-saturated photosynthesis and photon yield of oxygen evolution.

The chlorophyll fluorescence characteristics of each species at growth temperatures of 20 and 30 C were similar, while the fluorescence and photosynthetic characteristics of both species were higher at 20 C than at 30 C. Maximum rates of photosynthesis for *Epipremnum aureum* at 20 and 30 C were 11.5 and 6.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. In X *Fatshedera lizei* maximum rates of photosynthesis at 20 and 30 C were 16.9 and 12.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively.

X *Fatshedera lizei* leaves were more resistant than *Epipremnum aureum* to change in photosynthesis during photoinhibition. Photo-oxidative damage occurred in *Epipremnum aureum* leaves grown at 30 C after prolonged exposed to high PFD at 20 C or 15 C, whereas photoinhibitory treatments using higher leaf temperatures or lower PFD did not cause permanent damage. In each species the quenching of chlorophyll fluorescence induced by bright light depended upon an interaction with both growth and current leaf temperatures.

Both species were similar in sensitivity to photoinhibition. However, the chilling tolerant X *Fatshedera lizei* was able to recover more efficiently than the chilling sensitive *Epipremnum aureum* at low temperatures, irrespective of the growth temperature.

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I am grateful that in 2021 Nieves Vidal

discovered there were no copies of this

thesis in the University Library or the Archives.

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Table of Contents

List of Plates

List of Tables

CHAPTER ONE

General Introduction

"The world will never starve for want of wonder;
but only for want of wonder."

Tremendous Trifles
G. K. Chesterton

1.0 Introduction

Botanists have described more than 265,000 plant species and a million cultivars growing in diverse habitats tolerating extremes of light and temperature as they colonise niches over the majority of the planet (Raven, 1987). Foliage plants represent an arbitrary section of the plant kingdom exploited commercially because of their amenity value and utilised primarily for interior decoration or interior landscape purposes. While foliage plants may have flowers, these are of secondary importance compared to the features of the vegetative structures (Conover, 1980).

The foliage plant industry has its roots deep in the mists of antiquity. Historical records show that exotic plants have been cultivated in countries of the Old World far away from their natural habitat. The cultivation of ornamental plants may be traced back to temple drawings from Sumeria and Egypt where amenity horticulture was already practised about 3,500 years ago. In that era, Egyptian traders imported plants from distant countries by ship. Our view of these events may be short-sighted and underestimate how long ornamental plants have been

important to humankind. It is difficult for us to go back into history before the time of written records where:

> "the gardener Adam and his wife smile at [our] claims of long descent" (Tennyson, 1832).

In the 6th century B.C. the Hanging Gardens of Babylon were built for Nebuchadnezzar II and filled with plants from all over the known world. These gardens were esteemed as one of the seven wonders of the ancient world (Graf, 1970).

Much later, from about the 16th century, wealthy traders from Europe became involved in plant introduction for the aristocracy, seeking exotic plants from other places including tropical countries. At that time it was very fashionable for the wealthy members of society to have displays of rare and exotic plants in their orangeries. As the plant's requirements for light and heat, without noxious fumes became apparent, the environment in the orangeries was improved. There was a gradual change towards a crudely temperature-regulated structure that admitted more light which greatly enhanced the survival of tropical plants. Before the middle of the 18th century, vastly improved conditions for plant growth were available in structures such as 'The Crystal Palace' (M.A. Nichols pers. com., 1992) and closely resembling the modern greenhouse. Growers attempted to utilise principles of environmental control known at that time to regulate plant growth (Allan, 1970).

The first half of the nineteenth century saw astounding progress in the development of horticulture. A large number of new plants from all corners of the globe were brought to Europe now that plants could be grown in conditions that were similar to those in their own habitats. Plant hunting expeditions had no lack of financial support or interest. Plants from these searches became essential inputs for commercial nurseries who sought new plants in large numbers for plant fanciers.

Foliage and flowering plants have now become popular in many countries, particularly where climatic conditions preclude the year round enjoyment of a outdoors garden. Furthermore, increasing urbanisation of people, coupled with a renewed interest in growing plants has been responsible for the increased interest in ornamental plants worldwide (Beckett, 1987). The demand for foliage plants has been augmented by increasing environmental awareness and recognition of the important part that plants play in not only beautifying the environment, but also in making it safer for habitation by removing air pollutants like formaldehyde and other toxic materials liberated from many modern building construction materials (Wolverton *et al.*, 1984, 1989).

The demand for all types of potplants has increased steadily since 1945. There has however been tremendous growth in demand for foliage plants that began in the 1970s (Smith and Scarborough, 1981) and has continued through to the present day. In 1991, foliage plant production within the United States alone, was worth in excess of $US 500 m. More than half the production in the US originates from about 800 growers in Florida, utilising 1700 ha. of growing area (Conover, 1992). The annual value of the foliage plant industry at the international level probably exceeds $US 1 billion dollars, with major areas of production in North and South America, Europe and Asia.

Although the foliage plant industry in New Zealand is small (< $NZ 10 m) by international standards, it has produced crops for the domestic and export markets for many years. The local industry probably owes its inception to the Shetlander, John Nicholas Anderson who founded a houseplant business in 1889 in Napier. This family business flourished eventually becoming one of the largest foliage and flowering plant producers in the Southern Hemisphere (Anderson, 1979).

In the last three decades controlled environment facilities have been developed using high intensity lighting systems that satisfy the spectral requirements for normal plant growth and development. This has enabled scientists to examine the

effects of one or more environmental factors on plant growth, in environmental physiological studies, that may be extrapolated back to greenhouse or field conditions (Downs and Hellmers, 1975; Warrington, 1977). Recent technological innovations in greenhouse management and design have made it possible to monitor and regulate the environmental conditions with a degree of precision that allows control and optimisation of plant growth and development. Growers are not necessarily interested only in maximisation of plant growth *per se*, but in balancing heating and other production costs with production time to maximise economic return. Cost-benefit analysis has shown that environmental conditions that maximise dry matter production may not coincide with the highest yield of marketable produce. This applies equally to flowering and fruiting crops as it does to foliage plants. However, significant changes in the cost of fuel or market prices will have a major influence on the economics of production (Slack and Hand, 1983). If the capacity to control the environment is to be fully utilised in protected cropping it is essential that the parameters for each environmental factor controlling the set points be ascertained with confidence. Where the optimum environmental requirements of a crop are unknown, it is not possible to utilise the full potential of the sophisticated environmental controllers now available.

Environmental factors pertinent for crop production are known for only a limited number of agronomically important crops including capsicum (Nilwik, 1981a,b), maize (Warrington and Kanemasu, 1983a,b,c), tomato (De Koning ,1986; Heuvelink, 1989) and cucumber (Slack and Hand, 1983; Uitgave, 1987). Information describing the environmental response of ornamental greenhouse-grown crops is limited to a few flowering crops, such as: sunflower and zinnia (Hammer and Langhans, 1976), chrysanthemum (Karlsson *et al.*, 1989, Larsen and Gertsson, 1992), French marigold (Armitage *et al.*, 1981), Easter lily (Lieth and Carpenter, 1990), Petunia (Kaczperski *et al.*, 1991) and rose (Jaio *et al.*, 1988, Hopper and Hammer, 1991). In contrast, information on foliage plants is sparse because of their low economic worth relative to that of potted flowering plants. It may also be related to the relatively low production costs in the major production areas of the tropics compared with those in temperate regions.

With the increasing economic worth of foliage plants, it is surprising that detailed growth studies describing their environmental responses have not been more widely investigated, especially as production often takes place under conditions that are quite different to those in natural habitats. Furthermore, Biale (1978) reported the realisation that basic knowledge was a vital key required to explain and advance horticulture. These precepts can be traced back to Hale's Vegetable Staticks in a treatise on "The theory and practice of horticulture" (London, 1840), where it was stressed that horticultural practices should be based upon sound physiological principles.

It is in response to the increasing interest in foliage plants and the dearth of information on their environmental physiology that stimulated the current investigation. In a comparative study, the influence of light and day/night combinations of temperature and their interactions on the growth and development of *Epipremnum aureum* and X *Fatshedera lizei* were examined. The specific impacts of temperature and light on photoinhibition of photosynthesis were investigated in an attempt to understand the basis of the growth response obtained and to explain the markedly different environmental responses of the two species. A tentative schema has been developed to explain these relationships as well as the differences in growth habit between foliage species. From these studies it is hoped that further insight may be provided about the environmental physiology of these crops which will facilitate a more enlightened approach to decision-making processes in greenhouse crop production and management.

CHAPTER TWO

General Literature Review

"The shortest and surest way of arriving at real knowledge is to unlearn the lessons we have been taught, to remount first principles, and to take nobody's word about them."

Letter to Alexander Pope.
H. J. V. Bolingbroke

2.0 Introduction

Relevant literature pertaining to the effect of light and temperature on the growth and development of foliage plants including *Epipremnum aureum* and X *Fatshedera lizei* is presented in this chapter. As far as practicable this was based on investigations by researchers utilising other foliage plants. However, a significant body of the literature relevant to this study comprises results obtained from a variety of other plants other than foliage plants.

Plants are unique in their ability to produce their own basic requirements for growth from simple inputs of light, temperature, water, carbon dioxide (CO_2), and mineral nutrients by converting solar energy into stored chemical energy that drives the anabolic and catabolic processes that determine plant growth (Berry and Raison, 1981). Light is one of the essential requirements of photosynthesis and the moderator of photomorphogenic responses (Moss, 1984; Govindjee and Eaton-Rye, 1986; Thompson and White, 1991).

The absolute requirement for any of these environmental factors is largely predetermined by the basic physiology of the plant. This is regulated by the

interaction of genetic and environmental factors, and determines the plasticity of the plant to diverse environments (Bunce, 1986; Boardman, 1977).

> "Perhaps we should assume that evolution has perfected photosynthesis for high productivity in resource-limited natural environments" (Gifford, 1987).

However, it is possible that when a plant is not restricted by these natural limitations, then productivity may be enhanced. Björkman (1989) suggested that the failure to apply mechanistic knowledge of photosynthesis to crop improvement was in a large part due to insufficient knowledge of the factors determining photosynthetic adaptation to an unfavourable environment. This is certainly true for ornamental plant species (like Epipremnum and Fatshedera) that fall outside the main thrust of academic and economic pursuit.

2.1 History and Botanical Information

2.1.1 Epipremnum

Epipremnum aureum (Linden and Andre) Bunt. (*Scindapsus aureus*) is a variegated tropical vine belonging to the arum family, Araceae, and originating in the Solomon Islands. In its natural habitat this plant inhabits hot tropical jungle conditions where it grows along the forest floor and up tree trunks. It experiences a hot humid climate with minimal moisture or chilling stress. As vines mature they develop much larger leaves than the juvenile form. They also experience much higher photon flux density (PFD) as they grow higher (up to 12 m) in the canopy (Everett, 1981).

Considerable confusion has existed in the nomenclature of this species which is closely related to the Asian genus Raphidophora and the American Monstera. This species flowers very infrequently. Botanists have seen plants in flower in 1956 in Puerto Rico and in 1962 in Florida where detailed examination of the tiny flowers indicated it was neither *Pothos aureus* or *Scindapsus aureus*. It was then briefly renamed as *Rhaphidophora aurea* (Graf, 1970). Further research

indicated, however, that *Epipremnum aureum* was more appropriate (Everett, 1981; Beckett, 1987). In less than 30 years consumers have been thoroughly confused, as all of these names have been used for this plant in commercial trade (Poole *et al.*, 1985). For sometime to come, it is likely that 'Scindapsus' will be the generic name most often used in the nursery trade outside of the US.

2.1.2 Fatshedera

X *Fatshedera lizei* (Guillaum), is an intergeneric hybrid between two members of the aralia family, Araliaceae. This interesting plant originated about 1910 when Lizé Frères in the French nursery firm of Messers Nantes was accredited with accidently setting seed on *Fatsia japonica* Decne et Planch. 'Moseri' with pollen from a large leaved form of English Ivy, *Hedera helix* var. *hibernica* Kirchn. This hybrid has inherited some characteristics from each parent (Beckett, 1987; Dehgan, 1987), including considerable adaptability to varying temperature and PFDs (Araus, 1989). X *Fatshedera lizei* plants seldom exceed 2 m outdoors in mild climates, but under favourable greenhouse conditions may grow twice that height, and may occasionally produce sterile flowers (Everett, 1981).

(Hereafter each species will be referred to as either Epipremnum or Fatshedera).

Foliage plants originate from diverse habitats with respect to environmental conditions such as light, temperature, moisture and nutrient supply. However, in the absence of moisture stress, when stomatal conductance is high, and nutrient supply is not limiting, it is clear that light and temperature become the principle determinants of plant growth. In the following sections light and temperature will be considered in relation to their regulation of foliage plant growth.

2.2 Light

The rate of photosynthesis is determined primarily by the PFD and the energy available in the light spectrum between 400 and 700 nm (Thimijan and Heins, 1983; Powles, 1984; Dale, 1988). However, important morphological effects which may develop in radiation outside this spectral range can affect the rate of whole plant photosynthesis. For instance, in many species in a typical deep shade habitat, the balance between red and far-red light is altered as red light is filtered out by foliage closer to the canopy surface. This causes rapid internode extension as plants grow towards the light. In a review by Smith (1982) he concluded that the reduced fluence rate was responsible for many morphological responses affecting plant development and that a change in the red/far-red ratio was an important factor in shade acclimation.

In contrast to most controlled environment (CE) studies, there are very few naturally occurring habitats that do not experience both diurnal and seasonal variation in PFD. Plants do have some capacity to adapt to a particular light environment. This involves modulating the composition of their thylakoid membranes in a coordinated, integrated manner to make efficient use of the absorbed photosynthetically active radiation (PAR) (Anderson, 1986). This adaptive ability is reflected in the morphological changes in leaf orientation and in the partitioning of resources (such as carbon and nitrogen) among leaves, stems and roots (Boardman, 1977; Björkman, 1989). Both specific leaf area and leaf area ratio may also change in response to the light environment in conjunction with chlorophyll content and with other chloroplast components, including the size and the orientation of photosystem II antennae (Dale, 1988; Björkman, 1989).

Photon flux densities in the natural habitats of foliage plants may vary widely, ranging from $\approx$ 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$, in the extreme shade of tropical rainforests (Björkman *et al.*, 1972; Chow *et al.*, 1988) through to fully open sites where the PFD may reach in excess of 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, with no remission from bright light

at any time during normal daylight (Bunce, 1986; Anderson *et al.*, 1988). However, in many habitats the fluence rates may vary rapidly over two orders of magnitude indicating an inherent requirement for adaptability to changes in photon flux density (Anderson, 1986).

Plants have been classified as sun or shade plants according to their ability to adapt to the light environment experienced in their natural habitat (Boardman, 1977; Björkman, 1981). It has been shown, however, that the photosynthetic capacity of a plant is directly related to the environmental conditions, particularly the PFD, under which the plant is grown (Boardman, 1977; Bunce, 1986). Most plants have the capacity to adapt to different environmental conditions and depending on the species, this may be achieved by changes in leaf anatomy, physical characteristics and chemical composition. Changes can occur in some instances, even after leaves are fully mature (Syvertsen and Smith, 1984). However, some foliage plants appear to be obligate shade plants (*Aglaonema* spp., *Maranta* spp. and *Spathiphyllum* spp.) and do not normally acclimate to high light (Conover and Poole, 1990). These plants are characterised by a substantial investment in the light harvesting pigments and low capacity for electron transport compared with plants grown in bright light (Anderson, 1986; Anderson and Osmond, 1987).

2.2.1 Effect of low light

Foliage plants have been selected for their ability to adapt to indoor culture where warm temperatures are accompanied by very low light regimes. Acclimation of foliage plants has been practised with *Ficus benjamina* and other foliage plants to facilitate transition to new environmental conditions (Conover and Poole, 1975). Fonteno and McWilliams (1978) also reported that in all foliage plant species examined under decreasing PFD conditions there was an approximately exponential reduction in the light compensation point (LCP), where the net rate of photosynthesis exactly balances the total respiration rate over a 15 week period. Dark respiration also decreased, indicating that new growth would be

minimal at low PFD. Treatment of foliage plants with pesticides or brief exposure to low temperatures each caused a net CO_2 efflux for at least 3 days irrespective of the PFD. Acclimated plants were able to survive at PFDs between 2 and 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (W.S. Chow pers. com. 1991, Fonteno and McWilliams, 1978). At light levels less than the LCP, plant homeostatic equilibrium is not possible as the stored reserves are dissipated in maintenance respiration without replenishment.

Epipremnum growth and quality was improved at low PFD when the CO_2 concentration was elevated to 600 $\mu l \cdot l^{-1}$ (Schmidt and Brundert, 1984), suggesting that even at low PFD the influx of CO_2 into leaves could be an important limiting factor. Similarly, growth of Fatshedera was enhanced at 20 C by elevation of CO_2 from 600 to 1000 $\mu l \cdot l^{-1}$ (Verberkt, 1990). Epipremnum growth was not improved by supplementary light when exposed to 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 20 h per day at 24 C (Mortensen, *et al.*, 1988) indicating a light saturation response typical of deep shade plants (Boardman, 1977). Similar findings led Kristensen (1984) and Mortensen *et al.*, (1988) to conclude that Epipremnum was adaptable to growth at low PFD. Epipremnum adapted well to growth indoors irrespective of the PFD used during production (Kristensen, 1984), as indicated by the rapid rate of acclimation indicated by the reduction in LCP at low PFD. Similar findings have been reported for *Philodendron scandens oxycardium* and *Brassaia actinophylla* (Fonteno and McWilliams, 1978; Pass and Hartley, 1981). Fatshedera, in contrast to Epipremnum, has been reported to grow better at high rather than low PFD (Larsen, 1979).

2.2.2 Effect of high light

Typical light response curves for C_3 plants based on CO_2 fixation or O_2 evolution increase with increasing PFD up to a point where light saturation occurs, and no further increase in the effective rate of photosynthesis occurs with increased PFD (Powles, 1984; Krause and Weis, 1991). At some point above the light saturation point quenching of photosynthesis occurs with further exposure to additional PFD.

Impairment of photosynthetic activity by bright light has been recognised for a long time (Rabinowitch, 1945). This has however, been the object of extensive research since 1970 which has added greatly to our understanding of the mechanisms and factors involved in photosynthesis (Krause, 1988). In a review, Powles (1984) drew attention to the importance of interactions between light and temperature on photoinhibition of photosynthesis. Prolonged exposure to bright light usually results in reduced photosynthetic capacity that does not return to normal until environmental stresses are relieved. Exposure of leaves to low temperatures while in bright light exacerbates photoinhibition. Permanent damage to the thylakoid-light harvesting system occurs along with loss of chlorophyll at excessive PFD. This phenomenon has been reported in plants originating in the tropics (Lyons, 1973), and in shade-adapted plants (Dawson *et al.*, 1991), especially where exposure to low temperatures and high PFD coincide.

In some situations, foliage plants may tolerate exposure to higher PFD than in their natural habitat, provided there is sufficient air movement to maintain leaves at less than lethal temperatures (Carpenter and Nautiyal, 1969), or the exposure to high PFD is relatively brief (Harbinson and Woodward, 1984; Pearcy, 1990). A major disadvantage of the former approach is that stomates closed in moving air and remained closed at air speeds > 5 $km \cdot h^{-1}$ (Carpenter and Nautiyal, 1969).

Fatshedera plants are adaptable to relatively high PFD without apparent damage. After acclimation, light saturated photosynthesis (LSP) of Fatshedera was not influenced by incident PFD, while the LCP decreased as PFD decreased (Jeong *et al.*, 1983). In the same study, shoot growth of Fatshedera was maximised at 67% of full sunlight. The recommended PFD for Fatshedera plant production in Florida ranged between 740 and 1100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and between 650 and 830 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for Epipremnum (Joiner, 1981). In contrast, in another study recommended PFDs for production of Epipremnum ranged from 300 to 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Conover and Poole, 1990).

The morphology of foliage plants may be influenced by growth at high PFD. Leaves of *Aphelandra* spp. may be distorted or buckled at high PFD. Leaves of *Aglaonema* spp. and *Dieffenbachia* spp. may exhibit a heliotropic movement where they turn almost vertical to minimise light interception at high PFD. The size of individual leaves of *Philodendron scandens oxycardium* increased with increased PFD (Conover and Poole, 1974), while shorter, wider leaves of *Dracaena marginata* developed with increasing PFD (Conover and Poole, 1981).

2.2.3 Pigment development

The influence of light on chlorophyll and anthocyanin-related pigment development in leaves is well documented (Anderson *et al.*, 1973; Björkman, 1973; Boardman, 1977; Faragner and Chalmers, 1977; Armitage and Carlson, 1981). The leaf pigmentation of chimeric plants with zonal non-green leaves like *Codiaeum variegatum* and *Cordyline terminalis* may be masked by other principally green pigments when the PFD < 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The interaction of light and pigment production is made more complex by the ostensibly quite different responses of some chimeric plants (Anderson *et al.*, 1988). Variegated foliage, often caused by chlorophyll deficient chloroplasts, is an important attribute of many decorative foliage plants and hence these plants are widely grown. Chlorophyll development may be increased in variegated plants like Epipremnum by lowering the PFD to < 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In the related species *Syngonium podophyllum*, leaves were both whiter and larger at low rather than high PFD (Chase and Poole, 1987). Similarly, in some *Dracaena* spp. and *Peperomia* spp. the extent of the variegation appeared to increase at lower PFD (Conover and Poole, 1980, 1981; Shen and Seeley, 1983). Some Epipremnum cultivars do not tolerate exposure to high light as the white areas of the leaves are readily damaged (Poole *et al.*, 1985).

2.2.4 Photoperiodic response

Reports of photoperiodic responses of foliage plants are scarce and pertain only to plants produced as flowering foliage plants (Poole, 1971; Kerbo and Payne, 1976). Flowering of some foliage plants may be a very rare occurrence indicating that under normal circumstances these plants may have an extended juvenile period, or have adapted to a primarily asexual method of propagation with flowering restricted to environments where stress was minimal.

2.3 Temperature

Most information referring to the effect of temperature on plant growth and development refers to air temperature rather than leaf temperature. This reflects the information available and the problem of accurate measurement. No single leaf is completely representative of the entire plant. The leaves most often sampled will be near the top of the canopy exposed to high PFD and the highest air flow. Leaves from this position probably do not accurately represent the mean leaf temperature. Furthermore, the relationships between air temperature and plant growth are complex (Went, 1957).

While the light requirements of foliage plants have been reported, there appears to be few recommendations concerning temperature. This presumably reflects the relative simplicity of investigations concerned with shading or fluence rate, compared with the complexity of achieving different temperature treatments, especially in greenhouses.

In a general sense, our understanding of horticultural crop responses to temperature is improving all the time, but most interest has been focused on economically important edible crops such as cucumber (Uitgave, 1987) and on flowering plants such as chrysanthemum (De Jong and Jansen, 1992; Larson and Gertsson, 1992). Aside from minimum and maximum temperatures, broad temperature ranges form the basis of cultural conditions used in commercial

practice and only limited specific information on the response of foliage plants is available (Dawson *et al.*, 1991). Nonetheless, there is general agreement that plants derived from the temperate, subtropical and tropical regions of the world will each have different temperature optima for their growth and development (Eastin and Sullivan, 1984), responding differently to temperatures above or below the optima. Temperature is of paramount importance to foliage plants as it determines the natural distribution of each species and is a stricture imposed on the cultural requirements. This is particularly evident for those plants from tropical regions as maximum growth tends to occur near the upper thermal limit for growth. Greenhouse studies suggest Epipremnum shoot growth increased to a maximum at a day/night temperature of 32/24 C, while plant quality and shoot growth decreased at day temperatures in excess of 32 C (Poole and Conover, 1981,1988). In contrast, a related subtropical species, *Syngonium podophyllum* was much less responsive to increased temperature than Epipremnum (Chase and Poole, 1987).

2.3.1 Effect of low temperature

It has been suggested that differences between species in their growth response to temperature are dominated by the response of photosynthesis to temperature (Berry and Raison, 1981), while other workers have suggested that the primary effect of temperature is on leaf expansion (Milthorpe, 1959; Potter and Jones, 1977).

Chilling sensitive plants will frequently show signs of very slow growth and injury when exposed to temperatures below 15 C. Moisture stress and wilting of leaves at low temperatures can arise from reduced water uptake by the roots and transport. Development of plant injury depends on many factors including: the temperature and growth conditions prior to chilling, the age of the plant, light intensity, relative humidity during chilling, the rate of temperature change during chilling and the rate and timing of rewarming (Wilson, 1987). In foliage plants, symptoms of chilling injury are species dependent and quite varied. Typically

leaves may blacken and develop a water soaked appearance as epidermal cells collapse. Wilting or defoliation may occur within a few hours and plant response may be very rapid or take some days to develop (McWilliams and Smith, 1978; Fooshee and McDonnell, 1987; Wilson, 1987).

At low temperatures thylakoid protection in *Hedera* spp. may be related to increased glutathione production (Guy and Carter, 1982) and similar changes may be evident in related genera such as Fatshedera. In a range of cold hardened and unhardened plants, light dependent photosynthetic reactions were influenced more by chilling than by CO_2 uptake. Krause and Klosson (1983) concluded that a change in photochemical activity at the site of light interception in the photosynthetic pathway was probably the earliest sign of chilling injury. Adaptation of the photosynthetic apparatus to low temperature is probably more related to increased enzyme concentration rather than altered membranes (Berry and Björkman, 1980). The direct effect of thylakoid membrane composition on photosynthesis, and acclimation of photosynthesis to low temperature are both controversial (Rosinger *et al.*, 1982; Öquist, 1983; Bunce, 1986).

Foliage plants may be influenced by exposure to infrequent low night temperatures. For example, growth of Epipremnum was impaired by 3 nights per week at 10 C (Poole and Conover, 1986) probably as a consequence of the low temperature induced membrane damage and reduction in photosynthesis (Krause and Klosson, 1983). Chilling injury of Epipremnum is reported to appear as mottling of mature foliage when Epipremnum is exposed to temperatures below 13 C, while a brief exposure (< 1h) at 2 C caused severe damage (Poole *et al.*, 1985).

2.3.2 Effect of high temperature

When temperature is increased in excess of the optimum the normal balance between a net photosynthetic gain and respiratory loss is reversed and growth ceases. Normally, at higher temperatures disruption of normal metabolic activity

occurs before causing cell death (Gates, 1980). Aspects of heat resistance and susceptibility to heat stress have been reviewed by Alexandrov (1977) who concluded that fully developed cells were more resistant to stress than immature cells. Although it is useful to classify plants by temperature range, this alone would be an inadequate basis for classification. The nature of heat injury unlike chilling injury, is related to the duration of stress in an inverse exponential manner. Such an interrelationship needs to be incorporated into any discussion of thermal stress. The temperature of plant organs is often higher than the surrounding air (Levitt, 1972) and the differential can be exacerbated if transpiration is reduced when leaves are exposed to high PFD. The primary cause of damage is membrane dysfunction, probably protein and lipid denaturation (Levitt, 1972). This causes electrolyte leakage and impairment of membrane-bound enzymes. The interactions between high temperature stress and water stress makes their specific effects more difficult to resolve as they normally occur concurrently (Sullivan *et al.*, 1977).

Adaptation to growth at high temperature is greatly enhanced by prior exposure to high temperature (Berry and Björkman, 1980). This may be related to altered membrane structure and functioning (Rosinger *et al.*, 1982) or to production of isozymes of physiologically important enzymes with higher optimum temperatures.

The optimum temperature for Epipremnum root growth is above 21 C whereas air temperature should be between 21 and 35 C for good growth; provided the PFD was low, air temperatures could be as high as 38 C without incurring damage (Poole *et al.*, 1985). The importance of consistent temperatures on the production of high quality plant material has also been reported (Poole *et al.*, 1984). Optimum temperature for CO_2 fixation in *Hedera helix* was 18 C and in Epipremnum, *Ficus lyrata* and *Schefflera arboricola* was 15 C (Cuelemans *et al.*, 1985). Surprisingly, optimum growth temperatures for Hedera and Epipremnum have been reported to be less than 21 C, and between 24 and 27 C, respectively

(Mortensen and Larsen, 1989). Poole and Conover (1987) reported the best plant quality and growth of Epipremnum occurred at 32 C.

Light compensation point and respiration increased with increasing temperature, particularly in both *Hedera helix* and in *Fatsia japonica* (Matas, 1984). Both of these species are related to Fatshedera (Dehgan, 1987) and it is plausible therefore that Fatshedera may respond in some intermediate manner between these two species. Very few references have been located stating the optimum temperature for growth of Fatshedera. In constant temperature treatments, Sandved (1976) reported optimum growth at 18 C, with a minimum temperature above 12 C recommended to avoid low temperature damage. In more recent greenhouse studies at a constant 20 C, growth of Fatshedera was enhanced by supplementary light and CO_2 elevated to 700 $\mu l \cdot l^{-1}$ (Verberkt ,1990). The plasticity of this species suggests that it may be a useful subject when examining relationships between environmental physiology and plant growth.

2.4 Quantification of plant growth

Plant growth analysis has long been used by plant physiologists where it has been a useful tool for describing plant growth in general and dry matter production in particular . The pioneering work of Gregory (1918), Blackman (1919), Briggs *et al.* (1920a,b) and Fisher (1921) set out in mathematical terms the foundation for the classical approach to growth analysis. This approach normally depended upon a large number of plants that were harvested relatively infrequently and allowed the application of growth analysis formulae to determine mean rates of growth and development between harvests. Relatively recently, a dynamic or functional approach to growth analysis, based on curve fitting procedures has been developed concomitantly with increased computing capabilities (Hammerton and Stone, 1966; Radford, 1967; Hunt, 1979). This technique allows the mathematical description of plant growth at any instant during the time course of a study. This approach is now widely accepted inspite of relatively few comparisons between the classical and the functional

approaches (Hunt and Parsons, 1977; Causton and Venus, 1981). The advantages of the curve fitting (functional) approach include: fewer assumptions are needed than when using the classical approach, as the fitted curves are all that is required to adequately represent the relationships of leaf area, leaf weight and total plant weight with time. The functional approach, based on regression analysis, uses all the information from each harvest, whereas the classical approach used only the information from adjacent harvests and required pairing of plants for appropriate analysis (Causton *et al.*, 1978).

In addition, Hunt (1979) suggested that while the functional approach provided a convenient way of summarising a complex process and reduces a large data set to a few representative parameters, if the growth function is an inappropriate description of the data, then the conclusions drawn from the data could be incorrect. Thornley (1976) and Causton *et al.*, 1978) also cautioned against use of the functional approach as an empirical model where the mathematical function has no special biological significance, but where the primary aim has become accuracy of fitting. While Williams (1975) also warned

> "in general, curve fitting should be indulged only where there are clear-cut objectives, and where the practitioner is aware of the pitfalls".

The relevance of parameters fitted to polynomial models of different orders may be difficult to compare, even where environmental conditions are regulated in controlled environment studies (Hurd, 1977). Although a compromise between precision and pragmatism, it is better to select the most appropriate equations with biological meaning to describe the growth data in a convenient manner, replacing the original data disturbed by irregular errors with a smoothed continuous function (Richards, 1969; Hunt, 1973).

The problem of biological interpretation arises when fitted functions are not derived from a biological basis. The functional approach may use functions chosen somewhat arbitrarily to describe the data. Exponential curves are the simplest biologically meaningful function to deal with mathematically. They give

rise to a constant relative growth rate and are appropriate for quantifying the early growth of many organisms. Exponential polynomial functions are commonly employed as they are readily fitted using regression techniques and confidence intervals can be estimated (Causton and Venus, 1981). Although in biological systems the formation of a plateau at a maximum or minimum is universal, it may not be evident in all data sets or fitted functions. As polynomial models have no satisfactory way of dealing with an asymptotic function, models have been developed to take into account the ontogenetic change in relative growth rate as a crop develops (Hunt, 1982).

Many empirical functions have been developed to flexibly describe the growth of plants over extended periods of time and in different environmental circumstances. The Richards function appears as one of the more appropriate models of this type where the data are asymptotic, as the parameters of the fitted function may be interpreted in a biologically meaningful manner (Causton *et al.*, 1978).

Growth analysis of plants is not an end in itself, but in this study forms part of an investigation of how the vegetative growth of two foliage plants is influenced by light and temperature.

Plants function as temperature integrators provided the diurnal temperature variation is within the linear portion of the temperature response curve (Johnson and Thornley, 1985; Feng *et al.*, 1990). The overall rate of plant growth and development may be the sum of the rates at each temperature over a 24 h period. Such relationships, however, have not been proven for many crop or ornamental plants.

Under closed canopy conditions crop growth rate may be determined primarily by the total quantity of intercepted light and not by the total leaf area per plant (Monteith, 1977). It is anticipated that plant production in an intensive nursery situation would seldom, if ever, reach a closed canopy situation as productivity

is assessed on individual plant performance. However, rapid development of leaf area is considered extremely important for early crop establishment and subsequent growth. Similarly, light interception and its utilisation in photosynthesis is considered of utmost importance in determining plant productivity. These aspects will be assessed in this study.

2.5 Rationale

From the foregoing review, it is clear that there is limited information about the growth response of foliage plants, including Epipremnum and Fatshedera, in closely regulated temperature treatments with contrasting light environments. This study was designed to characterise the environmental physiology responses of Epipremnum and Fatshedera by investigating the separate effects of light and temperature (*ceteris paribus*) on vegetative growth and on photosynthetic activity. This knowledge was then used to develop hypotheses to explain differences in plant performance. In the subsequent chapters the growth and development of these foliage plants has been examined at two different PFDs and over a range of day and night temperature combinations. This led to further examination of the effect of night temperature on these plants. The final experiments sought to identify the underlying physiological basis for differences in growth of Epipremnum and Fatshedera that were manifest as interactions between light and temperature in the photoinhibition processes associated with photosynthesis.

CHAPTER THREE

Growth and development of Epipremnum and Fatshedera as influenced by temperature and light.

"The activities of living beings seem to be directed towards the attainment of goals that lie in the future [but] their behaviour just reflects the fact that they have evolved under conditions which favoured great variability."

(Eckardt, 1975)

3.1 Introduction

In the nursery trade foliage plants form an important component of total plant sales. Epipremnum and Fatshedera are well established as important foliage plants and feature prominently in industry publicity (Anon, 1992a).

Domestic sales of ornamental plants in New Zealand now exceed $NZ 200 m per annum and foliage plants would account for 5-10% of these total sales. There has been significant growth (40%) in export receipts from the ornamental plant industry over the period from 1990 to 1991 (Anon, 1992b) thus increasing industry confidence. The export potential of ornamental plants such as camellia and zantedeschia are of considerable economic importance particularly as these plants can be produced commercially outdoors in many parts of New Zealand. However, the challenges in optimising efficient plant production lies in the areas where we are not so well advantaged, particularly with greenhouse crops of tropical origin. In the prevailing free market economy New Zealand horticulturists are expected to develop and maintain a competitive edge over the rest of the world with regard to the production of ornamental plants with an inherently high energy requirement, it is essential that studies examining the fundamental environmental physiology of these crops be carried out to optimise production. Failure to support this industry with basic research in the longer term will contribute to retrenchment of grower-initiatives that create both domestic and

export opportunities for ornamental plant production. This applies particularly where our export competitors arise from production areas supported by a significant research base.

In addition, knowledge of how light and temperature interactions influence plant growth would enable growers of ornamental plants and other protected crops to plan production schedules more efficiently for the domestic and overseas markets.

The need for basic knowledge is recognised, but its importance has not been appreciated (Biale, 1987). Plant growth and development are acknowledged as the primary determinants of economic yield and have been a focus for the attention of plant physiologists and horticulturists (Landsberg, 1977). However, the transfer of information and technology from the researcher to the commercial grower does not occur readily (A.H. Hughes pers. com., 1992) and there is still much to be done in this area with many fruitful areas awaiting investigation.

3.1.1 Plant response to environmental conditions

Environmental conditions in greenhouses have been established on an empirical basis primarily dictated by considerations of plant origin and ecology. Greenhouse environments have traditionally been programmed to maintain a warmer day than night temperature due to the general belief that better plant growth and development resulted (Schimper, 1898). Conservation of photosynthates produced during the light period was the physiological explanation offered in support of this management strategy (Went, 1957). However, this may not be entirely valid as many plants appear to grow just as well at constant temperature as under conditions with no diurnal variation (Friend and Helson, 1976; Warrington and Kanemasu, 1983a,b).

The temperature regimes used in the production of greenhouse crops are of prime scientific and economic interest because of the impact they have in regulating plant development. (Post, 1939; Parups, 1978; Gent *et al.*, 1979).

The effect of temperature on plant growth has been studied for more than a century, albeit infrequently, and with widely differing results and interpretation. Some of the earliest plant science literature suggested much of the (extension) growth in crop plants occurred at night (Sachs, 1872). Similarly, development of chrysanthemum flowers are influenced by night temperature (Cathey, 1955).

Control of plant growth has also been attributed to the influence of light (Cremer, 1976; Christ, 1978; Lecharny and Jacques, 1980), temperature (Post, 1939; Went, 1957; Cremer, 1976), leaf water status (Powell, 1976; Parrish and Wolf, 1983), photosynthate and endogenous rhythms (Cremer, 1976) and plant growth regulators (Purohit, 1985).

In some crops detailed analyses have been conducted on different cultivars to identify those attributes that may be manipulated to produce an increased harvest index. This has most application where only a portion of the plant is harvested and sold, such as in a cut flower. However, an increase in production cannot be realised simply by altering the harvest index (De Jong and Jansen, 1992). In the case of foliage plants where the whole plant is sold, the grower may be interested in the possibility of altering the partitioning of dry matter into different parts of the plant including, for example, an enhanced leaf area. Comprehensive studies of this nature on foliage plant production are conspicuous by their absence.

3.1.2 Influence of diurnal temperature variation

Early studies by Went (1944) noted that the pattern of plant development under constant temperature conditions may be different where a temperature differential exists. Went proposed that plant growth could be altered by diurnal variation in

temperature, and may be influenced by the particular temperature regimes experienced during the light or the dark period. The beneficial effect of diurnal temperature variation on the growth of tomato plants was the first reported instance of thermoperiodism observed in a controlled environment facility (Went, 1944). These observations led to the concept of thermoperiodicity and Went suggested that many plants could have different temperature optima for processes occurring in the light and the dark periods.

Many experiments have been conducted to investigate the effect of diurnal variation on plant growth and development. Beneficial effects of diurnal variation have been demonstrated in lettuce (Verkerk and Spitters, 1973), tomato (Klapwijk *et al.*, 1978), cucumber (Challa, 1976; Toki, 1975) and in other species (Knapp, 1956). Heron *et al.* (1972) reported in tobacco that fresh weight, dry weight and leaf number were affected more by the night temperature than the day temperature. They concluded that diurnal variation enhanced growth and development.

The universal nature of thermoperiodicity in the plant kingdom has been contested by numerous investigators who failed to demonstrate any significant advantage from diurnal temperature treatments with a wide range of crops including bean (Dale, 1964), tomato (Calvert, 1964; Hussey, 1965), *Festuca* spp. (Robson, 1973), sunflower, cotton, maize (Rajan and Blackman, 1975), wheat, oat, pea (Friend and Helson, 1976), soybean (Warrington *et al.*, 1977), cucumber (Slack and Hand, 1983) and tropical grasses (Ivory and Whiteman, 1978).

In spite of widespread questioning, publications continue to appear in print supporting the thermoperiod concept. Recent reports using cucumbers (Krug and Liebig, 1980), rose (Van den Berg, 1984), lily (Wilkins, 1973; Erwin and Heins, 1985) and chrysanthemum (Karlsson and Heins, 1986) support the hypothesis that specific benefits exist for plant growth with a diurnal temperature differential. These results demonstrated that increased shoot extension growth occurred when day temperatures were lower than night temperatures. The morphology of

plants may also be altered by differential day/night temperatures, in particular, leaf shape (Filcher, 1954; Njoku, 1957), leaf orientation and flower size (Erwin and Heins, 1985).

To accommodate this evidence, Heins *et al.* (1989) proposed a new term 'thermomorphogenesis' to reflect the way in which temperature influences plant morphology. The term theromorphogenesis is intended to be consistent with the parallel term photomorphogenesis which describes the effect of light on plant morphology. Stem elongation responses have been reported in a range of plant species including chrysanthemum (Karlsson *et al.*, 1989), fuchsia (Erwin and Heins, 1988), poinsettia (Berghage and Heins, 1988), Easter lily (Erwin *et al.*, 1989), campanula (Moe, 1989) and tomato (Koning, 1988). A diurnal temperature differential is also reported to influence flower initiation and flower number (Moe, 1989), leaf orientation (Erwin *et al.*, 1989) and leaf pigmentation (Heins *et al.*, 1989).

These findings raise the question of why do some aspects of plant development, such as shoot growth, benefit from diurnal temperature variation while other factors, such as RGR and leaf development rate, do not?

Krug and Liebig (1980) suggested the reported inconsistencies arose from variation between species and cultivars. However, mature plants show little or no response to diurnal variation, whereas thermoperiodic effects have been reported in immature crops (Went, 1944, 1945; Calvert, 1964; Hussey, 1965). This may explain some of the inconsistencies between reports on thermoperiodism. The particular temperature in relation to an optima (Dale, 1964; Calvert, 1964; Hori and Arai, 1971), the magnitude of the diurnal variation (Knapp, 1956) and the length of the low temperature period (Toki, 1975; Challa, 1976) each may influence the nature of a thermoperiodic response. It may be concluded that any attempt to evaluate the response of plants to diurnal temperature variation would need to be comprehensive and test a wide range of environmental conditions. The value of investigating a wide range of temperature and light conditions was

demonstrated by Ashby and Oxley (1935) using the simple aquatic plant *Lemna minor.*

It would also be of particular interest to consider if plants can distinguish between exposure to a particular temperature during the light or dark period as this could challenge the traditional approach to plant production in greenhouses.

Higher night than day temperatures (23/27 C) lead to reduced shoot growth in tomato plants with minimal effect on the time to a leaf area index of 1 or on time to first harvest (Krug and Liebig, 1980). Heuvelink (1989) using tomatoes and Thomas and Raper (1978) using soybean concluded that development was less influenced by inverted day/night temperature regimes than dry weight. Differences in tomato shoot length were related to reduced internode extension rather than to the number of leaves developed. Thomas and Raper (1978) reported similar results with soybean. Recently, Erwin *et al.* (1991) and co-workers at Michigan State University have sought to exploit the relationship between day/night temperature differentials and internode extension as a practical means of plant growth control, popularly known as the "DIF temperature control program".

3.1.3 Effect of environmental conditions on greenhouse production

Increasing costs of production in protected cropping has caused growers and researchers to be more vigilant in their efforts to improve production efficiency and to effectively limit the rise in fuel consumption costs. This problem may be approached in several ways including making better use of the available energy inputs. For instance, better greenhouse construction will improve light transmission and heat retention with the potential to reduce the energy requirements for crop production. If greenhouse heating could be scheduled with night temperatures higher than the day temperature in combination with energy conservation measures during the night this could provide an alternative production strategy that may result is less energy wastage.

The greenhouse environment may be highly tuned to ensure energy wastage is minimal, but it may be difficult to optimise plant growth under these conditions. Particularly as the cultural requirements for many important greenhouse crops have not been well defined and conditions for optimal growth cannot be specified with confidence. These empirical recommendations can be used as a guide to plant response, but a systematic approach to environmental physiology would permit the construction of a more robust model to manage growth. Improvements in crop management based on a physiological response to PFD and temperature have considerable potential to produce improved plant growth with the opportunity to reduce in heating requirements. However, insufficient information is available to permit this to be carried out at present.

Manipulation of the greenhouse environment to modify crop production is not a new idea. Before the advent of chemical growth regulators, Davidson (1960) considered using low night temperature during part of the production schedule to reduce Poinsettia internode extension. This work may also be viewed as one of the earliest recorded attempts to conserve energy in greenhouse production while attempting to produce poinsettias at lower than normally accepted night temperatures.

Many plants appear to act as temperature integrators providing that growth and development is occurring in the linear part of the temperature response curve and that plants respond more to the mean daily temperature than to the individual fluctuations in temperature. Growth outside the linear range may be slower than anticipated unless the shape of the temperature response curve is defined (Orchard, 1976).

Development of Easter lilies and geranium plants in a range of thermoperiods was correlated directly with the daily accumulated heat-sum (Armitage and Carlson, 1980; Wilkins *et al.*, 1980). This has been incorporated into the standard production schedule of many commercial producers. Leaf emergence rate has also been modelled as a function of time in constant temperature treatments in

a range of crops including lily (Erwin and Heins, 1990), and wheat and barley (Volk and Bugbee, 1991). The direct translation of results derived from the constant temperature environment to the natural fluctuations in temperature of an uncontrolled environment has been questioned by Volk and Bugbee (1991). They cite the temperature dependence of leaf development in lilies as reason for concern. Clearly this is not an issue with all crops as development rate of beans was not influenced by diurnal temperature variation (Yourstone and Wallace, 1990a,b).

The processes collectively acting to regulate plant development, experience diurnal temperature variation in all but a few unusual habitats. Watson (1956) considered that those factors which influence the formation of adequate leaf area were probably the most significant determinants of dry matter production in crop plants. However, Milthorpe (1959) reported that leaf area expansion was determined by the rate of leaf unfolding which in turn was regulated by the temperature and the assimilation rate of upper leaves. This indicates a close linkage between the environment and plant development.

Despite a general awareness of the importance of environmental physiology in plant production, information applicable to foliage plant production in greenhouses is limited. The current study was undertaken to characterise the growth and development of Epipremnum and Fatshedera in different day/night temperature and light regimes in an attempt to explain their markedly different environmental responses.

3.2 Materials and Methods

3.2.1 Plant material

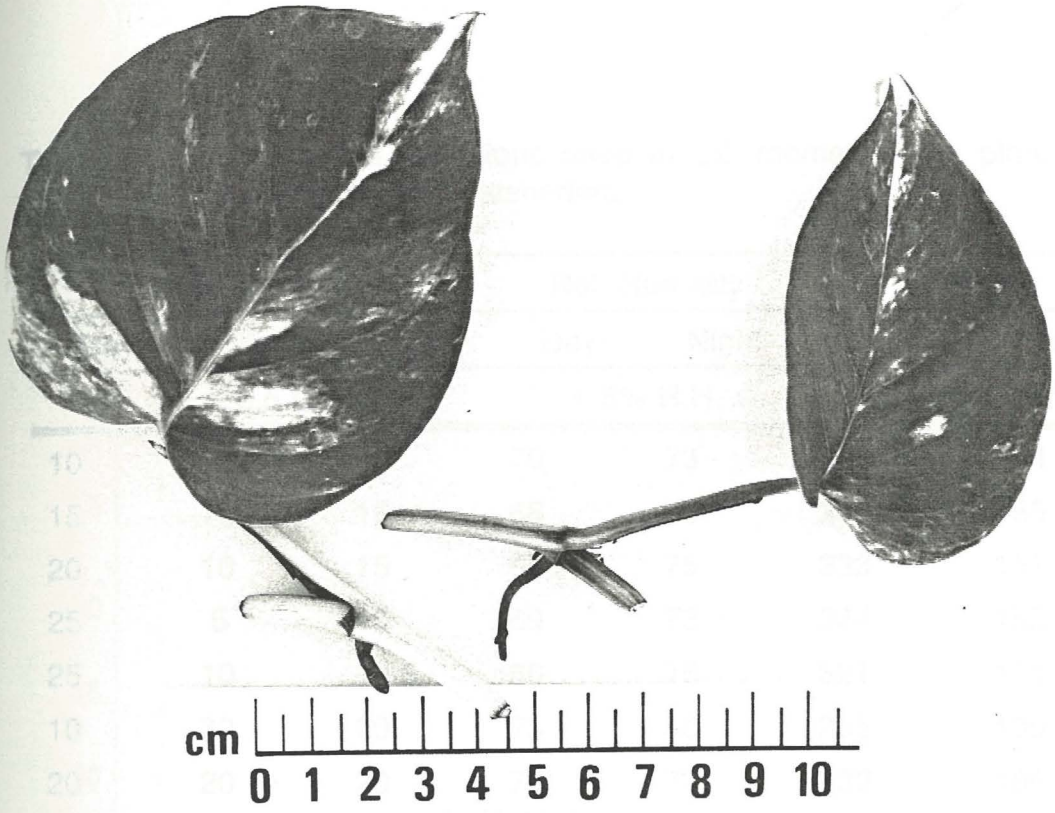
Stock plants of *Epipremnum aureum* and *Fatshedera lizei* were grown in a greenhouse heated at 15 C and ventilated at 25 C under ambient PFD (max ≈1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and ambient photoperiod conditions during autumn and winter. Plants were grown in a potting medium of 60% Hauraki peat and 40% Waikato river pumice (1-10 mm diameter) supplemented with 3 $kg \cdot m^{-3}$ Osmocote™ (8-9 month), 1 $kg \cdot m^{-3}$ Osmocote™ (3-4 month), 3 $kg \cdot m^{-3}$ dolomite lime and 0.1 $kg \cdot m^{-3}$ Micromax™ (Sierra Chemicals, Europe B.V. Heerlen, Nederland). Plants were watered automatically from the base by capillary watering and leached by weekly overhead watering.

Experimental plant material was propagated vegetatively from single node cuttings treated basally with 1% IBA powder (Plate 3-1). Cuttings were rooted in 30% Hauraki peat and 70% Waikato river fine pumice (≤2 mm diameter) under intermittent mist with bottom heat (≈ 21 C) in greenhouse conditions similar to those used for the stock plants.

Rooted cuttings were transplanted into 1.2 liter pots of containing a growing medium of 75% pea gravel, 15% peat and 10% vermiculite, and received up to four daily applications of a modified North Carolina State University nutrient solution (Brooking, 1976).

3.2.2 Growth environment

Both species were grown in walk-in controlled environment (CE) rooms maintained at a range of environmental conditions (Table 3-1, Fig. 3-1) in the DSIR Climate Laboratory (Anon, 1981). A 12 h photoperiod synchronous with the mid point of the change-over to day temperature period was provided by a water-screened array of four 1 Kw high pressure discharge "Metalarc" lamps and four



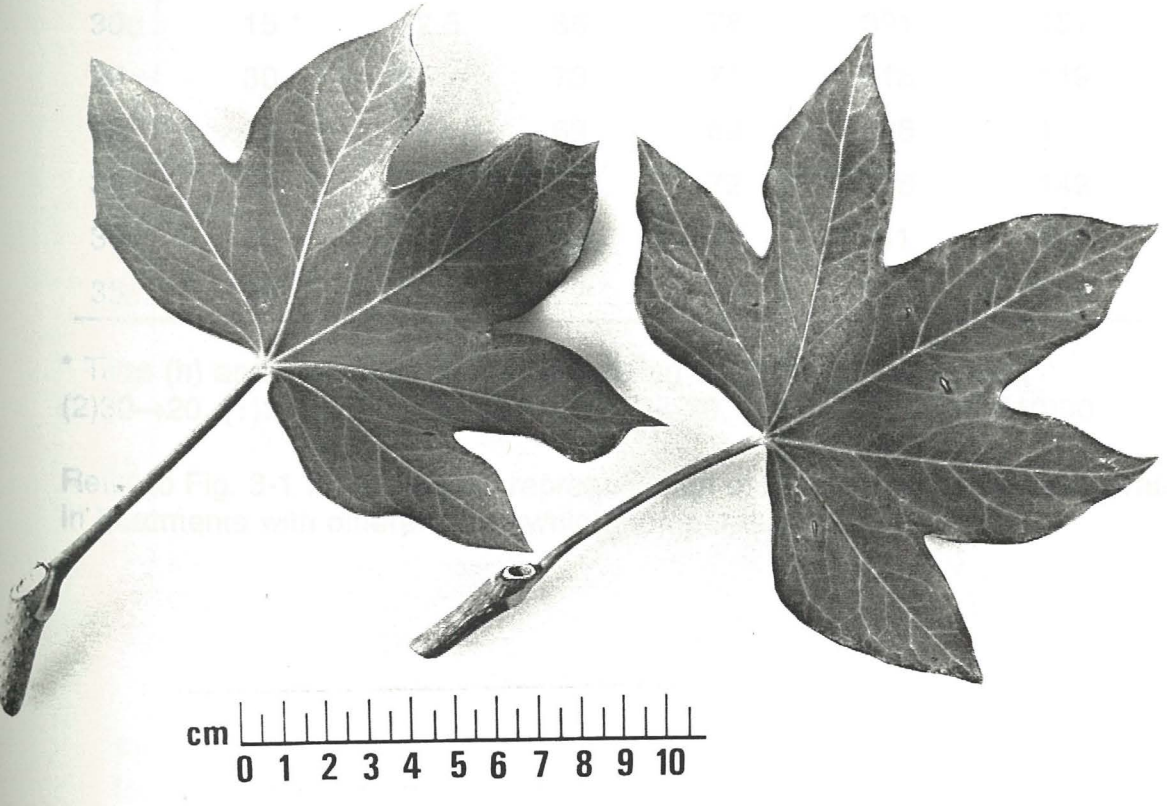


Plate 3-1. Typical propagation material of Epipremnum (upper photo) and Fatshedera (lower photo) used to produce plants for the current study.

Table 3-1 Environmental conditions used in CE rooms for the plant growth studies with Epipremnum and Fatshedera.

Temperature			Rel. Humidity		PFD	
Day	Night	Mean	Day	Night	High	Low
	± 0.5 C		± 5% R.H.		$\mu mol \cdot m^{-2} \cdot s^{-1}$	
10	10	10	70	73	328	154
15	15	15	68	70	330	155
20	10	15	68	75	333	157
25	5	15	69	73	324	152
25	10	17.5	66	78	321	151
10	30	20	73	66	295	139
20	20	20	72	70	332	156
25	15	20	71	69	331	156
30	10	20	68	75	318	149
30	15 *	22.5	66	78	321	151
20	30	25	73	71	318	149
25	25	25	69	69	326	153
30	20	25	69	72	318	149
30	30	30	69	70	311	147
35	25	30	72	71	314	148

* Time (h) and Temperature (C) scheduling for split-night treatment
(2)30→20, (1)20, (2)20→10, (4)10, (2)10→20, (1)20, (2)20→30, (10)30

Refer to Fig. 3-1 for schematic representation of the time course of temperature in treatments with differential day/night temperatures.

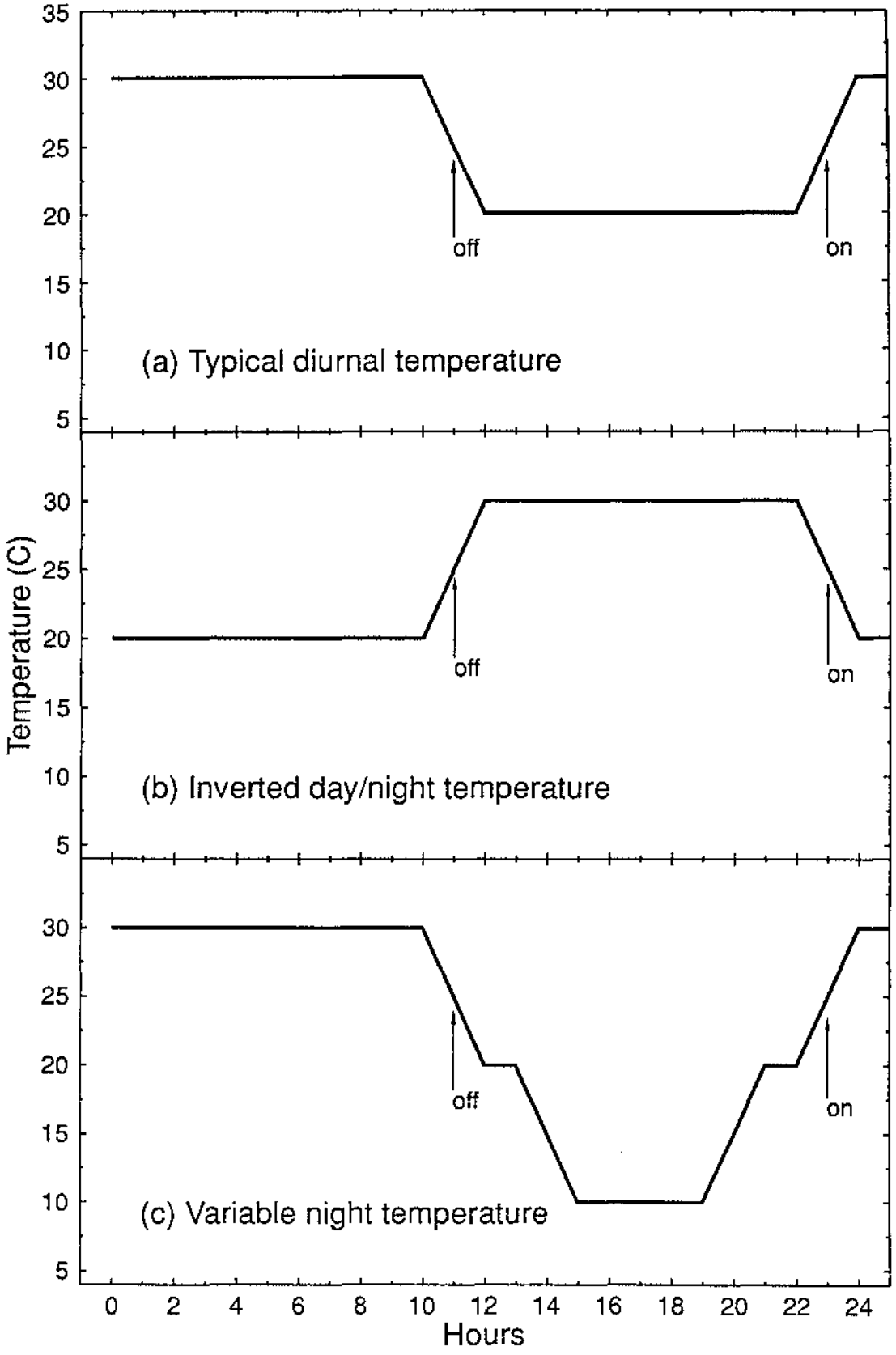


Fig. 3-1. Typical temperature regimes used in these experiments (a) for 30 C day and 20 C night temperature, (b) 20 C day and 30 C night temperature, (c) variable night temperature (30 C day, mean 15 C night). (on = beginning of photoperiod, off = end of photoperiod)

1 Kw tungsten halogen lamps (all supplied by GTE Sylvania, Drummondville, Que, Canada).

In each CE room, plants were positioned on six trolleys, three being exposed to an average PFD of 320 ± 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (measured with a Li-Cor LI-185 meter and a 190S quantum sensor (Li-Cor, Lincoln, Nebraska, USA)) at the top of the plants.

Low PFD treatments within each temperature treatment were achieved by screening three trolleys with green polypropylene shade cloth (Sarlon-Reid, Auckland, N.Z.) giving an average PFD of 150 ± 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the top of the plants (Warrington et al. 1978; Greer and Laing, 1988a) (Plate 3-2).

Plate 3-2. Shaded and non-shaded trolleys with plant material in a standard controlled environment room.

The high and low PFD in each CE room were equivalent to a daily light integral (DLI) of 14.0 and 6.8 mol[photons]·m^{-2}·day^{-1}, respectively. The water vapour pressure deficit (VPD) was controlled by the air conditioning equipment in each room (Table 3-1). Carbon dioxide was monitored continuously but not controlled during the study and ranged between 330 and 360 µl CO_2·l^{-1} air. Air flow down through plants in each CE room was 0.3 - 0.5 m·s^{-1} measured with an Alnor Instruments thermoanemometer.

3.2.3 Experimental design

In each temperature treatment, 16 plants of each species were randomly assigned to each temperature x PFD treatment. In each CE room the environmental treatments were replicated producing 3 blocks. On 3 successive occasions from the beginning of the experiment, four plants of each species selected at random from each replicate within each block, were destructively harvested. The position of the remaining plants was adjusted over the total area within the replicate to restore uniform spacing and avoid inter-plant competition.

The uniformity of growth room conditions and lack of replication in CE studies has been questioned by some investigators (Hammer and Urquhart, 1979; Lee and Rawlings, 1982). The number of treatments utilised in this study and the time required to complete each treatment precluded any possibility of replicating each treatment. In CE facilities with appropriate standardisation, the variation due to time and between CE rooms could be relatively small and generally not significant (Warrington and Kanemasu, 1983a; Dreesen and Langhans, 1991). Therefore, while using the same facilities (but not necessarily the same CE rooms) as Warrington and Kanemasu (1983a), it was assumed that differences arising in the current experiments were attributable primarily to the effects of temperature and PFD, as systematic spatial and temporal effects were assumed to be small.

The environmental conditions used in chapters three and four have been represented schematically (Fig. 3-2).

3.2.4 Plant Analysis

Shoot length, leaf area, and dry weight of the leaves, stems and roots (after washing to remove potting medium) from individual plants were recorded at each harvest. The number of leaves larger than 1 cm^2 on each plant were recorded at the final harvest.

Leaf area was measured with a Li-Cor model 3100 leaf area meter. Samples were vacuum dried (24 h at 2 mm Hg; 40 C) to constant weight and equilibrated at room temperature before recording.

3.2.5 Data Analysis.

Temperature treatments were arranged in each CE room as a randomised complete block design where each trolley within a PFD treatment represented an individual block. Data were analysed by analysis of variance using the general linear model procedure of SAS Institute, N.C. to establish whether there were significant block effects. As each temperature treatment (CE room) was unreplicated, data from each treatment were then combined, treating the temperature treatment as a simple block effect. Sequential estimates of plant dry weight (W) and leaf area (L_A) from each block (and each treatment) for the 1st, 2nd and 3rd harvests were fitted to a stepwise growth analysis program (Hunt and Parsons, 1974). Data from the initial harvest collected at the beginning of the experiment (time = 0 days) was not included as the plant material was not acclimated to the environmental conditions and therefore was not representative of growth in each treatment. Data for each of the variates was transformed logarithmically to render their variability more homogeneous with time. Estimates of RGR, LER, LAR, NAR and their standard errors (from the Hunt and Parsons

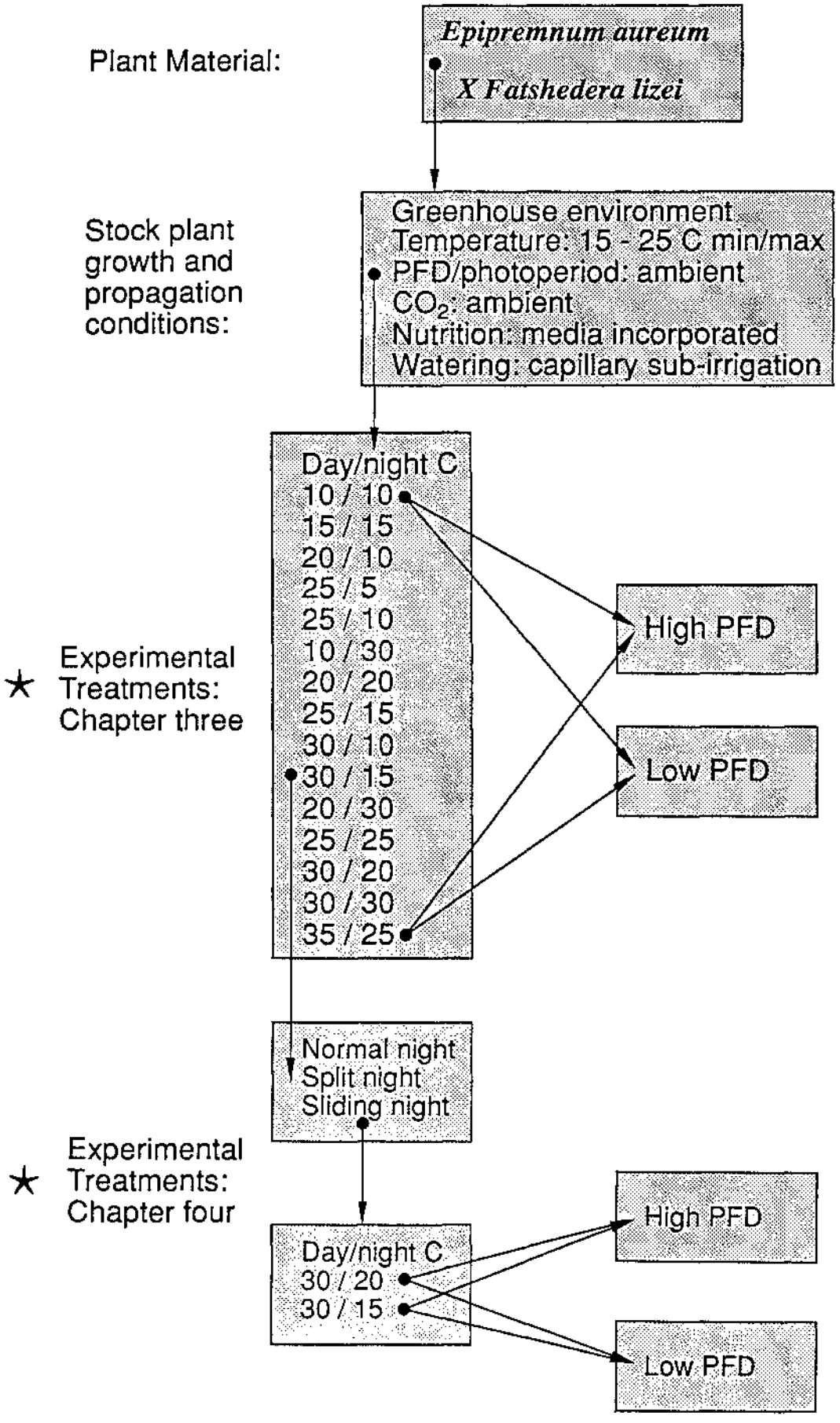


Fig. 3-2. Schematic representation of treatments used in chapters three and four. High and low PFD treatments were used within all temperature treatments.

program) were comparable with values from instantaneous functions developed in an independent analysis. The instantaneous functions were derived from polynomials fitted to leaf area (L_A), leaf weight (L_W) and total plant dry weight (W), using equations of the form $\log_e L_A$, $\log_e L_W$ and $\log_e W$ at any time (t). The least squares method was used to fit the following growth functions:

Relative growth rate (RGR) calculated from the slope of the equation:

$$\log_e W = f_W(t) \qquad (3.1)$$

$$RGR = f_W'(t) \qquad (3.2)$$

Similarly, the relative leaf area expansion rate (LER) at any instant was equal to the slope of the following function:

$$\log_e L_A = f_L(t) \qquad (3.3)$$

$$LER = f_L'(t) \qquad (3.4)$$

Inspection of the analysis of variance tables revealed that in all cases the linear fit to the exponential model was the most appropriate (P<.001). Based on this assumption five derived functions were fitted using the following equations:
Leaf area ratio (LAR)

$$LAR = \frac{L_A}{W} = \exp\left[f_L(t) - f_W(t)\right] \qquad (3.5)$$

Net assimilation rate (NAR)

$$NAR = f_W' * \exp\left[f_W(t) - f_L(t)\right] \qquad (3.6)$$

Leaf area partitioning coefficient (LAP)

$$LAP = \frac{LER}{NAR} = \frac{f_L' * \exp[f_L(t) - f_W(t)]}{f_W'} \qquad (3.7)$$

Specific leaf area (SLA)

$$SLA = \frac{L_A}{L_W} = \exp[f_A(t) - f_W(t)] \qquad (3.8)$$

Leaf weight ratio (LWR)

$$LWR = \frac{L_W}{W} = \exp[f_L(t) - f_W(t)] \qquad (3.9)$$

The notation in the equations above follows Hunt (1990).

The regression coefficients for RGR and LER were analysed as dependent variates using the Manova command within the General Linear Model (GLM) procedure (SAS Institute Inc. N.C.) as described by Eskridge and Stevens (1987) and Yourstone and Wallace (1990a,b).

The following additional parameters were calculated from the data collected at each harvest:

New leaf production per day (LFP) = $(LF_n - LF_1) / (t_n - t_1)$

Mean leaf area (MLA) = (L_{An} / LF_n)

Shoot growth per day (HP) = $(Ht_n - Ht_1) / (t_n - t_1)$

Mean node length (NOL) = SL_n / LF_n

Shoot-root ratio (SHR) = Shoot dry weight / root dry weight

Efficiency of dry weight production = $W_n / (DLI \times t_n)$

Where t_1 = time (days) at harvest 1, t_n = time at a subsequent harvest

LF_n = leaf number at t_n, L_{An} = leaf area at t_n, SL_n = Shoot length at t_n, W_n = dry weight at t_n and DLI = daily light integral.

Plate 3-3. Growth of Epipremnum (upper photo) and Fatshedera (lower photo) in a preliminary experiment at constant 20 C and at 30 C (day)/10 C (night) temperature and at high and low PFD after 45 days. Treatments, left to right: 20 C high and low PFD and 30/10 C high and low PFD.

Plate 3-4. Typical growth of Epipremnum (upper photo) and Fatshedera (lower photo) in constant temperature and high and low PFD after 52 days. Treatments, left to right: 20 C high and low PFD, 25 C high and low PFD and 30 C high and low PFD.

Plate 3-5. Typical growth of Epipremnum (upper photo) and Fatshedera (lower photo) in day/night temperature treatments 30/10 C and 10/30 C after 52 days. Treatments, (upper photo) left to right: 30/10 C; high and low PFD, 10/30 C; high and low PFD and 30 C; high and low PFD, (lower photo) 30/10 C and 10/30 C at high PFD.

3.3 Results

This research programme compared the relative importance of constant temperature and diurnal temperature on vegetative growth and development at two PFDs. Data quantifying growth and development were collected from plants grown under constant day/night temperature or with various differential day/night temperature combinations.

3.3.1 Relative growth rate

Plots of logarithms of the total dry weight (W) at each harvest show a significant linear pattern of increase over time (Fig. 3-3). This response was indicative of exponential growth and of a constant relative growth rate for both Epipremnum and Fatshedera in almost all temperatures and PFD treatments. An exception occurred at 10 C where Epipremnum exhibited a net decrease in $\log_e$ W (Fig. 3-3a). Fatshedera also only grew very slowly at 10 C as evident by the small increase in $\log_e$ W over time. As the mean temperature and the PFD increased, the slope of each fitted line increased. Invariably, W was higher in Fatshedera than Epipremnum over time by approximately the same magnitude in all temperature treatments between 10 and 20 C. The difference in W between each species tended to diminish in the low PFD treatments at constant 25 and 30 C but was maintained at high PFD (Fig. 3-3). In each species the relationship between the relative growth rate and temperature was described by a quadratic function (Fig. 3-4). In Epipremnum the RGR increased with increasing temperature reaching a maximum value at 29.6 C (from the fitted quadratic function) at low PFD, while at high PFD a peak value did not occur within the temperature range investigated. Differentiation of the fitted function indicated a maximum value occurred at about 36 C. The curvilinear relationship of RGR to temperature in Fatshedera peaked at 23.0 and 22.2 C at high and low PFD, respectively.

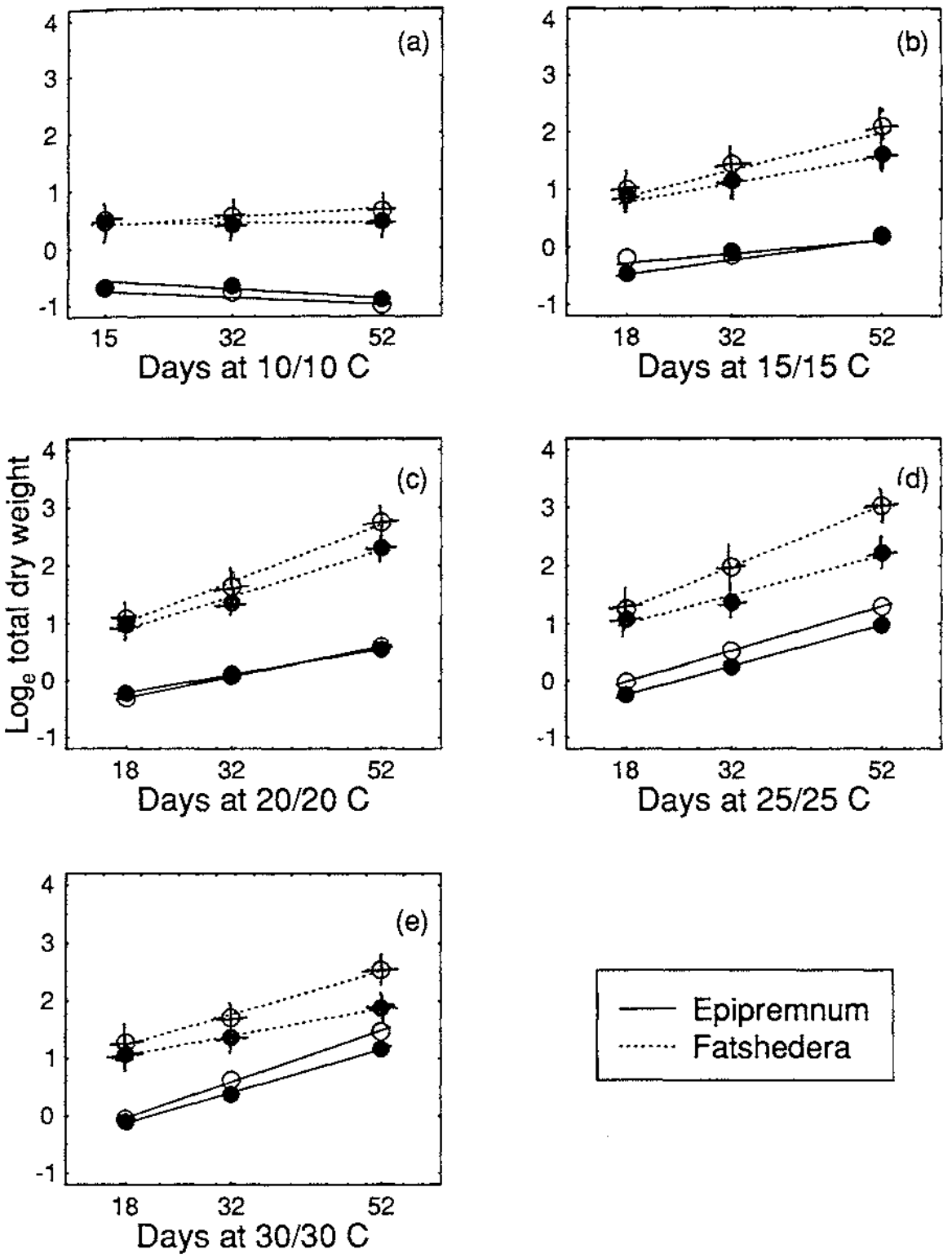


Fig. 3-3. Influence of constant day/night temperature (10-30 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in $\log_e$ of total dry weight in Epipremnum (solid line) and Fatshedera (dashed line). Each fitted line represents a functional relationship based on 36 plants and 3 harvests.

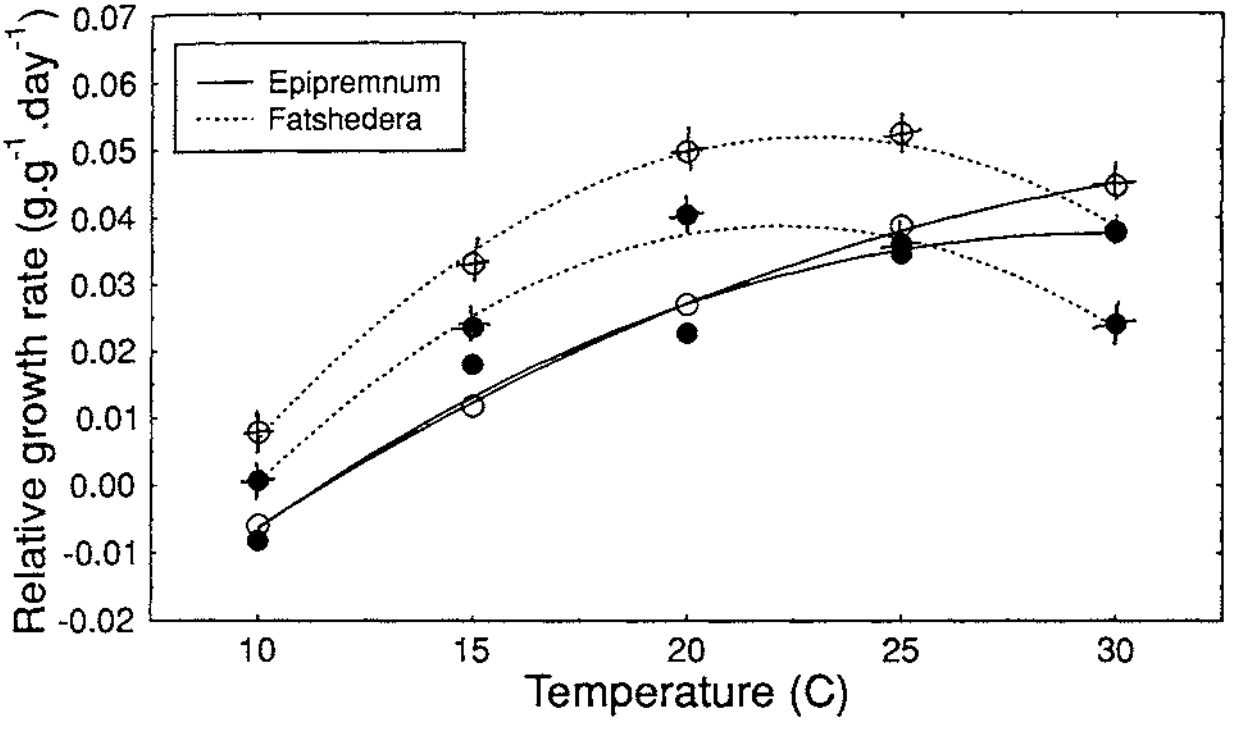


Fig. 3-4. Influence of constant temperature (10 to 30 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on relative growth rate (g.g^{-1}.day^{-1}) in Epipremnum (solid line) and Fatshedera (dashed line). Fitted functions for Epipremnum and Fatshedera at high PFD are $y = -0.054 + 0.0055x - 0.0000075x^2$ ($r^2 = 0.999$), $y = -0.062 + 0.0067x - 0.00011x^2$ ($r^2 = 0.966$) and at low PFD $y = -0.088 + 0.012x - 0.00026x^2$ ($r^2 = 0.993$), $y = -0.087 + 0.011x - 0.00025x^2$ ($r^2 = 0.982$), respectively. Each data point represents the mean of 12 plants. Lines were fitted using least squares regression.

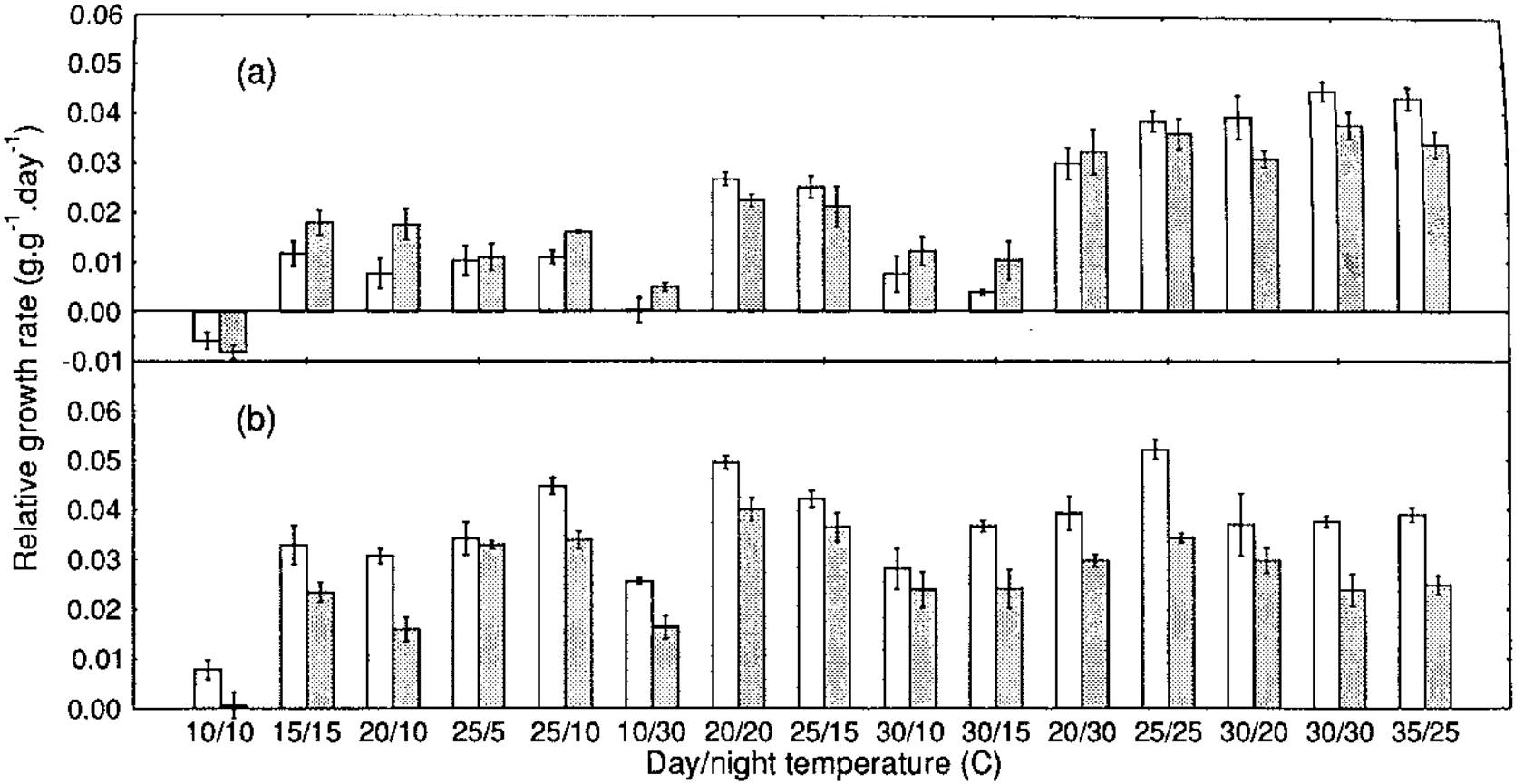


Fig. 3-5. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on relative growth rate ($g.g^{-1}.day^{-1}$) on (a) Epipremnum and (b) Fatshedera. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

Relative growth rates in all other temperature treatments were constant for the duration of the treatments (Fig. 3-5). Highly significant differences existed between the temperature treatments, PFD treatments, the species, and the species x PFD interaction ($P \leq 0.0001$). The overall mean RGRs for Epipremnum and Fatshedera were 0.020 and 0.031 $g \cdot g^{-1} \cdot day^{-1}$, respectively. As noted in the constant temperature treatments, RGR tended to increase with increasing mean temperature at both high and low PFD. In both species at any mean temperature RGR was usually higher in treatments with a constant temperature than with a diurnal temperature with the same mean. In both species where the day or the night temperature was at 10 C, even for a brief period of 4 h (refer to Fig. 3-1 profile c), this resulted in a marked reduction in RGR. In most treatments growth data could be related to the environmental treatments, but growth data for the 25/7 C treatment originating in the first run carried out in late spring was anomalous to treatments examined later, and not considered further. The species x temperature interaction was evident in the differential sensitivity of Fatshedera to high temperature and Epipremnum to low temperature.

In Epipremnum at low temperature (< 20 C) or when the day temperature was markedly lower than the night temperature, RGR was usually higher at low PFD than at high PFD. Where the temperature was ≥ 20 C during the day and plants were not exposed to chilling temperatures during the night, RGR was higher at high PFD and increased with increasing mean temperature (Fig. 3-5a).

In Fatshedera, RGR was always higher at high PFD compared with low PFD and no evidence of photoinhibition at low temperature was found. The relationship between RGR and temperature in treatments with a day/night differential suggests that a high RGR in Fatshedera is somewhat less dependent on temperature than in Epipremnum (Fig. 3-5b).

In both Epipremnum and Fatshedera higher night temperatures than day temperatures tended to reduce RGR compared with other treatments with the

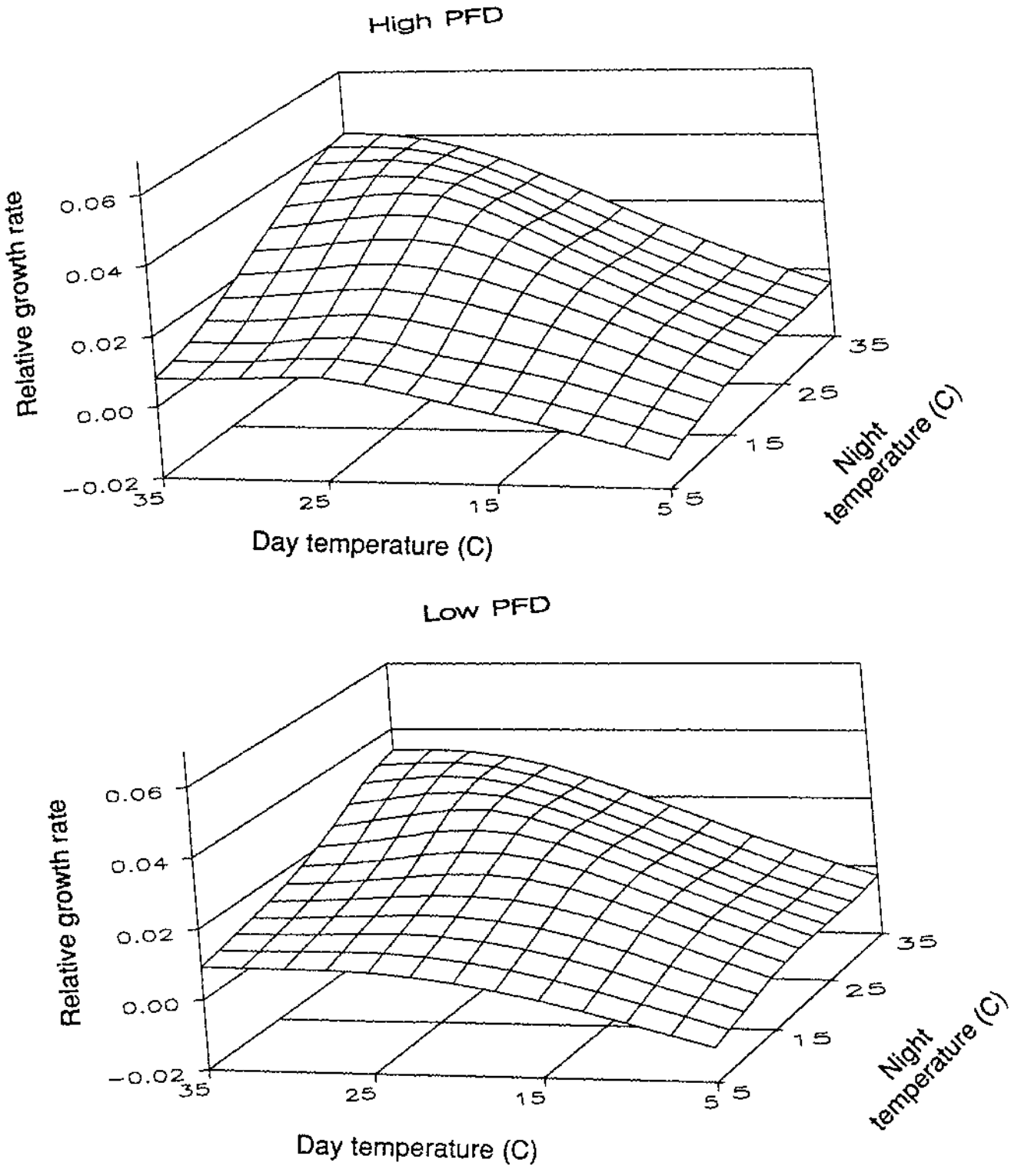


Fig. 3-6. Response surface representing the effect of day and night temperature on the relative growth rate ($g.g^{-1}.day^{-1}$) of Epipremnum at high and low PFD. The surface was generated by spline interpolation of data fitted to CE treatments (Table 3-1).

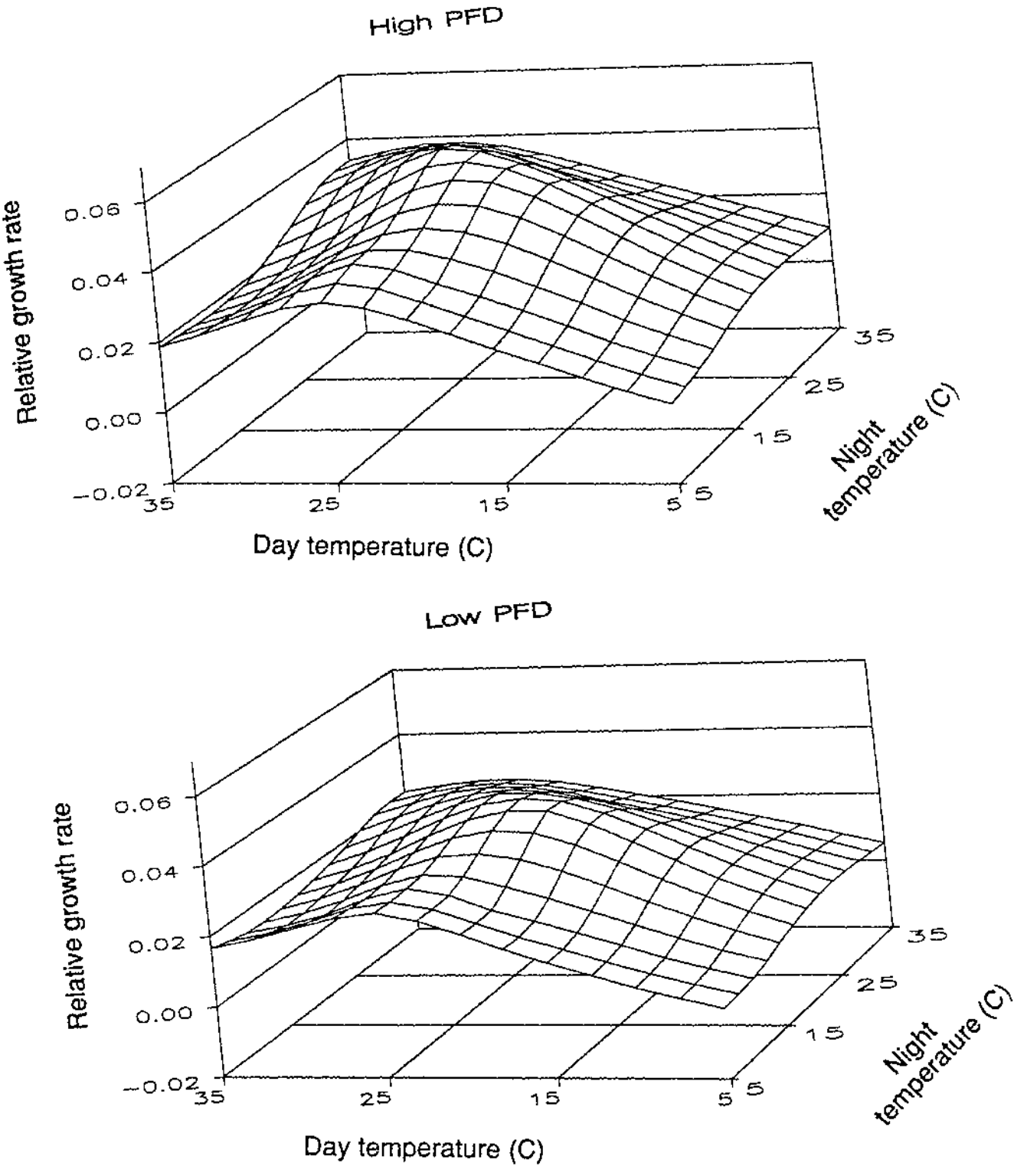


Fig. 3-7. Response surface representing the effect of day and night temperature on the relative growth rate ($g.g^{-1}.day^{-1}$) of Fatshedera at high and low PFD. The surface was generated by spline interpolation of data fitted to CE treatments (Table 3-1).

same mean temperature. The RGR of each species in relation to a particular combination of day and night temperature at high or low PFD can be described by a quadratic response surface. Data from all temperature treatments were used to generate the response surface (this included computer prediction of some temperature treatments not included in this study). The response surface for the effect of day and night temperature on RGR in Epipremnum shows a relatively flat surface with RGR increasing as day and night temperature increased. This is evident from the near-symmetry of the response on either side of the constant temperature treatments at high and low PFD (Fig. 3-6). A similar trend was found in Fatshedera. However, there was a significant difference between the shape of the response surfaces for Epipremnum and Fatshedera. The RGR in Fatshedera increased with increasing temperature and peaked at a constant temperature of about 25 C and then decreased at higher temperatures. A small thermoperiodic response in Fatshedera is indicated where RGR was higher at 25 C during the day than at night. However, RGR was always higher in constant temperature than in treatments with a day/night differential at the same mean temperature (Fig. 3-7).

3.3.2 Relative Leaf area expansion rate

Natural logarithms of the total leaf area (L_A) plotted against time were similar in their pattern to Log_e W in the majority of the temperature treatments. A linear relationship indicated that exponential leaf growth was occurring throughout the treatment period investigated and was equivalent to a constant relative leaf growth rate or leaf area expansion rate (LER). Leaf area data for the constant temperature treatments is presented to illustrate this finding (Fig. 3-8). At 10 C negligible leaf growth of Epipremnum and Fatshedera occurred during the time course and progressively higher LER occurred as growth temperature increased in both species. The temperature optima for LER in Epipremnum was outside the range of temperatures investigated, however it is probably closely related to the optima for RGR as these two factors are highly correlated ($P \leq 0.0001$). The peak

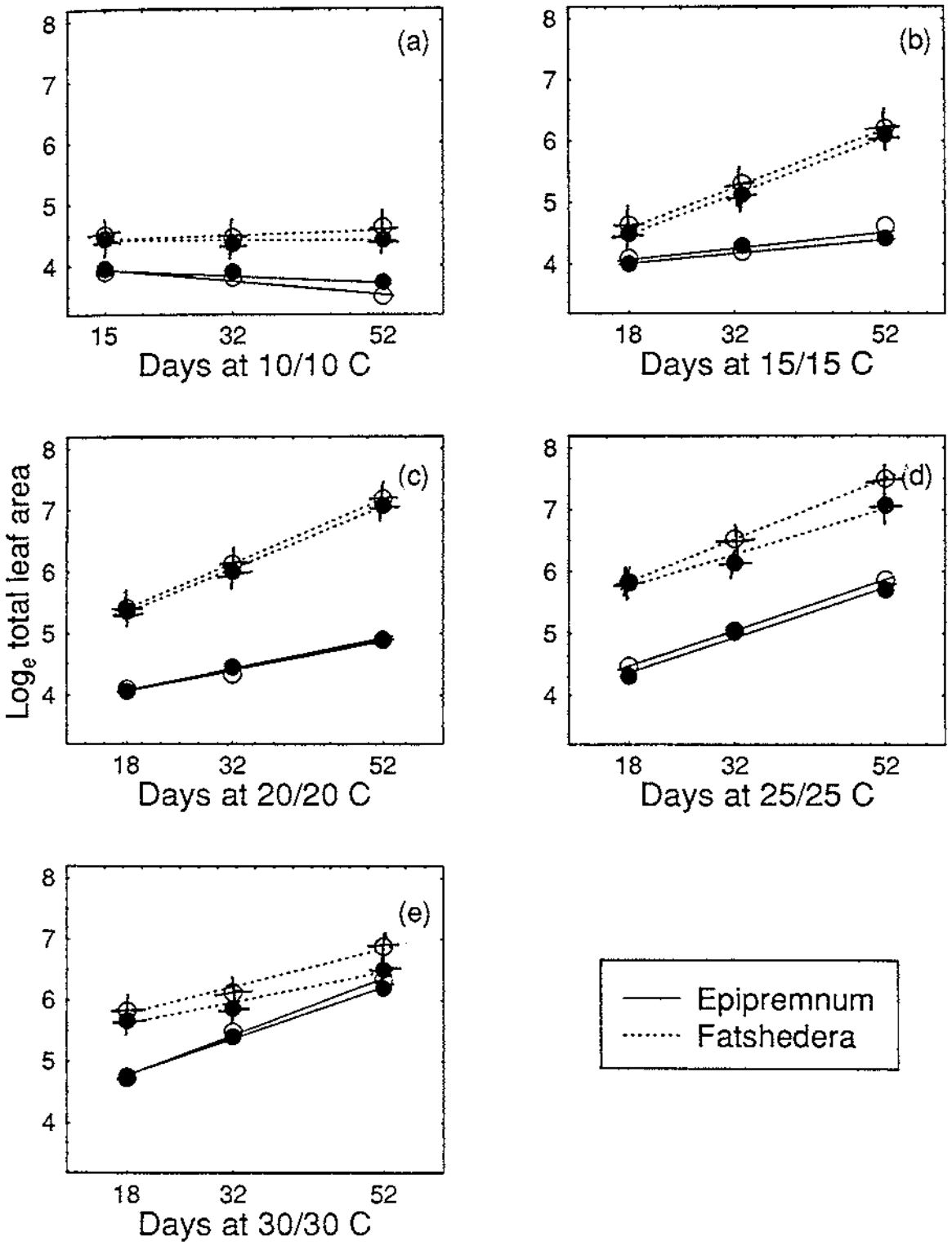


Fig. 3-8. Influence of constant day/night temperature (10-30 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in log$_e$ of total leaf area in Epipremnum (solid line) and Fatshedera (dashed line). Each fitted line represents a functional relationship based on 36 plants and 3 harvests.

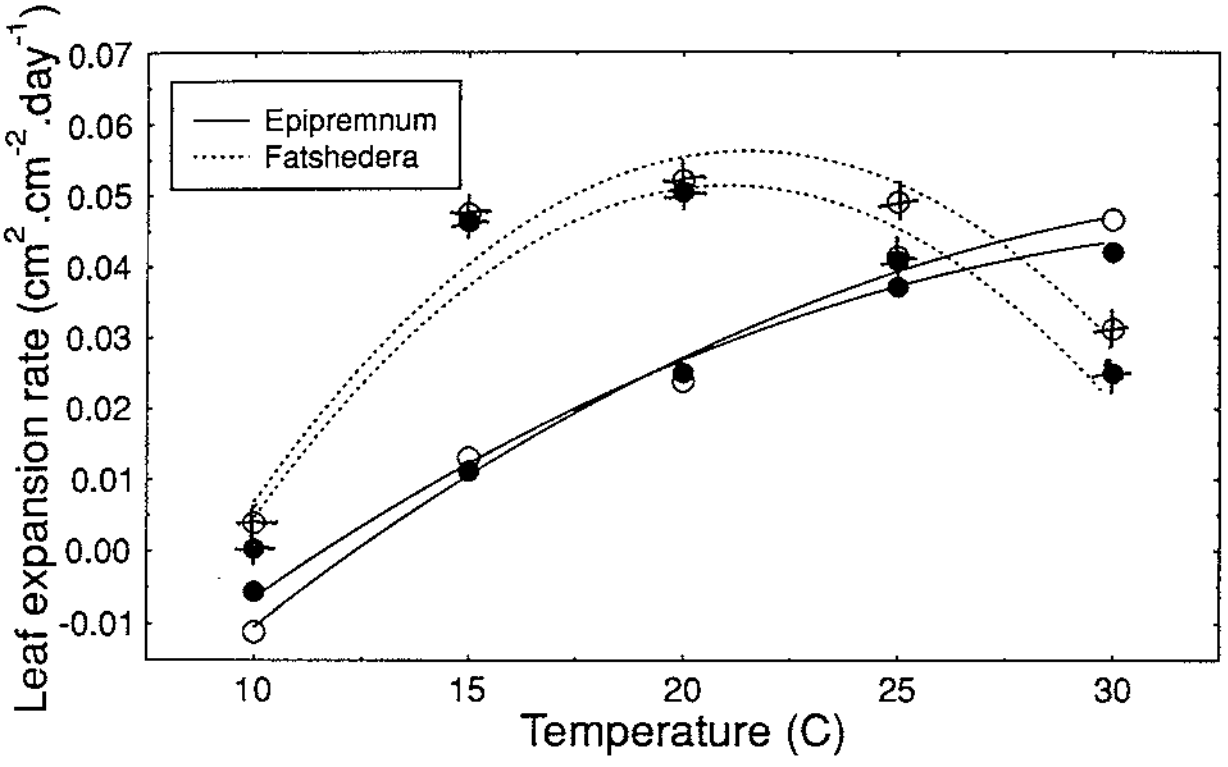


Fig. 3-9. Influence of constant temperature (10 to 30 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on leaf expansion rate (cm^2.cm^{-2}.day^{-1}) in Epipremnum (solid line) and Fatshedera (dashed line). Fitted functions for Epipremnum and Fatshedera at high PFD are $y = -0.065 + 0.0064x - 0.0000088x^2$ ($r^2 = 0.989$), $y = -0.115 + 0.015x - 0.00037x^2$ ($r^2 = 0.951$), and at low PFD $y = -0.056 + 0.0058x - 0.0000083x^2$ ($r^2 = 0.988$), $y = -0.117 + 0.0160x - 0.00038x^2$ ($r^2 = 0.886$), respectively. Each data point represents the mean of 12 plants. Lines were fitted using least squares regression.

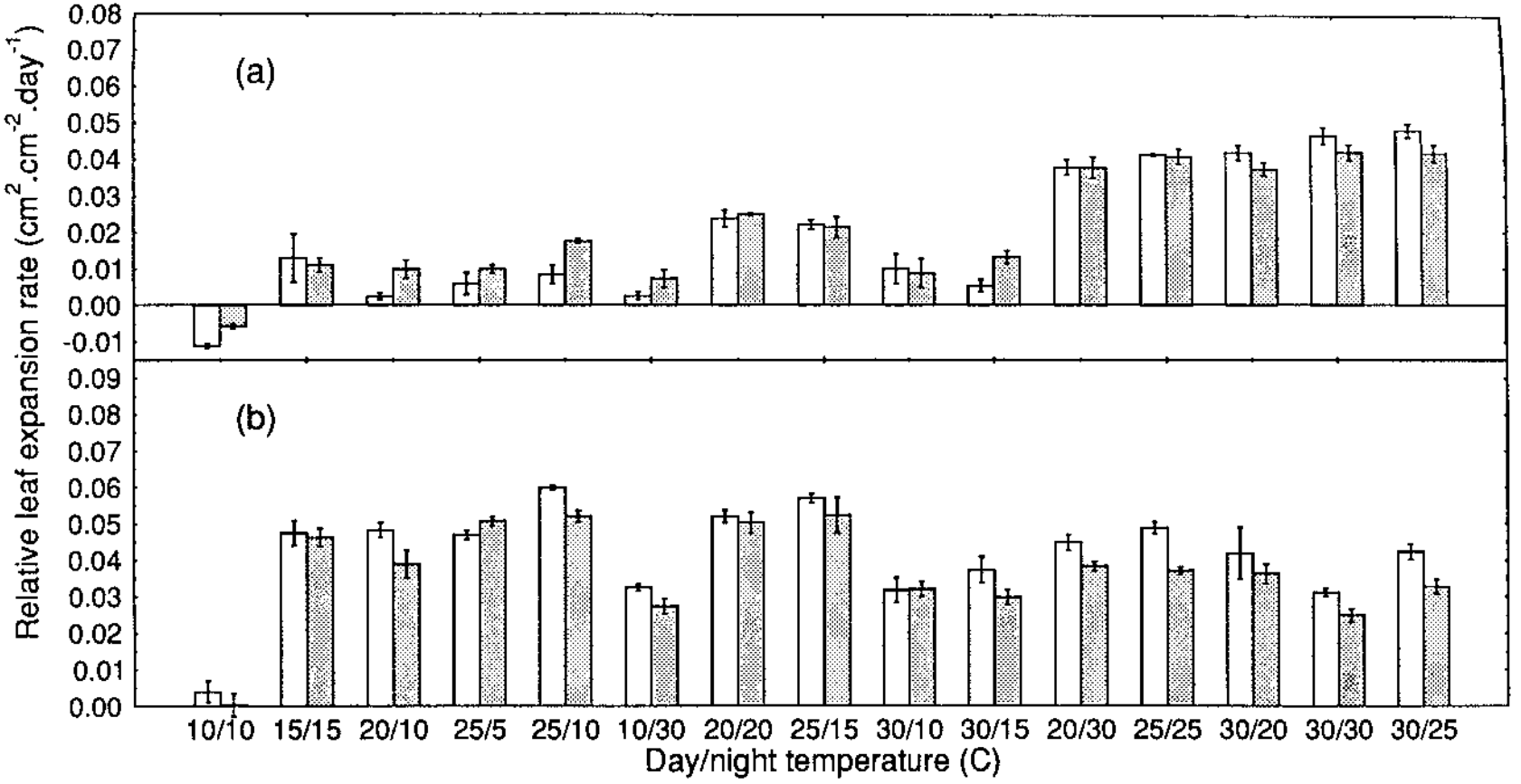


Fig. 3-10. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on relative leaf expansion rate (cm^2.cm^{-2}.day^{-1}) on (a) Epipremnum and (b) Fatshedera. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

rate of leaf expansion in Fatshedera (when derived from the fitted curves, refer to Fig. 3-8) occurred at 21.5 and 21.1 C at high and low PFD, respectively. Analysis of variance results indicated a significant effect of temperature and species ($P \leq 0.0001$) on LER. Interaction between species and PFD and PFD, as a main effect, were not significant across all temperature treatments. The mean LER for Epipremnum (0.021 $cm^2 \cdot cm^{-2} \cdot day^{-1}$) was almost half the rate found for Fatshedera (0.039 $cm^2 \cdot cm^{-2} \cdot day^{-1}$) over all treatments (Fig. 3-10).

The pattern of LER response to temperature, in treatments where a day/night temperature existed, closely parallels RGR; this is particularly apparent in Epipremnum. However, in Fatshedera attenuation of LER with increased temperature tended to be more pronounced than in RGR at the same temperature (compare Figs. 3-5 and 3-10).

Exposure of both species to 10 C either during the day or night markedly inhibited LER. Higher night temperature than day temperature generally reduced LER to a lower level than temperature treatments with the same mean, whereas in treatments with a higher day than night temperature LER was often comparable with constant temperature treatments. As noted with RGR in Epipremnum at low temperatures (≤20 C), there was a trend towards LER being higher at low PFD than at high PFD.

A significant positive correlation ($P \leq 0.0001$) and linear relationship existed between relative growth rate (RGR) and leaf expansion rate (LER) in both species and each PFD. The relationship between RGR and LER in all temperature and light treatments was relatively stable resulting in significant correlation coefficients (r^2 between 0.701 and 0.937 for Epipremnum, and between 0.684 and 0.709 for Fatshedera). Regression lines for each species and PFD treatment were not significantly different ($P=0.001$) when tested for homogeneity of slopes.

The temperature response surfaces illustrating the relationship between LER and combinations of day/night temperature (not presented) were very similar to RGR at high and at low PFD (Figs. 3-6, 3-7).

3.3.3 Leaf area ratio

Significant effects for temperature treatment, species and PFD ($P \geq 0.0001$) on LAR were found in these experiments whereas significant interactions between species and PFD were absent. Change in LAR over time was described by a functional relationship (Eq. [3.5]). This formula was used to calculate expected values at day 30 (corresponding to the middle harvest). Leaf area ratio tended to remain almost constant over time between 10 and 15 C in Epipremnum and Fatshedera. At higher temperatures LAR increased over time.

A quadratic function described the relationship between LAR (at 30 days) and temperature in the constant temperature treatments (Fig. 3-11). In Epipremnum the parabolic relationship of LAR with temperature resulted in minimum values at 18.1 C and 16.9 C for high and low PFD, respectively. In Fatshedera LAR increased in a curvilinear manner with increasing temperature. Maximum values for LAR derived from these functions occurred at 30.6 and 26.6 C in high and low PFD treatments, respectively (Fig. 3-11).

Over all temperature treatments LAR was markedly lower (26%) in Fatshedera than in Epipremnum (Fig. 3-12). Within Epipremnum there was a trend towards higher LAR with increasing mean temperature. As noted in the constant temperature treatments, LAR increased in Fatshedera but peaked at less than 30 C. Leaf area ratio tended to be higher in treatments where 25 C or higher was utilised at least for part of the diurnal cycle (Fig. 3-12).

Leaf area ratio was significantly higher ($P \leq 0.01$) at low PFD compared with high PFD, although this was less apparent in low temperature treatments where differences tended to diminish as plant growth was relatively slow (Fig. 3-12).

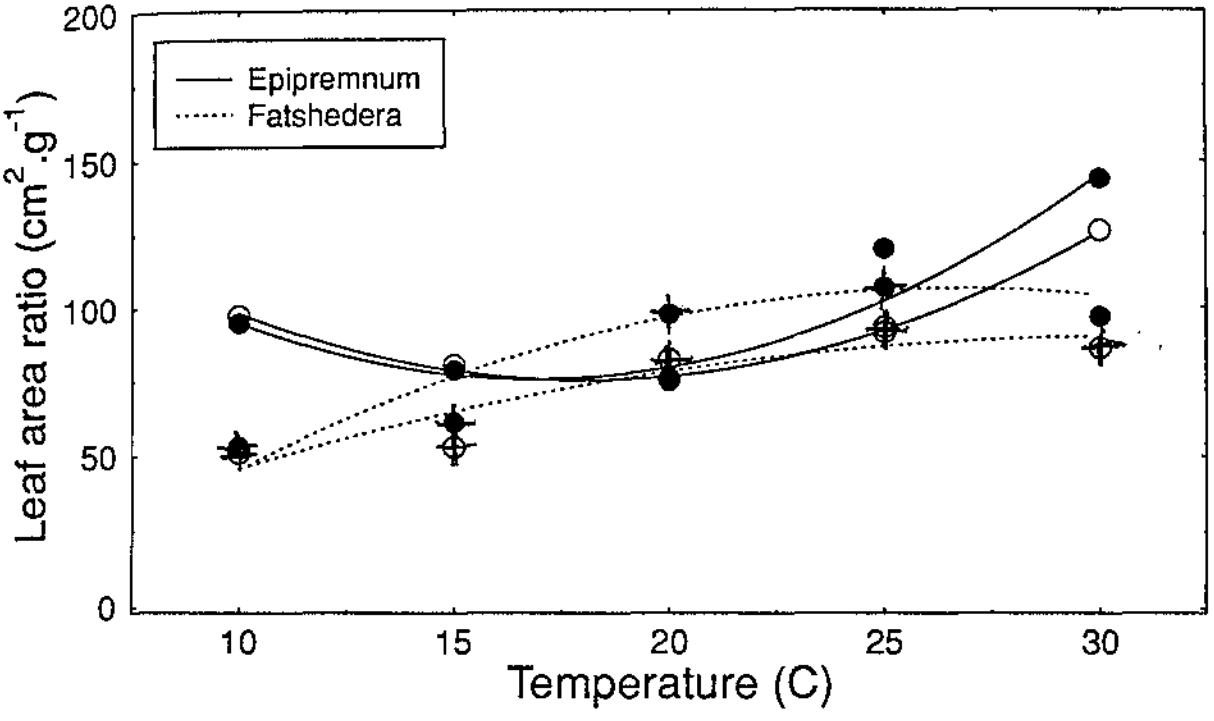


Fig. 3-11. Influence of constant temperature (10 to 30 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on leaf area ratio (cm^2.g^{-1}) in Epipremnum (solid line) and Fatshedera (dashed line). Fitted functions for Epipremnum and Fatshedera at high PFD are $y = 190.2 - 12.72x + 0.35x^2$ ($r^2 = 0.996$), $y = -7.26 + 6.37x - 0.104x^2$ ($r^2 = 0.846$), and at low PFD $y = 190.9 - 13.6x + 0.40x^2$ ($r^2 = 0.984$), $y = -49.6 + 11.7x - 0.22x^2$ ($r^2 = 0.825$) respectively. Each data point represents the mean of 12 plants. Lines were fitted using least squares regression.

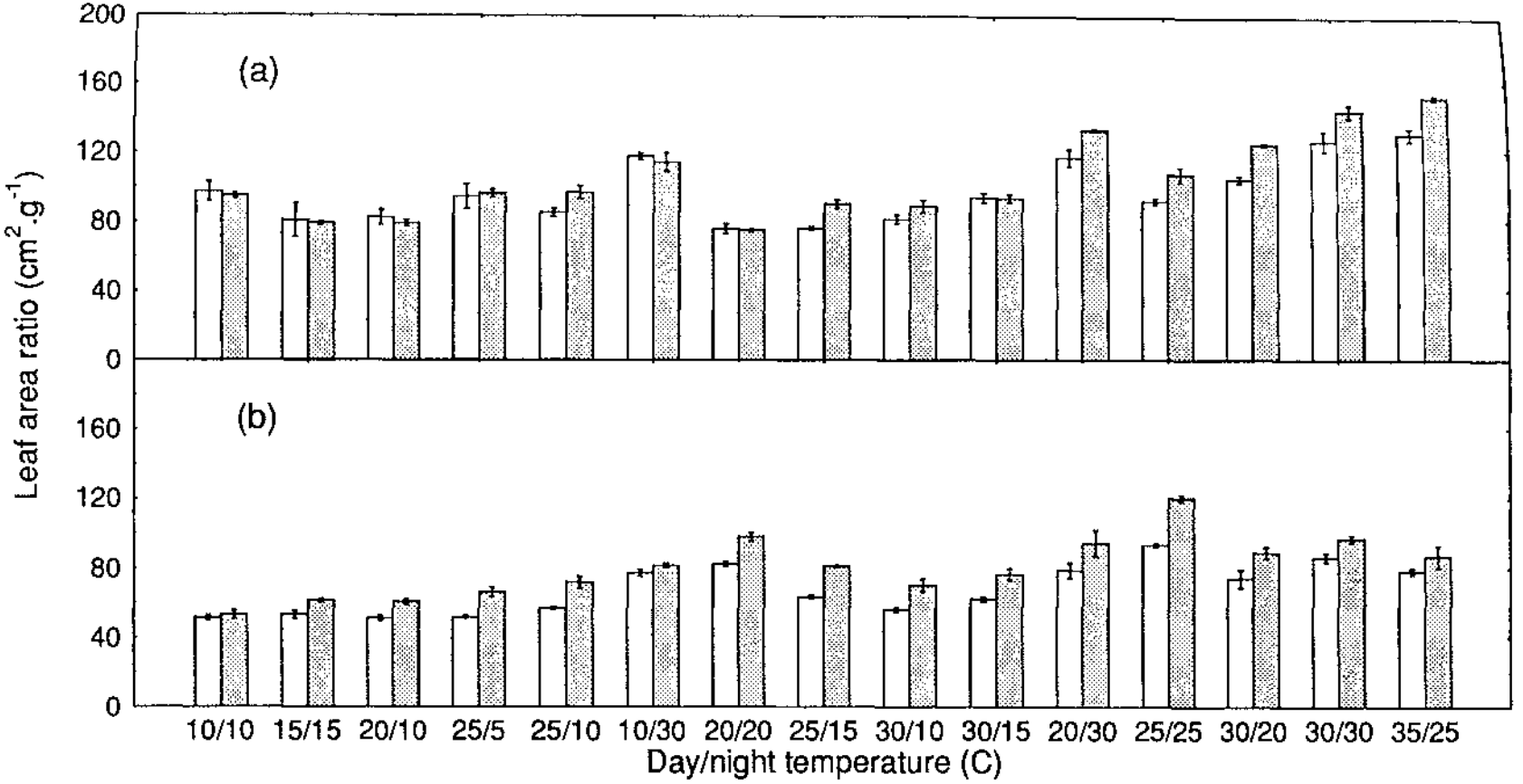


Fig. 3-12. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on leaf area ratio ($cm^2.g^{-1}$) on (a) Epipremnum and (b) Fatshedera at 30 days. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

Within each species a significant linear relationship ($P \leq 0.01$) existed between leaf area ratio (LAR) and RGR at each PFD over all temperature treatments. The correlation between LAR and RGR for each species (but not for PFD within species) were significantly different ($P \leq 0.001$).

3.3.4 Leaf area partitioning coefficient

The leaf area partitioning coefficient representing the daily change in LAR was generated using Eq. [3.7]. The derived values of LAP increased in an approximately linear manner during time within the treatments and the data presented is for the middle harvest at day 30. The influence of PFD on LAP was highly significant ($P \geq 0.001$), whereas both species and temperature treatment effects were not significant (at $P=.05$). Leaf area partitioning coefficient was significantly higher ($P \leq 0.001$) at high PFD than at low PFD.

Quadratic curves were fitted to the constant temperature treatment data for each species and each PFD (Fig. 3-13). In Epipremnum, the daily change in LAP increased, in a curvilinear manner with increasing temperature. As the temperature increased the margin between LAP in the high and low PFD treatments increased. In contrast, in Fatshedera the difference between LAP in the high and low PFD was almost constant across the temperature range investigated. As the temperature increased from 10 to 30 C LAP for Fatshedera increased to a maximum value of 22.2 and 22.5 C for high and low PFD, respectively.

As noted with LAR, LAP was markedly higher at low PFD than at high PFD. This trend was evident in almost all temperature treatments (Fig. 3-14). In Epipremnum LAP tended to increase in with increasing mean temperature. In Fatshedera LAP tended to be influenced less by the temperature treatments than PFD.

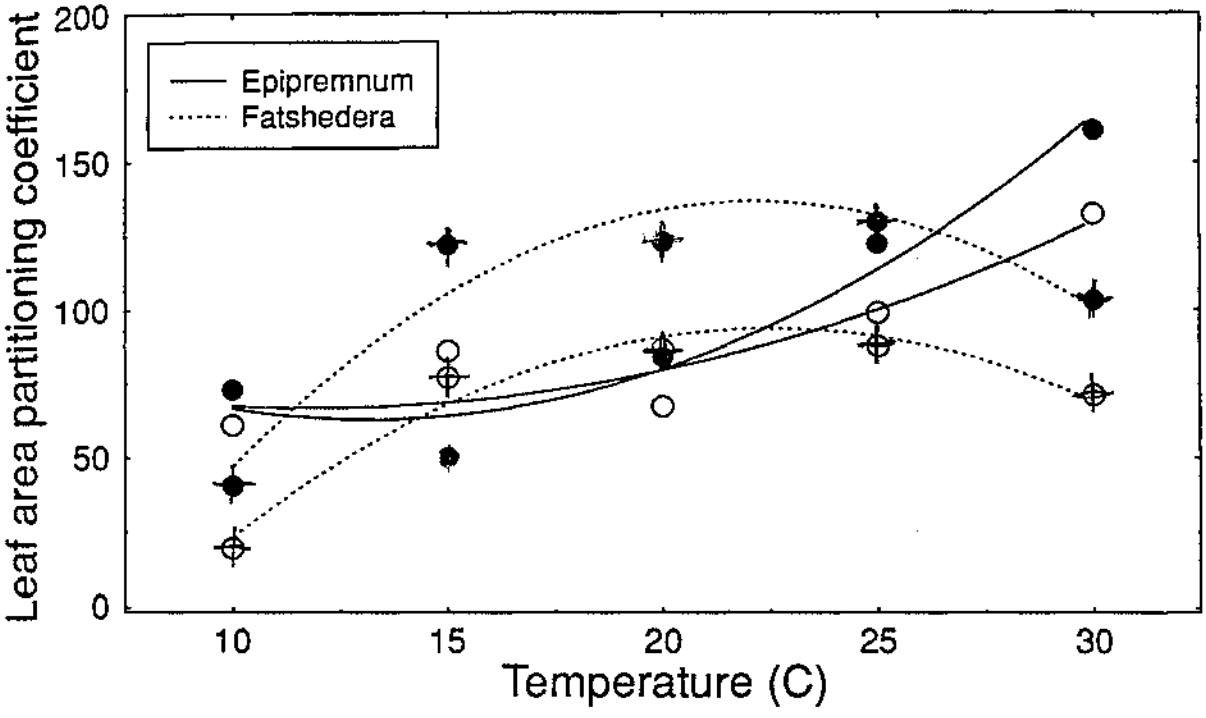


Fig. 3-13. Influence of constant temperature (10 to 30 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on leaf area partitioning coefficient in Epipremnum (solid line) and Fatshedera (dashed line). Fitted functions for Epipremnum and Fatshedera at high PFD are $y = 93.9 - 4.55x + 0.19x^2$ ($r^2 = 0.847$), $y = 605 - 50.31x + 1.16x^2$ ($r^2 = 0.907$), $y = -133 + 20.13x - 0.44x^2$ ($r^2 = 0.960$) , and at low PFD $y = 125 - 9.54x + 0.36x^2$ ($r^2 = 0.953$) $y = -159 + 26.70x - 0.60x^2$ ($r^2 = 0.916$), respectively. Each data point represents the mean of 12 plants. Lines were fitted using least squares regression.

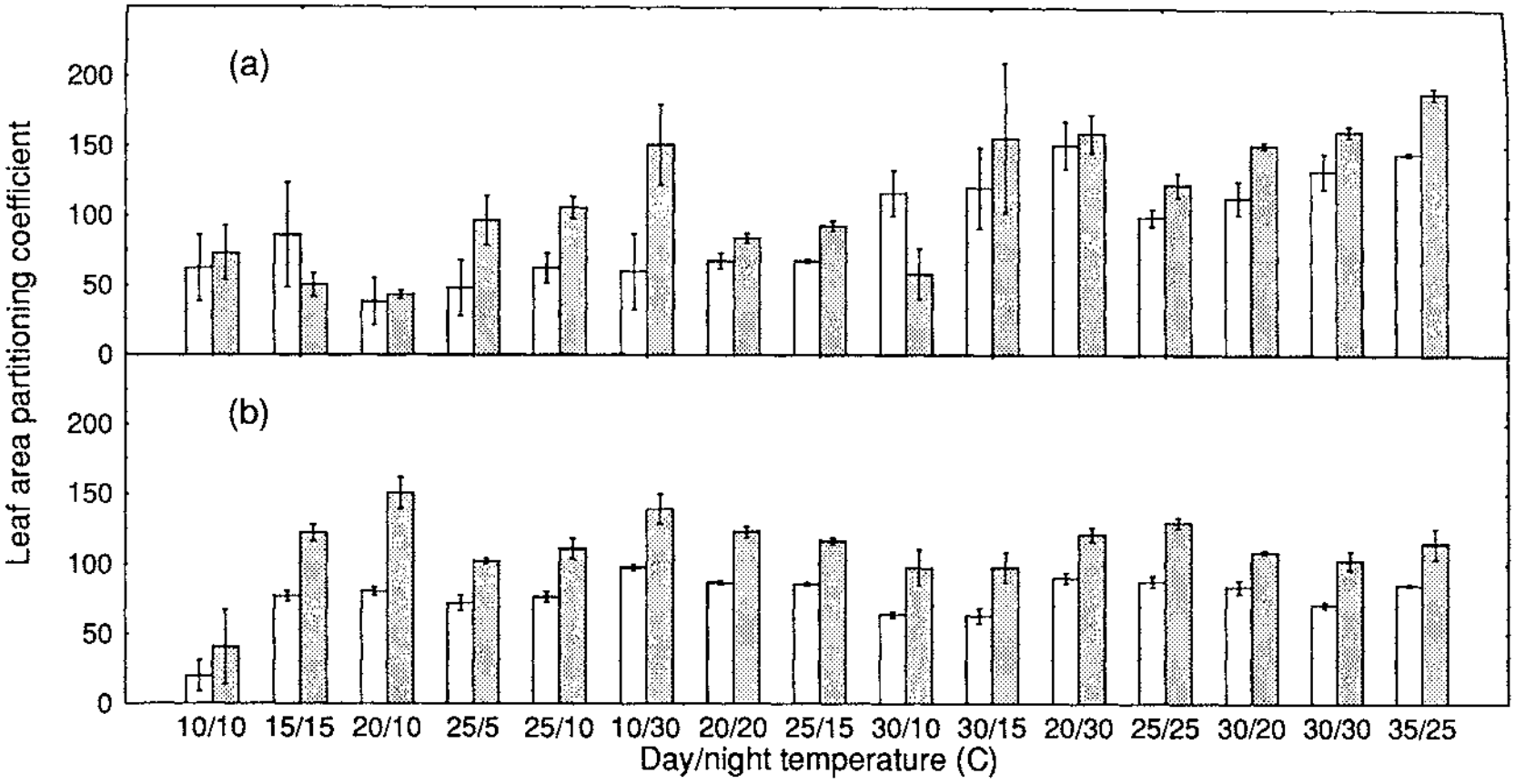


Fig. 3-14. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on leaf area partitioning coefficient on (a) Epipremnum and (b) Fatshedera at 30 days. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

A linear relationship existed between RGR and LAP in both species and in each PFD with data pooled from each temperature treatment. However, the relationship between RGR and LAP was relatively weak as reflected in the low values of the regression coefficients (r^2 = 0.030 to 0.114 for Epipremnum and r^2 = 0.064 to 0.358 for Fatshedera), and in the lack of significance (P=0.05) when regression lines were tested for homogeneity of intercepts and slopes.

3.3.5 Net assimilation rate

Analysis of variance results for NAR indicated that the effects of temperature, species and PFD, and their interactions were all highly significant (P≤0.0001).

Change in NAR over time was described by a functional relationship (Eq. [3.6]) and data derived for day 30 (corresponding to the middle harvest) are presented here. Net assimilation rates in both Epipremnum and Fatshedera were almost constant over time in treatments between 10 and 15 C whereas at higher temperatures NAR decreased in an almost linear manner with increasing time.

Quadratic curves described the response of NAR to temperature in both species (Fig. 3-15). Derivatives from these fitted curves reveal that in Epipremnum maximum rates of NAR occurred at 25.7 and 23.5 C at high and low PFD, respectively. There was relatively little difference between the values at high and low PFD, except at 25 C and above. The temperature optima for Fatshedera were similar being 21.5 and 21.3 C at high and low PFD, respectively. A consistent increase in NAR occurred in Fatshedera, at high PFD relative to low PFD, at temperatures greater than 10 C.

Evaluation of NAR in all temperature treatments shows that, on an area basis, NAR was markedly higher at high PFD in almost all treatments, except where Epipremnum was exposed to temperature below 20 C (Fig. 3-16). At these low temperatures, NAR tended to be higher at low PFD. Exposure of Epipremnum

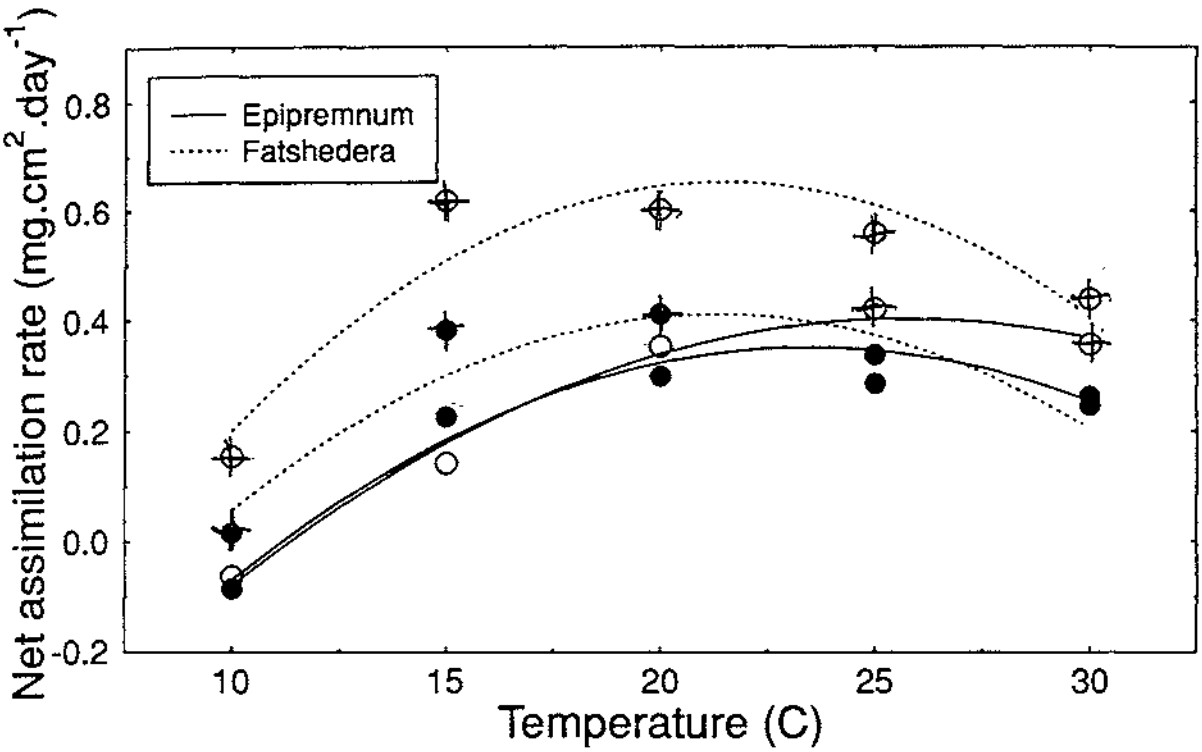


Fig. 3-15. Influence of constant temperature (10 to 30 C) and PFD (open symbols = 710 μmol.m^{-2}.s^{-}1, closed symbols = 320 μmol.m^{-2}.s^{-}1) on net assimilation rate in Epipremnum (solid line) and Fatshedera (dashed line) at day 30. Fitted functions for Epipremnum and Fatshedera at high PFD are y = -0.00088+0.00010x- 0.00000019x^2, (r^2 = 0.986), y = -0.00092 + 0.00015x - 0.00000034 (r^2 = 0.866) , and at low PFD y = -0.00092 + 0.000108x- 0.00000023x^2, (r^2 = 0.976), y = -0.000843 + 0.00012x- 0.00000027, (r^2 = 0.817) respectively. Each data point represents the mean of 12 plants. Lines were fitted using least squares regression.

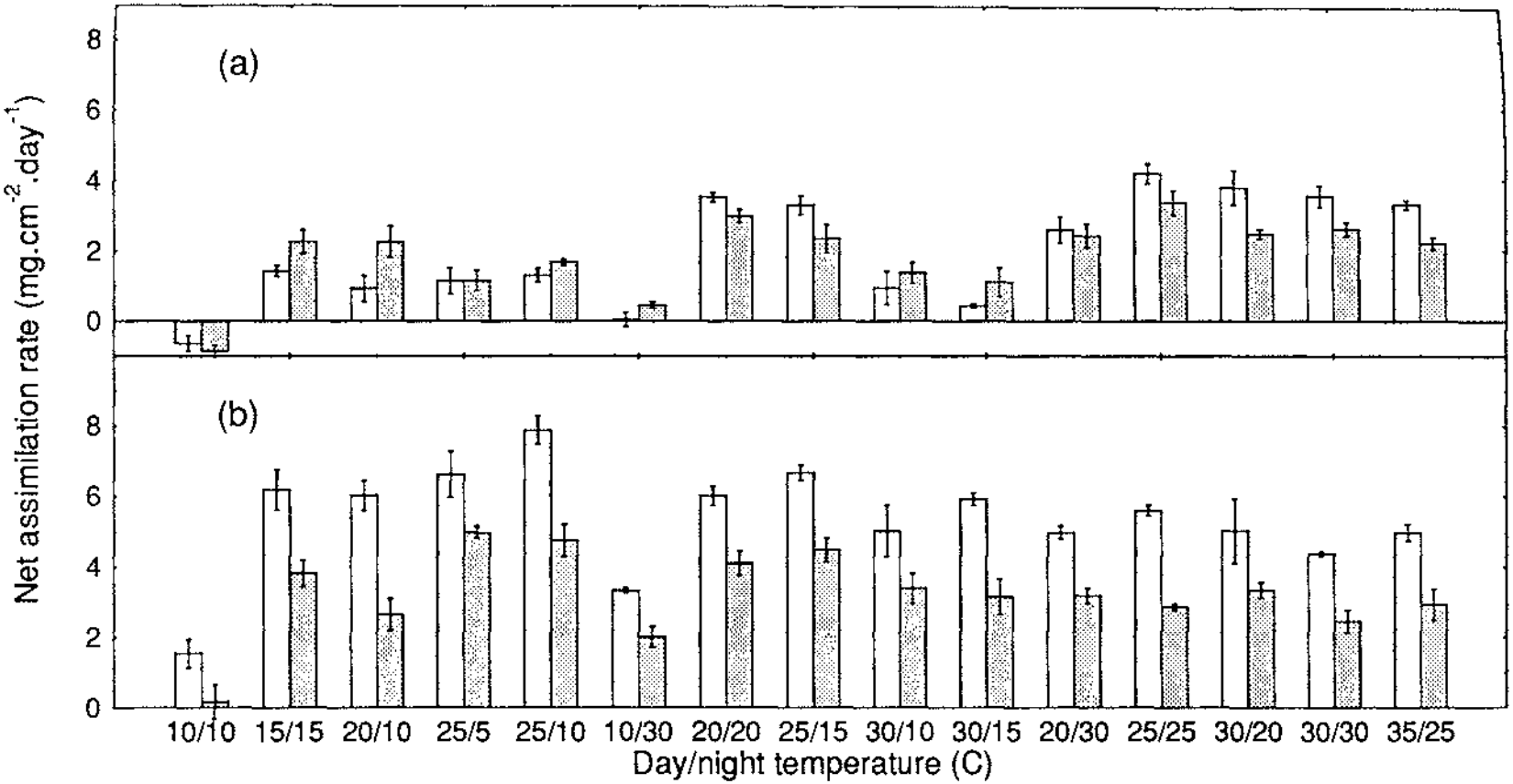


Fig. 3-16. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on net assimilation rate ($mg.cm^{-2}.day^{-1}$) on (a) Epipremnum and (b) Fatshedera at day 30. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

plants to 10 C markedly repressed NAR irrespective of the PFD. Highest rates of NAR were observed where the mean temperature was ≥ 20 C. In Fatshedera some reduction in NAR occurred when exposed to 10 C in the photoperiod, however highest rates of NAR occurred in treatments where the maximum temperature was 25 C.

A significant positive correlation ($P \leq 0.0001$) and linear relationship existed between RGR and net assimilation rate (NAR) in both species and for each PFD (r^2 values between 0.701 and 0.937 for Epipremnum and r^2 from 0.684 to 0.709 for Fatshedera). Slopes and intercepts of regression lines for each species and PFD were tested for homogeneity and were not significantly different ($P=0.05$) from each other.

3.3.6 Efficiency of dry matter production

Relative efficiency of light energy conversion into plant dry matter on an incident light basis was significantly higher in each species at low PFD. Analysis of variance results indicated that both temperature and species were highly significant ($P \leq 0.0001$) for efficiency of dry matter production.

In Epipremnum exposed to the constant temperature treatments the relative efficiency of dry matter production per mole of incident photons increased as a linear function of temperature up to a maximum rate of about a third of the rate found for Fatshedera (Fig. 3-17). In Fatshedera the relative efficiency of dry matter production was a curvilinear function increasing with increasing temperature up to a maximum value of 15 $mg \cdot mol^{-1} \cdot m^{-2}$ between 20 and 25 C then decreasing.

Plant response at high PFD suggests that each species may be adapted to grow better at low PFD. Fatshedera was usually more efficient than Epipremnum by a factor of between 2- and 6- fold in all temperature treatments. In Epipremnum

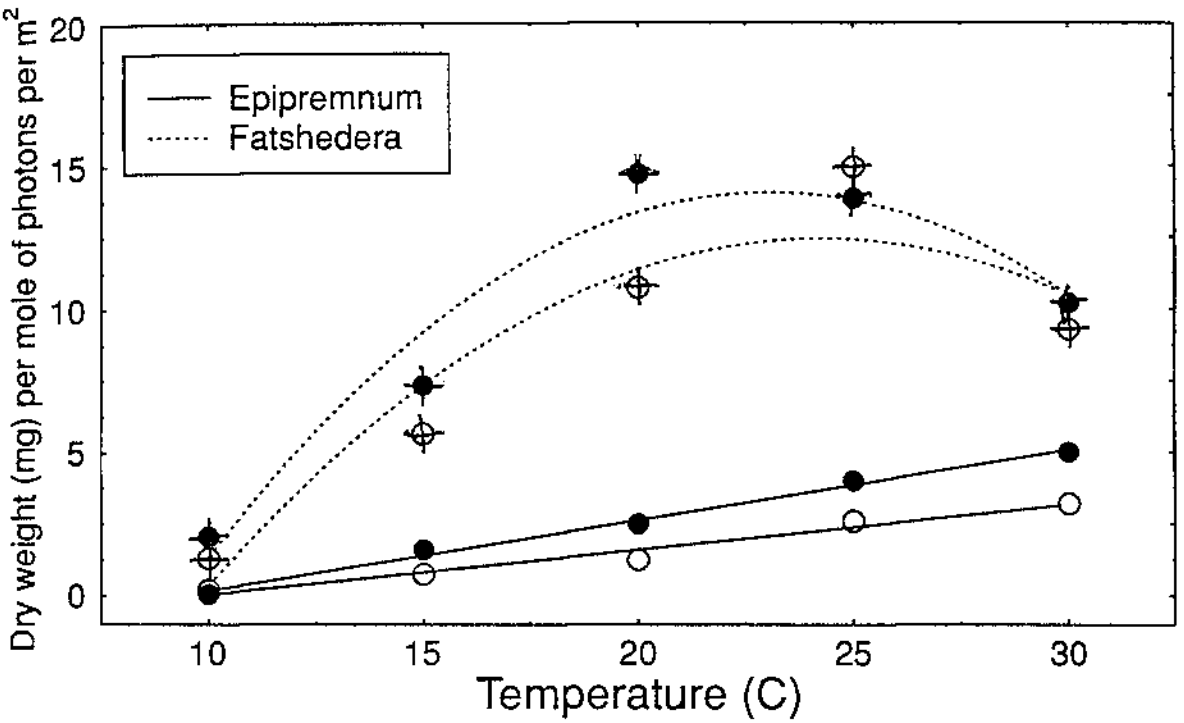


Fig. 3-17. Effect of temperature and PFD on dry weight production (mg) per mole of photons per m^2 for Epipremnum (solid line) and Fatshedera (dashed line) at a constant temperature (10 to 30 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}). Fitted functions for Epipremnum at high and low PFD were $y = -1.54 + 0.16x$, $r^2 = 0.968$, $y = -2.29 + 0.25x$, $r^2 = 0.994$, respectively. Fitted functions for Fatshedera at high and low PFD were $y = -22.63 + 2.89x - 0.059x^2$, $r^2 = 0.888$, $y = -2.79 + 0.303x - 0.0014x^2$, $r^2 = 0.945$, respectively. Each data point represents the mean of 12 plants at the final harvest. Lines were fitted using least squares regression.

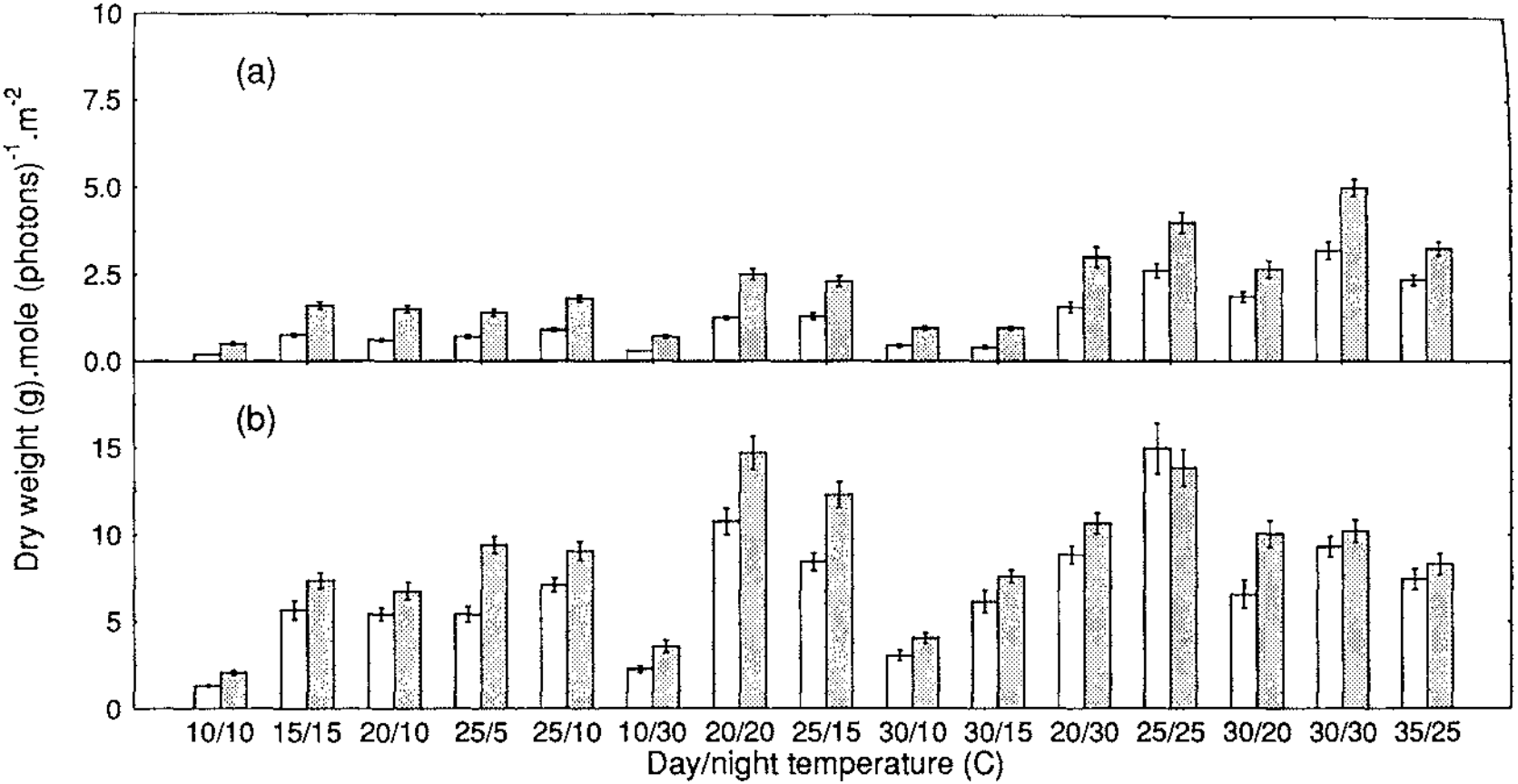


Fig. 3-18. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on dry weight per mole of photons per m^2 on (a) Epipremnum and (b) Fatshedera at day 30. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean. (Note the vertical scales for each species differ by a factor of 2).

the highest rate of dry matter production of 5 and 3.2 $mg \cdot mol^{-1} \cdot m^{-2}$ occurred at low and high PFD, respectively in plants grown at constant 30 C. Exposure to light at 10 C inhibited dry matter production and reduced the relative efficiency more than if exposed to 10 C in the dark. This was evident when comparing the 30/10 and 10/30 C treatments. A brief period (4 h) as experienced in the variable night treatment 30/15 C, or 12 h in the dark at 10 C were similar in their depression of overall efficiency (Fig. 3-18). A brief exposure of Fatshedera to 10 C (Fig. 3-1c) had less effect on depression of overall efficiency of dry matter accumulation than a full night at 10 C (Plate 3-5). This result suggests that there may be an important and significant difference in the tolerance of Fatshedera and Epipremnum to chilling temperatures.

The temperature response surfaces illustrating the relationship between efficiency of dry matter production on an incident light basis and combinations of day/night temperature (not presented) were very similar in form to data presented for RGR at high and low PFD (Figs. 3-6, 3-7).

3.3.7 Specific leaf area

Specific leaf area tended to increase over time in a manner described by the functional relationship defined in Eq. [3.8]. This formula was used to calculate expected values at day 30 (corresponding to the middle harvest) and are presented here.

Specific leaf area was influenced significantly ($P \geq 0.0001$) by the temperature treatments, species, PFD and harvest date.

Specific leaf area tended to increase with increasing temperature (Fig. 3-19) and was significantly higher in Epipremnum (196 $cm^2 \cdot g^{-1}$) compared with Fatshedera (110 $cm^2 \cdot g^{-1}$). Specific leaf area was significantly higher at low PFD than at high PFD in both species.

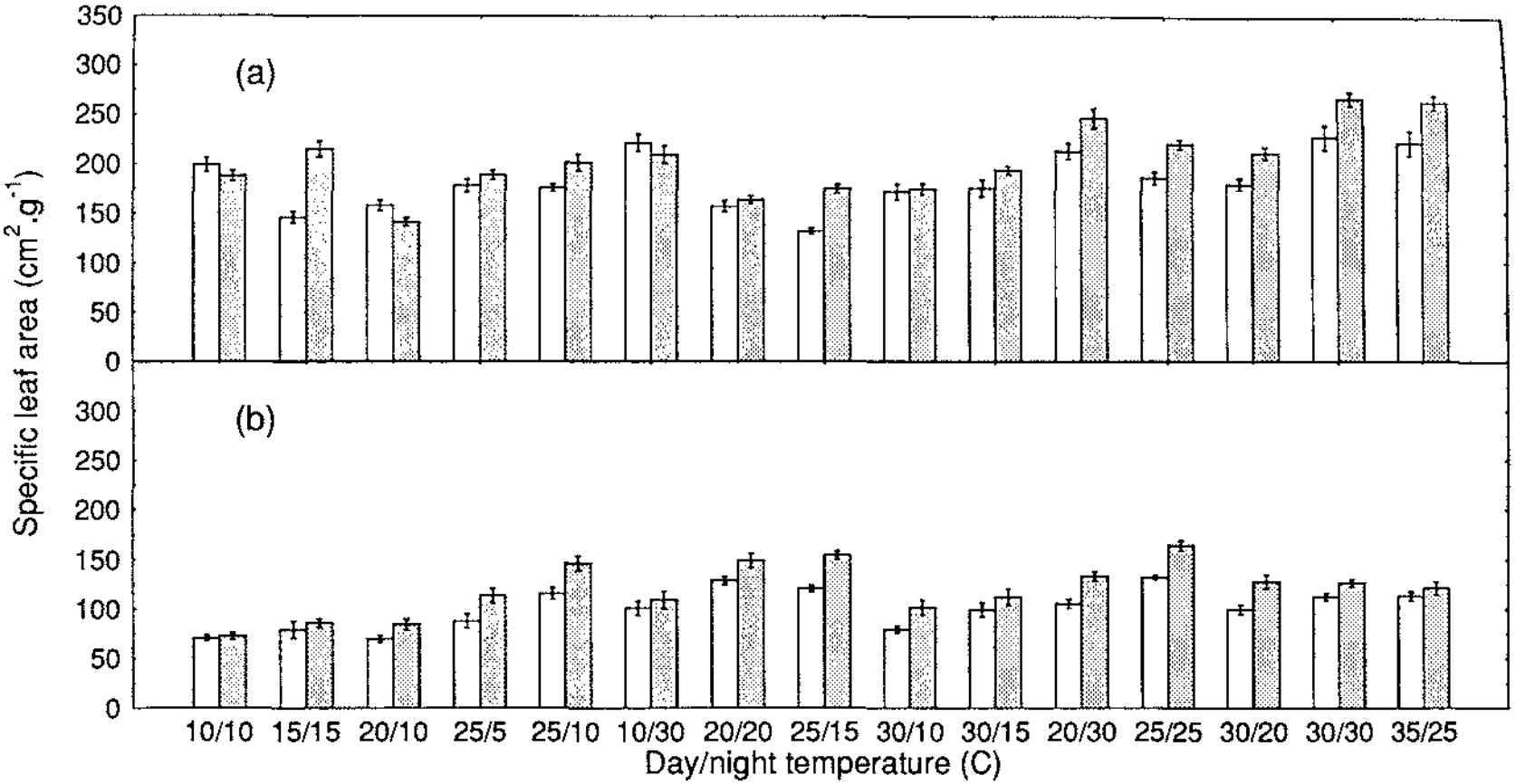


Fig. 3-19. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on specific leaf area (cm^2.g^{-1}) on (a) Epipremnum and (b) Fatshedera at 30 days. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

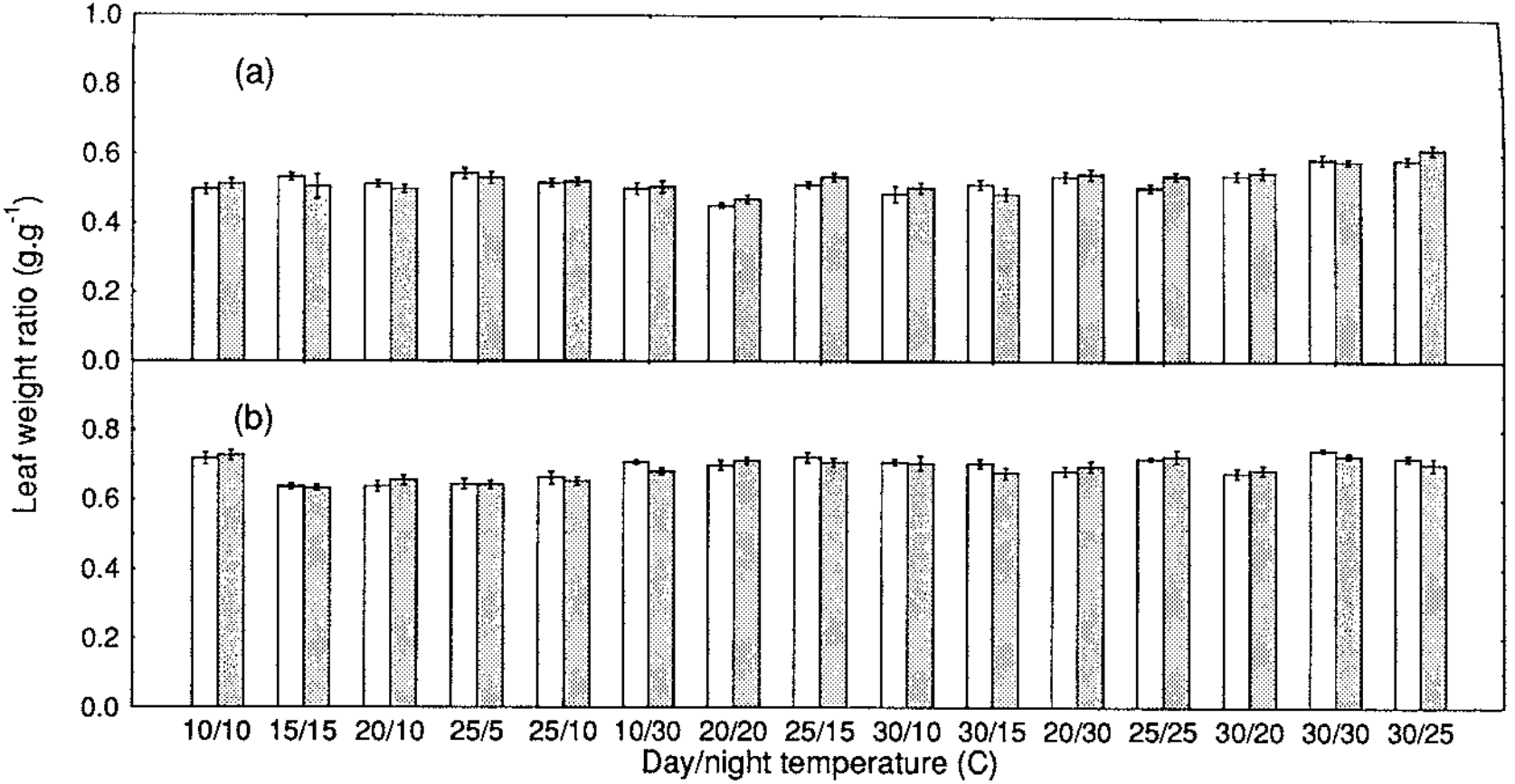


Fig. 3-20. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on leaf weight ratio ($g.g^{-1}$) on (a) Epipremnum and (b) Fatshedera at the second harvest. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

3.3.8 Leaf weight ratio

Instantaneous values for leaf weight ratio were derived in a similar manner to SLA using Eq. [3.9]. Leaf weight ratio for Epipremnum and Fatshedera although different, remained essentially constant in each temperature and PFD treatment within each species. Equation [3.9] was used to calculate expected values for LWR at day 30 (corresponding to the middle harvest) and are presented here (Fig. 3-20).

Analysis of variance indicated there were highly significant ($P \leq 0.0001$) treatment effects related to temperature and species, while no significant effects due to PFD were obtained. Mean LWR values for Epipremnum and Fatshedera were 0.58 and 0.70 $g \cdot g^{-1}$, respectively.

3.3.9 Shoot length

Shoot length was significantly influenced by temperature and PFD ($P \leq 0.0001$) and a significant interaction was found between species and PFD. This was evident as no effect of PFD on shoot length in Epipremnum (133 mm) compared with Fatshedera where mean shoot growth at low PFD (159 mm) was significantly lower than at high PFD (210 mm). Overall shoot length was significantly greater at successive harvests. The mean shoot length was significantly larger in Fatshedera (185 mm) than Epipremnum (133 mm) ($P \leq 0.0001$).

Total shoot length at the conclusion of the experiment was normalised to shoot length at 52 days (all data not presented) to allow growth to be compared at the same time. The effect of day/night temperature differential (at the same mean temperature) on shoot growth was investigated (Fig. 3-21). In both species there was a marked trend towards maximal shoot growth occurring in all constant temperature treatments, except at 15 C where only treatments utilising higher day than night temperature were investigated. A slight trend towards increased shoot

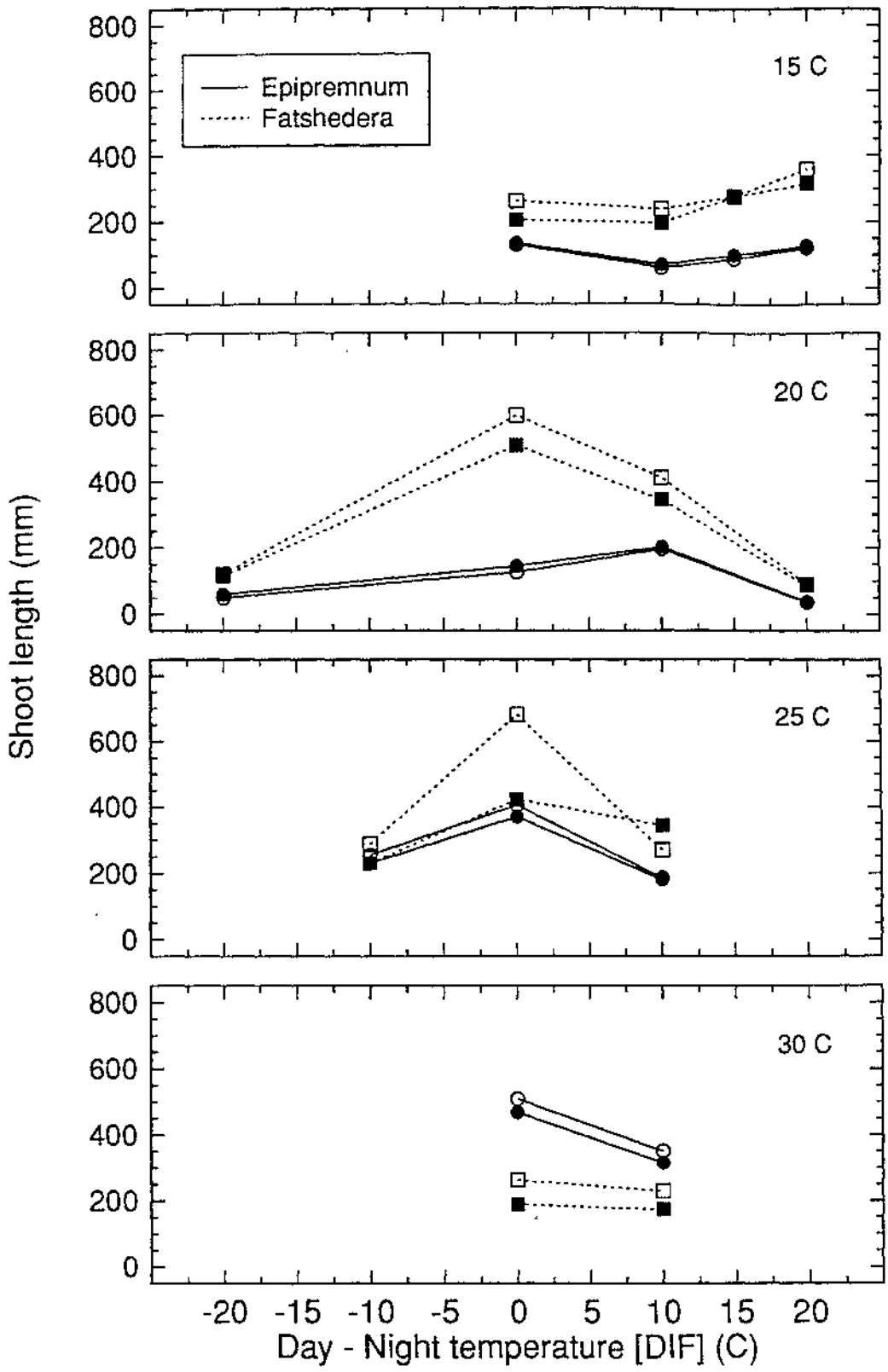


Fig. 3-21. Influence of difference between day and night temperature [DIF] on shoot growth (mm) of Epipremnum and Fatshedera at high PFD (open symbols) and low PFD (closed symbols) after 52 days at mean temperatures of 15 to 30 C. Each data point represents the mean of 12 plants.

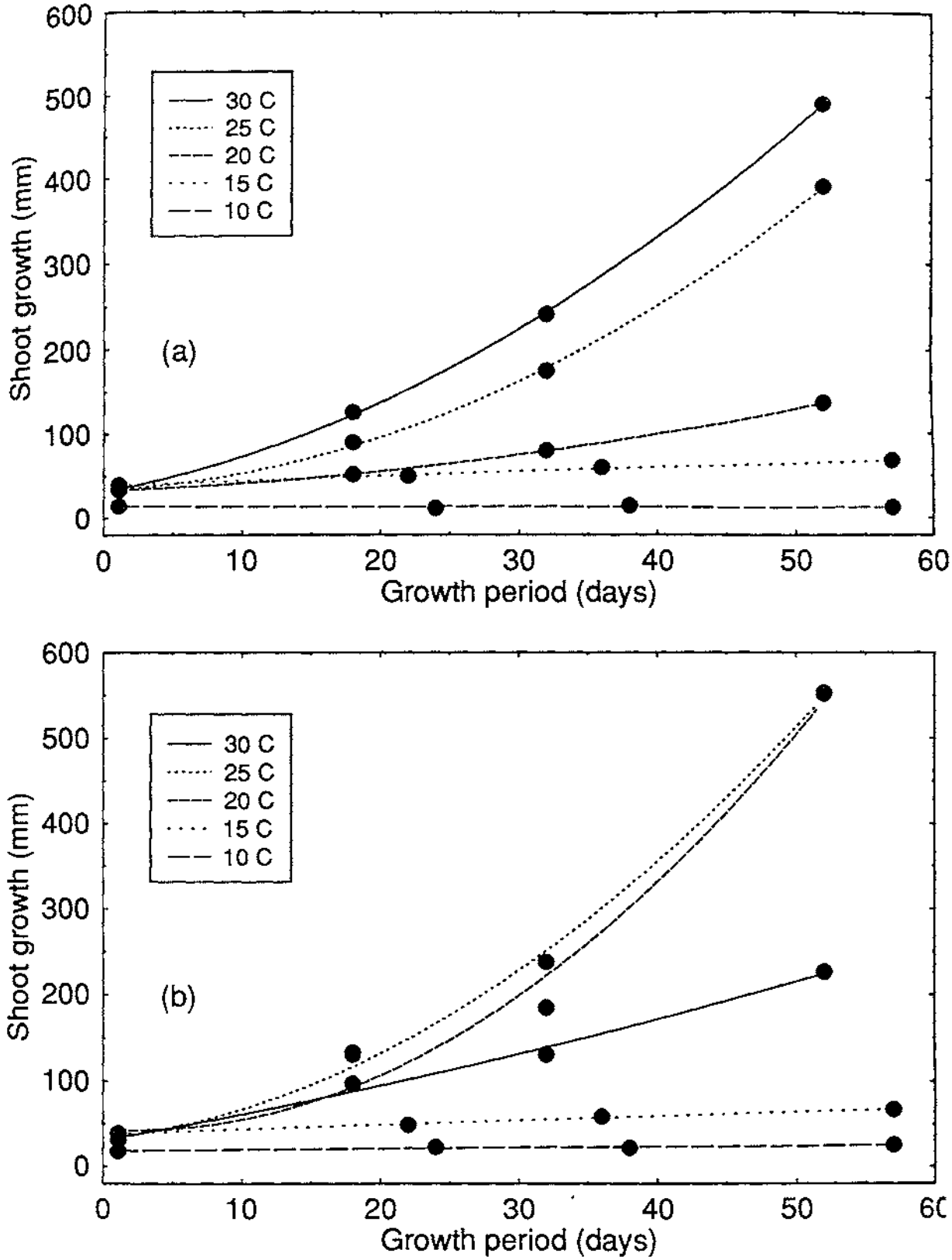


Fig. 3-22. Time courses of increase in shoot length (mm) in (a) Epipremnum and (b) Fatshedera at constant temperature (10-30 C). Data from from high and low PFD were pooled. Each data point represents the mean of 24 plants. Quadratic functions were fitted using least squares regression to data above 10 C. A linear function was fitted to data at 10 C.

growth in Fatshedera with increased day/night temperature differential. This effect was not maintained in Epipremnum as no quantitative increase in shoot length occurred with change in temperature differential.

Time courses of increase in shoot length were plotted for each constant temperature treatment with Data for each PFD being pooled (Fig. 3-22). At 10 C shoot length increased linearly with increasing time, whereas at higher temperatures a curvilinear increase occurred. In both species the rate of shoot growth increased as temperature increased, except in Fatshedera at 30 C where the shoot growth rate was intermediate between 15 and 20 C.

3.3.10 Mean shoot growth rate

Analysis of variance revealed highly significant effects of temperature, species and harvest on mean shoot growth per day. In contrast, no significant effect of PFD was found. Mean shoot length growth rates of 10.0 mm per day for Epipremnum and 11.2 mm for Fatshedera were significantly different ($P \leq 0.02$) overall temperature treatments.

After 30 days, significant differences between the mean rate of shoot growth were present among the temperature treatments (Fig. 3-23). Mean shoot growth per day was almost completely inhibited in both species when plants were exposed day temperatures of 10 C (Plates 3-4, 5-5). In Epipremnum, 4 h at 10 C was sufficient to reduce shoot growth rate, whereas 12 h was required for a similar effect in Fatshedera. At temperatures above 10 C, shoot growth rate in Epipremnum increased with increasing mean temperature up to 25 C, above which the rate of shoot growth increased rapidly. Fatshedera had highest rates of shoot growth at temperatures between 20 and 25 C and had higher rates than Epipremnum from 15 to 25 C. This confirmed the intolerance of Fatshedera to high temperature, and that of Epipremnum to low temperature (Fig. 3-23).

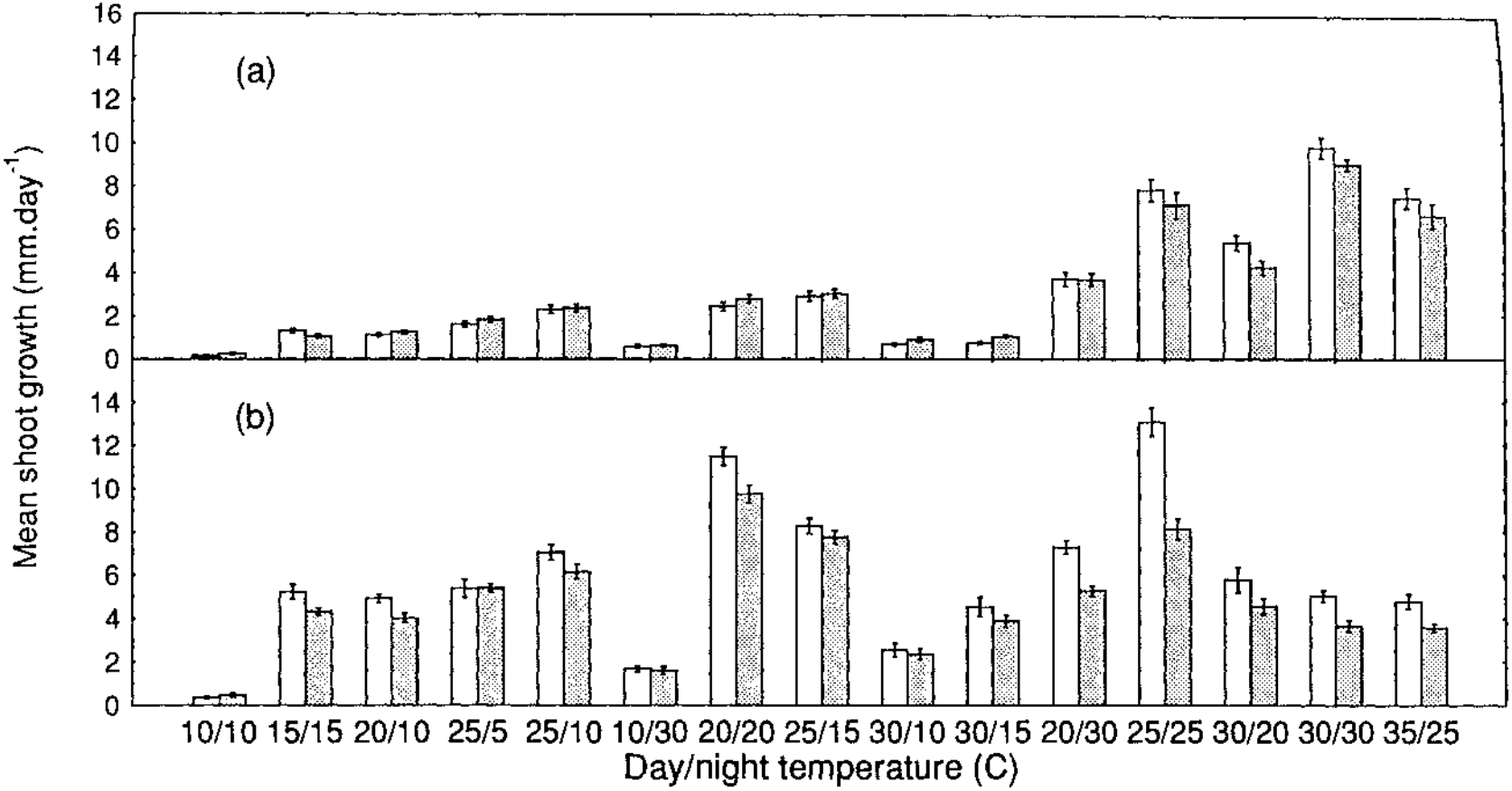


Fig. 3-23. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on mean shoot growth (mm) per day on (a) Epipremnum and (b) Fatshedera at day 30. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

3.3.11 Node Length

Highly significant (P≤0.0001) effects of temperature treatment and harvest on node length were present in the treatments whereas no significant effect of PFD or species or significant interactions were present (P=0.01). A mean node length of 28 mm occurred in both Epipremnum and Fatshedera and values tended to increase at each successive harvest. At low temperature, node length was significantly shorter than at higher temperatures, increasing from about 16 mm at 10 C to 38 mm at 30 C (Fig. 3-24).

3.3.12 Leaf appearance rate

The rate of development or leaf appearance rate (LFPD) was influenced significantly (P≤0.0001) by temperature and species. Overall, PFD and harvest date were not significant determinants of LFPD (P=0.01), however, there was a trend towards higher LFPD at higher PFD in Fatshedera, but not in Epipremnum.

Data collected after 30 days growth at each temperature showed significant differences between each species. Overall of the temperature treatments LFPD was significantly lower in Epipremnum (0.099) than in Fatshedera (0.165 leaves·day^{-1}) (Fig. 3-25).

Temperature was the dominant factor influencing the rate of leaf development in both Epipremnum and Fatshedera, as noted with other parameters. Rate of appearance increased with increasing temperature (Figs. 3-25, 3-26). Exposure of Epipremnum and Fatshedera to 10 C for part of the diurnal cycle (in light or dark) reduced LFPD dramatically (by up to 50%) compared with other temperature treatments at the same mean.

Rates of leaf appearance in the constant temperature treatments were plotted against temperature (Fig. 3-26). In Epipremnum, LFPD increased with increasing temperature and was fitted to a cubic function with maximum rates of 0.25 to 0.27

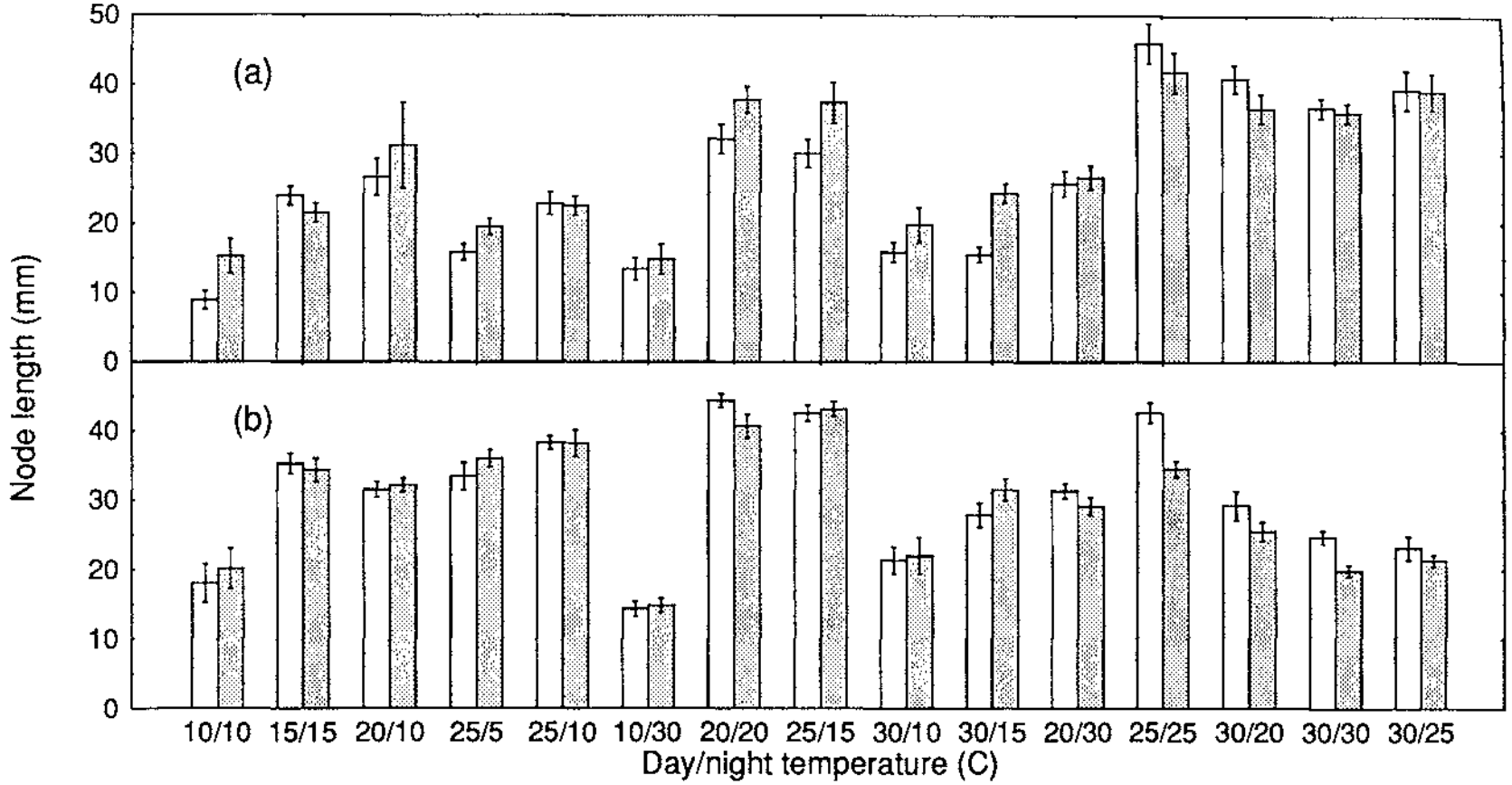


Fig. 3-24. Effect of PFD and day/night temperature combinations (10 - 30 C) on node length (mm) on (a) Epipremnum and (b) Fatshedera at day 30. (Nil shading = high PFD, dark shading = low PFD) Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

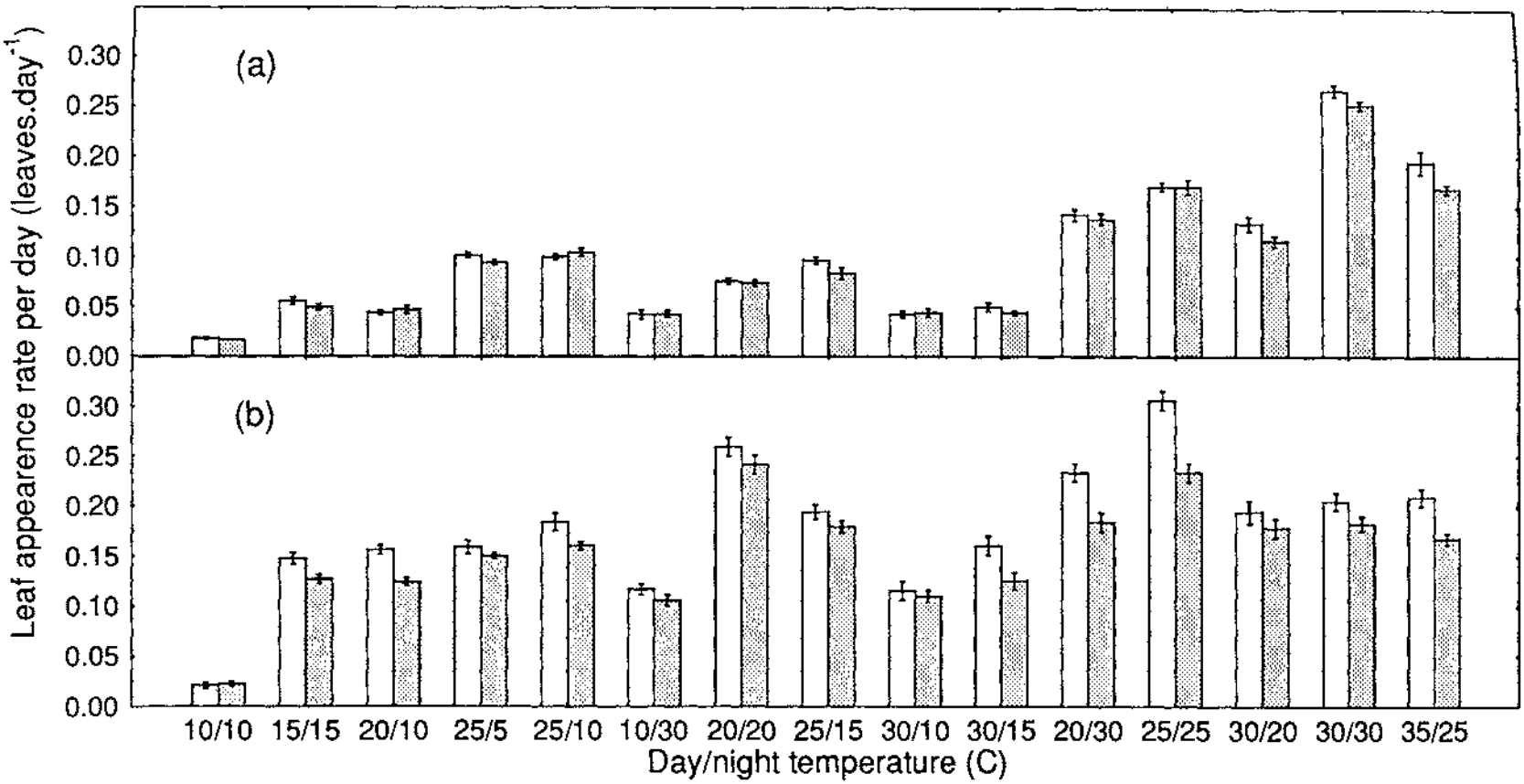


Fig. 3-25. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) of leaf appearence rate per day (leaves.day^{-1}) on (a) Epipremnum and (b) Fatshedera at day 30. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

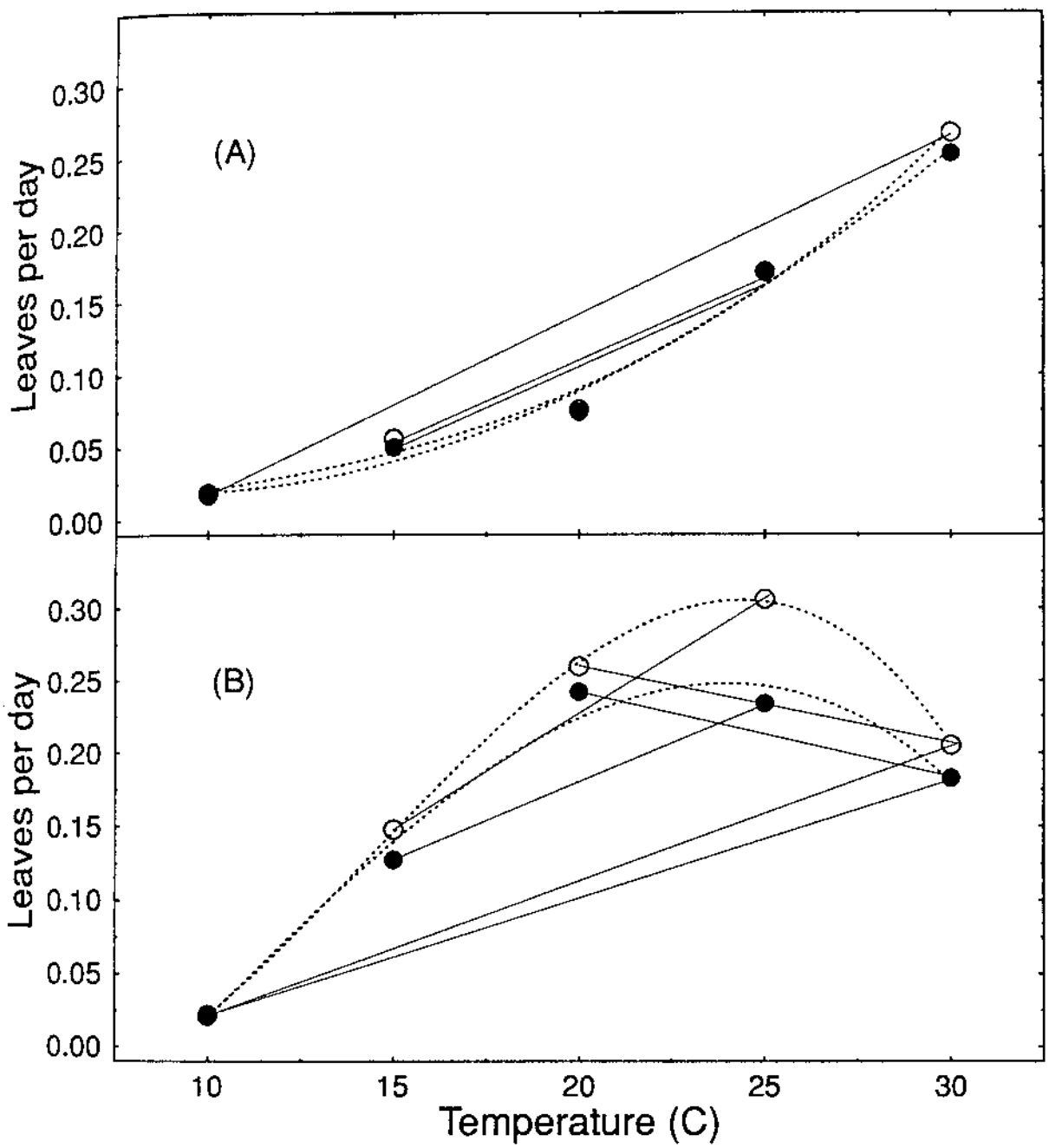


Fig. 3-26. Influence of constant temperature (10 to 30 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on leaf production per day in Epipremnum (A) and Fatshedera (B) at 30 days. Fitted functions for Epipremnum and Fatshedera at high PFD are $y = -0.013 + 0.0042x - 0.00021x^2 + 0.0000013x^3$ ($r^2 = 0.990$), $y = 0.015 - 0.028x + 0.0038x^2 - 0.0000088x^3$ ($r^2 = 0.999$), and at low PFD $y = 0.0704 - 0.0118x + 0.00071x^2 - 0.00000038x^3$ ($r^2 = 0.989$), $y = -0.219 + 0.0184x + 0.00089x^2 - 0.00000036x^3$ ($r^2 = 0.982$), respectively. Each data point represents the mean of 12 plants. Lines were fitted using least squares regression. Refer to text for explanation of the additional lines on each graph.

leaves·day^{-1} occurring at 30 C. Similarly, LFPD in Fatshedera increased with temperature, but differed in that maximum values of 0.30 and 0.25 leaves·day^{-1} were found at 25 C at high and low PFD, respectively.

Data from the constant temperature regimes could be used to predict the performance of plants in a wide range of differential day/night temperatures treatments, assuming the development during the day and night were independent and additive. The rate of development (for instance at 30/10 C) could be estimated from the point where a vertical line from the x-axis through the mean temperature (20 C) intersected with a line joining the values corresponding to the temperature differential (i.e., 30 and 10 C) (Fig. 3-26). The height of the vertical line corresponds with the rate of development. In Fatshedera there was good agreement between the actual (0.11) and predicted values (0.11). However, in Epipremnum using the same temperature combination the predicted values (0.14) over-estimated the actual rate (0.05 leaves·day^{-1}). In Epipremnum, reducing the day/night temperature differential while increasing the mean temperature, decreased the difference between the observed LFPD and the predicted values. In Fatshedera agreement between predicted and observed values depended on the mean temperature and the PFD. At a mean of 25 C, obtained using 20/30 C, the predicted rate of LFPD over-estimated the actual rate, whereas at 20 C the outcome depended on the PFD. At high PFD the predicted rate over-estimated the actual rate, whereas at low PFD there was good agreement.

3.3.13 Shoot/root ratio

Significant variation in shoot/root ratio was due to differences arising between each species and among temperature treatments ($P \leq 0.0001$), while the effects of PFD and harvest were not significant (at $P=0.05$).

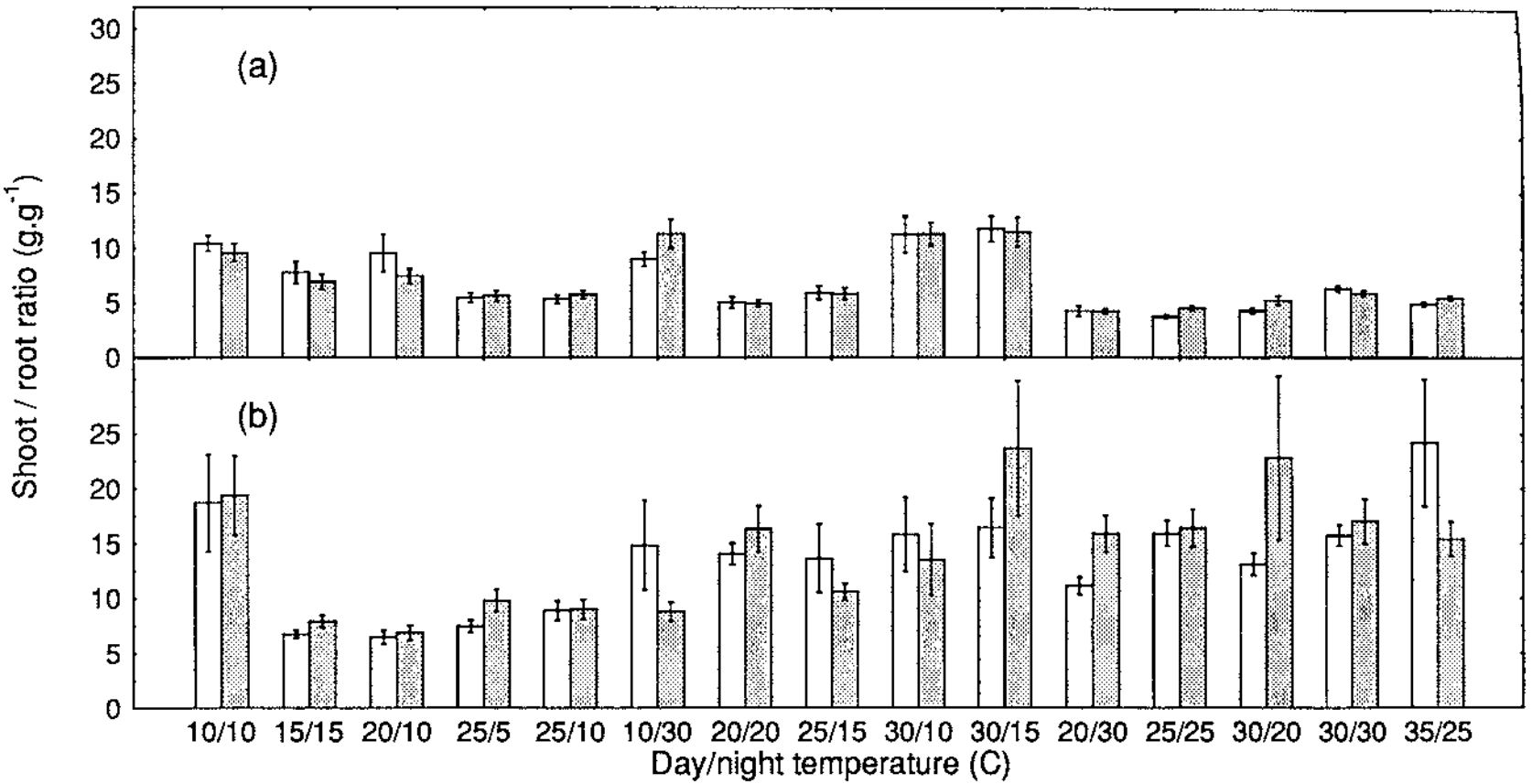


Fig. 3-27. Effect of PFD and day/night temperature treatments (with increasing mean temperature from left to right) on shoot/root ratio ($g.g^{-1}$) of (a) Epipremnum and (b) Fatshedera at day 30. (Nil shading = high PFD, dark shading = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

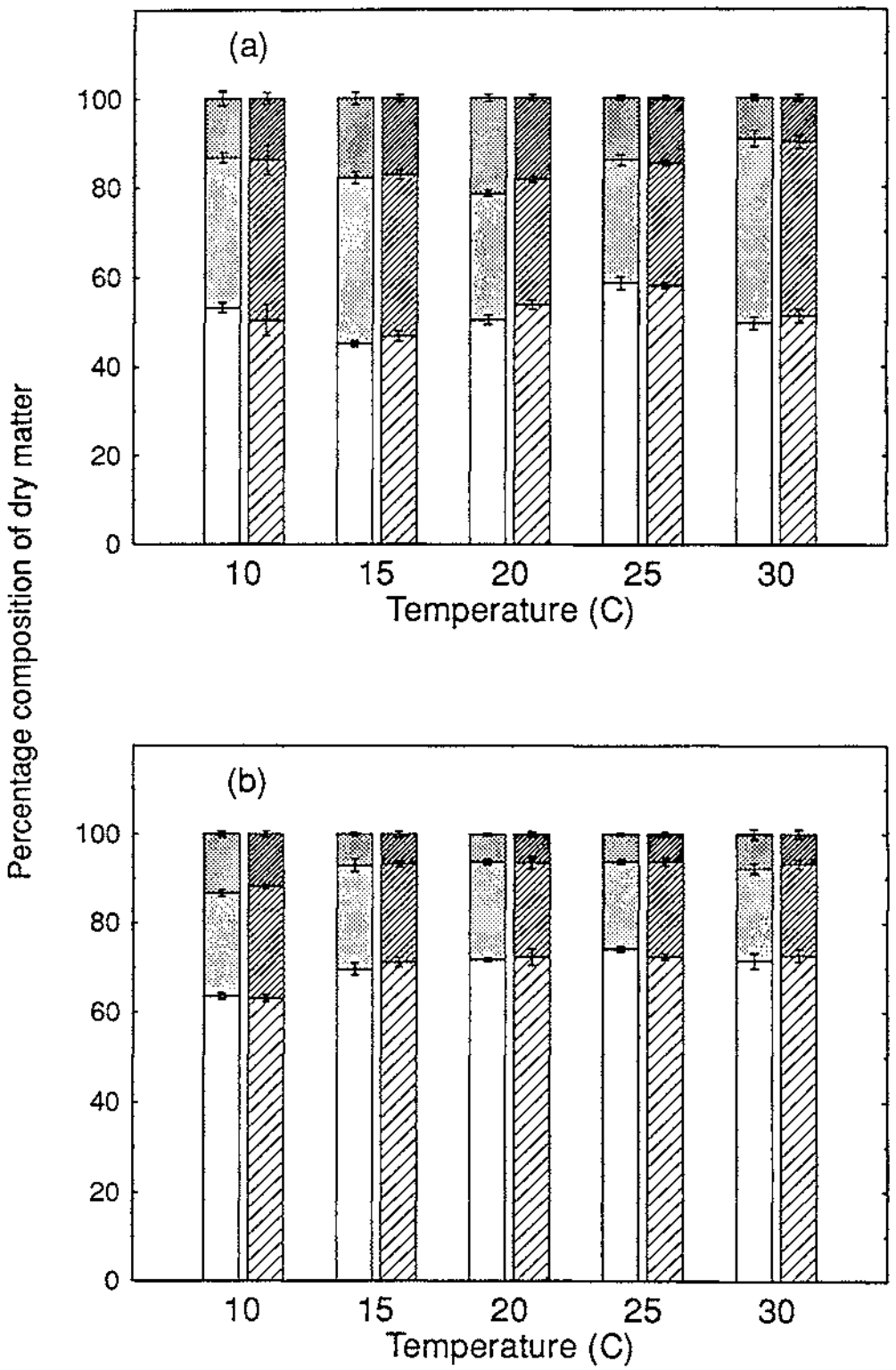


Fig. 3-28. Effect of PFD and constant temperature (10 - 30 C) on the dry matter partitioning between leaves, shoots and roots (base, middle and upper section of each bar) on (a) Epipremnum and (b) Fatshedera at 30 days. (Light shading = high PFD, diagonal lines = low PFD). Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

The shoot/root ratio in Fatshedera was generally higher (15.6) than in Epipremnum (7.6) at all temperatures and was relatively constant during each treatment (Fig. 3-27). In Fatshedera the shoot/root ratio was consistently high in treatments with a mean temperature of ≥ 20 C. High ratios were also found in treatments where plants experienced low day temperatures. In contrast, in Epipremnum no clear patterns were evident, except in treatments where plants experienced low day temperatures then, like Fatshedera, the shoot/root ratio was higher.

Shoot/root ratio in both Epipremnum and Fatshedera was higher in treatments where growth was relatively slow or was impaired by exposure to low or high temperatures. The higher shoot/root ratio in the slow-growing treatments probably resembled the shoot/root ratio of a recently rooted cutting (Fig. 3-28).

3.3.14 Partitioning between leaves, stem and roots

The partitioning of dry matter between leaves, stem and roots was influenced significantly ($P \leq 0.0001$) by temperature and species. Partitioning of dry matter between plant parts was not influenced significantly by harvest or PFD ($P=0.05$).

The proportion of dry matter allocated to leaf tissue was markedly lower in Epipremnum (54%) than in Fatshedera (69%). There was a correspondingly significant ($P=0.01$) increase in the proportion of stem and root in Epipremnum compared with Fatshedera (Fig. 3-28). The allocation of resources to roots was almost constant in Fatshedera across the temperature range, except at 10 C where it was almost double the quantity present at other temperatures. In Epipremnum the proportion of total plant dry matter allocated to roots was highest at 20 C.

3.4 Discussion

3.4.1 Introduction

The growth response of each species may be attributed primarily to differences within the aerial environment as the root systems were not restricted by lack of water, aeration or nutrients through selection of a suitable substrate and appropriate irrigation frequency (Brooking, 1976). The relative consistency of the carbon dioxide concentration and the vapour pressure deficit ensured differences in plant performance could be ascribed primarily to differences in temperature and PFD.

Fitting smooth curves to the primary growth data may lead to loss of information that could in some circumstances have biological significance, especially where substantial differences exist between the raw data and the fitted values representing responses to environmental treatments. The functional approach has been used to fit curves to the data collected in CE treatments where variation within each environment was considered relatively small compared to differences between environments. However, in common with most experiments of this type, precision of fitted functions could have been enhanced by additional harvests and increased replication of experiments.

3.4.2 Relative growth rate

Relative growth rate may be considered as an index of efficiency describing growth in terms of the rate of increase in dry weight per unit of dry weight. this measure of growth enables more meaningful comparisons between different sized individuals than is possible with absolute growth rate.

Under favourable conditions the RGR of each species is determined by the rate of carbon assimilation. This is largely determined by the potential photosynthetic activity of the leaves and may be used as a convenient basis to compare plant performance in different environments (Hunt, 1991).

In these experiments in all temperature treatments (except at 10 C) exponential growth of both W and L_A occurred over the period between 15 and 60 days. This is a comparatively long period for constant relative growth rate in woody plants (Barrow, 1977), but is often matched or exceeded by other herbaceous plants such as maize (Duncan and Hesketh, 1968), ryegrass (Troughton, 1971) and cotton (Raper *et al.*, 1977). These results indicate that in favourable environmental conditions the temperature and PFD treatments did not prevent exponential growth over an extended period, but were only responsible for modifying the rate that occurred in each treatment. However, exponential growth in whole plants could not be maintained indefinitely and it is envisaged that an asymptotic growth function would be required to describe the growth data over an extended period of time.

In these experiments RGR increased with temperature up to a maximum of 30 to 36 C for Epipremnum and 22 to 23 C for Fatshedera. These values are typical of many crop plants (Dale, 1964; Terry, 1968; Rajan and Blackman, 1975). While the temperature optima for Fatshedera could be determined readily, this was not possible with Epipremnum owing to the restricted range of high temperature treatments investigated in this study. The RGR was only half that reported in bean at PAR <20 $W \cdot m^{-2}$ (Dale, 1964). Mortensen (1992) obtained a similar patterns of dry weight increase in *Dieffenbachia maculata* and *Syngonium podophyllum.* In the current study, RGR in constant temperature treatments was higher than in other treatments with the same mean. The growth of many plants including bean (Dale, 1964) and tomato (Calvert, 1964; Hussey, 1965; Friend and Helson, 1976; Klapwijk and Wubben, 1978; Heuvelink, 1989) was also higher at constant temperature than with an inverted day/night temperature regime. Friend and Helson (1976) reported in a study of seven crops that plant growth was

greater at a high day and low night temperature than a low day and high night temperature at the same daily mean temperature.

It was established that inhibition of RGR occurred where Epipremnum and Fatshedera were exposed to chilling temperatures. These temperatures resulted in a severe limitation to plant growth, particularly in Epipremnum. Sensitivity to chilling temperatures was also reflected in the other growth parameters quantified in this study. Similar findings have been reported in chilling sensitive species such as maize (Long *et al.*, 1983) and tomato (Vallejos *et al.*, 1983). Recently, chilling related inhibition of plant growth has been linked to both the temperature dependence of photochemical activity and to carbon fixation (Brüggemann *et al.*, 1992a,b). In this study there was some evidence of low temperature-induced chlorophyll degradation particularly at high PFD possibly contributing to impaired photochemical activity (Plate 3-5).

Inhibition of RGR also occurred when Fatshedera were grown at temperatures in excess of 25 C and noted in the other growth parameters investigated in this study. The relative sensitivity of Fatshedera to high temperatures compared with Epipremnum probably reflects a more rapid rise in the inactivation of enzymes with increasing temperature compared with the activation energy of chemical reactions required for plant growth. The asymmetric temperature response curve for RGR could result from the net difference between these two opposing Arrhenius functions (Johnson and Thornley, 1985).

Thermoperiodic responses have been described by Went (1944), where increased stem elongation rates occurred when the temperature during the dark period was lower than during the day. Unfortunately Went did not examine plant dry weight in his early investigations, and other studies suggested that only a relatively poor correlation existed between stem height and dry weight (Bendix and Went, 1956; Kristoffersen, 1963). This study did not find any substantive evidence of a thermoperiodic response in the two foliage species. Maximal values for RGR occurred in the constant temperature treatments with no further increase

in RGR occurring with a day/night temperature differential. This was in agreement with findings of many other researchers (Dale, 1964; Calvert, 1964; Hussey, 1965; Rajan and Blackman, 1975; Friend and Helson, 1976; Warrington *et al.*, 1977; Ivory and Whiteman, 1978). The equal contribution of the day and night temperature to RGR is clearly evident for Epipremnum and Fatshedera from the symmetry of the response surfaces about the mid-line of each graph between equal day and night temperatures (Figs. 3-6 ,3-7).

3.4.3 Relative leaf area expansion rate

Relative leaf area expansion rate is analogous to RGR, representing an efficiency index describing plant growth in terms of the rate of increase in leaf area per unit of leaf area. Like RGR, LER depends upon photosynthetic and respiratory activity, nutrient supply and metabolic balance; in addition it is also concerned with internal correlation mechanisms that determine the growth of new meristems and organs (Evans, 1972). In this study LER was related to RGR in a linear manner. A similar relationship was reported using an *Impatiens* sp. (Hughes, 1959). The interdependence between leaf area and total dry weight was also evident in the similarity of the response surfaces representing the effect of day and night temperature on LER and RGR. The parallel growth of leaf area and dry weight in Epipremnum and Fatshedera not only suggests the close relationship of the two parameters, but also the similar temperature dependency in each species of all the underlying processes that culminate in the LER and RGR.

In this study, relative leaf growth rate increased with increasing temperature up to a maximum value and then decreased with further increases in temperature. The temperature dependency of LER was very similar to RGR. It has been suggested that differences between species in their growth response to temperature are reflecting the response of photosynthesis to temperature (Berry and Raison, 1981). Several investigators have found that leaf expansion is strongly influenced by temperature and is a significant factor determining growth

at low temperature (Milthorpe, 1959; Beauchamp and Lathwell, 1966; Potter and Jones, 1977). In this study the lower LER in Epipremnum than Fatshedera at low temperature reflected their relative tolerance and ability to grow at low temperature.

Leaf expansion rate has been related to the average daily temperature as reported in bean (Dale, 1964), cucumber (Milthorpe, 1959; Slack and Hand, 1983) and poinsettia (Berghage, 1989), but was not evident in fuchsia (Erwin *et al.*, 1991). In a recent paper Wolfe (1991) comparing chilling-sensitive and chilling-tolerant species reported that the relative importance of low temperature depended on species, time, intensity and duration of treatment.

Maximum rate of LER occurred in constant temperature treatments, and there was no evidence of a thermoperiodic response that could be related to specific increases in RGR arising from particular day/night temperature treatments. Leaf expansion rates in the inverted day/night treatments were generally similar in magnitude, but lower than in constant temperature treatments at the same mean temperature. A notable exception occurred where the low temperature period occurred during the light period, when both RGR and LER were reduced substantially. Chilling-dependent reduction in dry matter production and leaf area expansion may be linked to low temperature impairment of photosynthesis. Chilling-induced temperature stress may arise from either one or several of the following: direct thylakoid membrane damage or impairment of photosystem II reaction centres, disruption of dark reaction enzymes by reduced ribulose-1,5-biphosphate carboxylase/oygenase (Rubisco) activity, loss of bulk chlorophyll, or stomatal closure triggered by ABA or some related factor. These mechanisms may operate in plants arising from exposure to incipient chilling damage mediating feedback inhibition of photosynthesis by carbohydrate accumulation during chilling (refer to Chapter four). The low activity of Rubisco could be a significant factor in depression of photosynthesis and growth in chilling sensitive plants (Brüggemann *et al.*, 1992) including Epipremnum.

3.4.4 Leaf area ratio

Relative growth rate can be partitioned into a morphological component (LAR) and a physiological component (NAR). Leaf area ratio describes the leaf area per unit of total plant dry weight. In these experiments the maintenance of exponential growth in both Epipremnum and Fatshedera required LAR to increase over time to compensate for the time-dependent decrease of NAR.

The relationship between temperature and LAR was quadratic in both the high and low PFD treatments. This contrasts with a recent report suggesting that LAR was influenced by temperature at low PFD in a quadratic manner, but this relationship was not maintained at high PFD (Hunt, 1990). If this report represents a general principle, then it must be concluded that the PFDs utilised in this study were effectively both 'low' PFDs.

Leaf area ratio was lower in constant temperature treatments than in alternating temperature conditions in Epipremnum, but not in Fatshedera suggesting a differential thermoperiodic response. This contrasts with earlier findings that thermoperiodic effects were absent from both RGR and LER.

3.4.5 Net assimilation rate

The NAR is the assimilatory component of RGR being a measure of the productive efficiency of whole plants expressed as the net rate of photosynthesis integrated over time. This represents the rate of carbohydrate production less respiratory losses (equivalent to dry weight increase) between harvests on a leaf area basis. In these experiments the net assimilation rate generally decreased as plants developed over time. Similar findings have been reported in other studies (Thorne, 1960, 1961; Hughes and Cockshull, 1972) where NAR declined in both CE and natural environments in many different crops. The decline in CE indicates this is not related to an externally-limiting factor response or a seasonal

change in the environment, but rather a normal and inevitable consequence of plant growth where the proportion of non-photosynthesising components in the plant increases with plant size.

In this study NAR increased with increasing temperature up to a maximum rate and then declined. Similar trends have been reported by Dale (1964), Warren Wilson (1966), Terry (1968), Rajan *et al.*, (1973), Rajan and Blackman (1975), Thomas and Sprent (1984), Midmore and Prange (1992) and contrasts with the finding that in young tomato plants NAR was not influenced by temperature (Heuvelink, 1989). The reduction in NAR with increasing temperature, particularly in Fatshedera was probably due to respiration having a higher temperature coefficient than photosynthesis or could reflect a more rapid rise in the inactivation of enzymes with increasing temperature compared with the activation energy of chemical reactions required for plant growth (Johnson and Thornley, 1985).

Chilling-related inhibition of plant growth may be related to the temperature dependence of photochemical activity and carbon fixation (Brüggemann *et al.*, 1992a,b) as this would be expected to depress NAR as noted in this study when plants were exposed to 10 C.

The highly significant correlation between NAR and RGR found in these results could have been anticipated as these two factors are interrelated and not independent. This raises the question as to why this was not considered in other studies (Potter and Jones, 1977; Heuvelink, 1989) and not evident in chrysanthemum in findings by De Jong and Jansen (1992).

In the current study the combination of high NAR and high LAR usually contributed to a high RGR. Accordingly, the light intercepting capacity and the efficiency of its use are responsible for high RGR. Similar findings have been reported by Jarvis and Jarvis (1964) when comparing growth of *Helianthus annuus* with *Betula verrucosa* and *Populus tremula*. Another study comparing

shade-avoiding and shade-tolerating plants also reported a similar relationship between RGR, NAR and LAR (Corré, 1983). While this evidence supports the findings with Epipremnum and Fatshedera, it is clearly not typical of most plants as demonstrated recently when Poorter (1990) summarised 60 plant growth studies, and found that variation in RGR among species was largely accounted for by LAR (80-90%) and the balance by NAR (10-20%).

3.4.6 Efficiency of dry matter production

The relative efficiency of light energy utilisation in different environmental conditions may be readily evaluated in CE studies. The constant pattern of increased efficiency of dry matter production at low compared with high PFD is consistent with the adaptation of both Epipremnum and Fatshedera as facultative shade plants.

The large difference between each species in their relative efficiency of dry matter production per mole of incident light suggests there could be important differences in the response of each species to PFDs that exceed the photosynthetic requirements.

Efficient utilisation of light is probably never more important than in determining crop productivity in intensive greenhouse production. In protected cultivation the opportunity exists to maximise productivity through understanding the environmental physiology of crops and its application to management strategies. It is therefore surprising how few references on this topic exist in the literature for ornamental greenhouse crops; begonia (Hershey and Merritt, 1987; Merritt and Kohl, 1989), chrysanthemum (Kohl and Mor, 1981; Kohl and Thigpen, 1979; Munoz, 1974), geranium (Merritt and Kohl, 1985, 1989), kalanchoe (Munoz, 1974), and petunia (Merritt and Kohl, 1982, 1983; Leith *et al.*, 1991). Strangely, most of these references neglected to consider the roots as an important part of the plant. This must limit the validity of some of the conclusions drawn from this

work when attempting to apply results to other crops. Hershey and Merritt (1987) suggested roots were of minor importance since they were not part of the marketable yield. Using seedling begonias they showed a productive efficiency of 9.5% which is comparable with the highest measured values of 9.8% for maize (Loomis *et al.*, 1971) and 10 % for petunia (Leith *et al.*, 1991).

If the conversion of photosynthetically active radiation into dry weight were to proceed without loss then the conversion rate could be calculated assuming the energy output in PAR from metal halide and tungsten halogen lamps was similar to a typical value for sunlight of 218 $Kj \cdot mol^{-1}$ (Thimijan and Heins, 1983, Merritt and Kohl, 1989) divided by a typical heat of combustion for herbaceous plants of 16.8 $Kj \cdot g^{-1}$ (Loomis *et al.*, 1971) yielding about 13 $g \cdot mol^{-1}$.

Productivity efficiency of Epipremnum and Fatshedera on a per plant basis may be evaluated by assuming that each plant occupied about 0.04 m^2. On this basis, Fatshedera at 20 C produced 1.5 $g \cdot mol^{-1}$, about 20% of the dry matter reported for petunia (Leith *et al.*, 1991), while maximum productivity of Epipremnum (at 30 C) was about 10% of the overall efficiency of petunia. Previous studies have consistently shown that in crops such as chrysanthemum a leaf area index >3 is required for maximum light absorption capacity (Kohl and Mor, 1981; Kohl and Thigpen, 1979). Although not recorded in these experiments it is expected that LAI would be lower than values reported above. A relationship between increased productivity efficiency and increased number of growing points per plant has been presented by Merrit and Kohl (1983). The linking of these two factors could be an important determinant of the efficiency of light trapping and conversion to dry matter in this study as leaves were restricted to an alternate arrangement on to a single stem in Epipremnum and Fatshedera.

Although recognised, the relationship between low production temperatures and quality of foliage plants has seldom been reported (Conover and Poole, 1981). Infrequent cool nights did not reduce the quality or size of Epipremnum, but with three cool nights per week the reductions in these factors were readily discerned

(Poole and Conover, 1986). This could suggest that the deleterious effects of low night temperatures may be restored slowly during warm days in between the cool days. Few signs of chilling stress occurred provided at least half of the potential recovery from an earlier cold period was allowed for before the next period of chilling stress occurred, otherwise the deleterious effects of chilling may accumulate.

Results presented in this study for Epipremnum, that demonstrate exposure to 10 C during the night or the day caused a marked repression of photosynthetic activity, this may be related to chlorophyll degradation in Fatshedera and to photo-oxidative damage in Epipremnum (Plate 3-5). The same effect was not evident following exposure of petunia plants to low temperatures (4 C) during the dark period (Leith *et al.*, 1991), but apparent in young geranium plants at 7 C (Merritt and Kohl, 1989). In the current study and in a related investigation by Poole and Conover (1983) Epipremnum grew slowly at 15 C. The temperature response of Epipremnum was similar to a related species. Sandved (1976) recommended a minimum temperature of 15 C to avoid chilling injury in *Philodendron scandens* and also suggested Fatshedera was more chilling-tolerant, being able to grow at 12 C without damage.

3.4.7 Specific leaf area

The SLA is an index of the ratio of leaf area to leaf dry weight (i.e., a measure of the relative thickness or density of leaves).

Specific leaf area in Epipremnum was largely independent of temperature and leaves were about half the thickness of Fatshedera. The findings in this study suggest that SLA may contribute to growth reduction in the inverted day/night temperature treatments in Fatshedera as noted in tomato by Heuvelink (1989). However, the opposite was found in Epipremnum. In view of the relative stability of LWR, this could be interpreted as indicating the effect on NAR, and hence the

efficiency of light interception, was more important in controlling RGR in Epipremnum than it was in Fatshedera.

Although SLA in Epipremnum did not vary systematically with mean temperature, leaf thickness may be an important factor in the avoidance of temperature-related stress in Fatshedera. Leaves were significantly thinner near the optimum temperature for growth compared with higher or lower temperatures. It has been proposed that leaf thickness and chlorophyll content may be critical factors in the protection of photosynthetic pigments from destruction under light saturating conditions and under cool growing temperatures during exposure to high PFD (Bunce *et al.*, 1977; Armitage *et al.*, 1981).

3.4.8 Leaf weight ratio

Leaf weight ratio quantifies the leafiness of the plant on a dry weight basis and represents the proportion of the total plant invested in photosynthesis. It provides an estimate of the proportion of potential photosynthetic area in relation to the total weight of respiring plant material. Leaf weight ratio was almost constant in Epipremnum and Fatshedera and was insensitive to changes produced by temperature and PFD treatments examined in this study. The morphology of Epipremnum and Fatshedera can be considered as a simple repeating leaf-stem sequence. As plant growth occurs the proportion of leaf to stem and other 'non-photosynthetic' tissues would remain in a stable ratio.

The stability of this ratio suggests that it is highly regulated within each species. Such tight control is probably determined by the genome and is recognised as occurring widely in other plants (Dale, 1964; Evans, 1972; Thomas and Sprent, 1984; Heuvelink, 1989; Vlahos *et al.*, 1991; Midmore and Prange, 1992).

3.4.9 Partitioning of dry matter

Partitioning of assimilates within a plant is the final result of many processes interacting together and over time. Although it is possible to describe how assimilates are partitioned, the mechanisms controlling the processes have yet to be resolved (Daie, 1985; Patrick, 1988). Kramer and Kozlowski (1979) reported that each species has a characteristic shoot/root ratio. This ratio may be disturbed by environmental stress and the plant may respond by directing assimilates into the organs that are most repressed by the stress in an effort to maintain the ratio by compensatory growth (Hunt and Nicholls ,1986).

The shoot/root ratio tended to be higher in those temperature treatments where plants were exposed to high or low temperature stress. If the hypothesis of Hunt and Nicholls (1986) is correct, then it may be concluded that in these treatments the shoots are the primary site of stress. The results of this study indicate that there may be more than one species-specific response of the shoot/root ratio to temperature. Both Epipremnum and Fatshedera had higher shoot/root ratios when exposed to 10 C. At other temperatures the ratio remained almost constant in Epipremnum, while in Fatshedera the ratio increased to a higher almost constant level above 20 C. Similar response patterns in other species have been reported by Cooper (1973). The temperature optima for root growth may be lower than for shoot growth (Terry, 1968; Nielsen and Humphries, 1966) and hence the sink strength would also be lower. This may partially explain the interspecific differences in shoot/root ratio. The temperature optima for Fatshedera shoot growth was about 25 C, and the optima for roots appears to occur at about 20 C. At temperatures above the optima for shoot growth the ratio would be increased and would be regulated by the relative reduction in growth rate for the shoots and the roots. In contrast, growth of Epipremnum in greenhouses was maximised at air and root temperatures of 21 and 27 C, respectively (Conover and Poole, 1986). This suggests that empirically derived principles related to temperate crops may not always be directly applicable to tropical plants (Nielsen and Humphries, 1966; Terry, 1968).

Variation in shoot/root ratio increased between plants in some treatments in an uncontrolled manner, suggesting that some unexplained heterogeneity existed within these particular treatments. In this study, distribution of dry matter was not affected by plant age or PFD. This contrasts with young legumes where increased PFD was associated with increased partitioning into stems and decreased partitioning into roots with that to leaves remaining unchanged (Cooper, 1967). In lettuce, the partitioning to leaves increased at low PFD (Lorenz and Wiebe, 1980).

3.4.10 Plant development rate

Leaf appearance rate in Epipremnum and Fatshedera increased in a curvilinear manner with respect to temperature and in the constant temperature treatments was described by cubic functions. Similar equations were used by Tollenaar *et al.*, (1979) and Karlsson *et al.*, (1991) to describe the maximum rate of leaf unfolding in maize (0.57 leaves·day^{-1} at 31-32 C) and hibiscus (0.23 leaves·day^{-1} at 32 C). Frond unfolding in nephrolepis fern peaked at about 0.38 fronds·day^{-1} at 25 C (Erwin *et al.*, 1990) and a similar temperature optima has been reported for poinsettia (Berghage *et al.*, 1989) and fuchsia (Erwin *et al.*, 1989). Warrington and Kanemasu (1983) fitted a cubic function to leaf initiation rate and a quartic function to leaf appearance rate in maize - a maximum leaf appearance rate of 0.43 leaves·day^{-1} at 33 C was similar to that determined by Tollenaar *et al.* (1979).

The temperature range in this study was appropriate to determine the maximum rate of leaf unfolding for Fatshedera (from the fitted function) of 0.31 leaves·day^{-1} occurred at 24 C. With Epipremnum the maximum of 0.27 leaves·day^{-1} was recorded at 30 C. For many plants the leaf development rate was determined to be a linear function of mean daily temperature between approximately 10 and 30 C (Friend *et al.*, 1962; Tollenaar *et al.*, 1979; Rawson and Hindmarsh, 1982; Karlsson *et al.*, 1988, 1989, 1991; Lieth and Carpenter, 1990).

The results of this study indicate that in treatments utilising different day/night temperature conditions the rate of leaf appearance in Epipremnum and Fatshedera was determined by the sum of the rates of development over the time intervals spent at any particular temperature. Furthermore, the results indicated that leaf appearance rate was not influenced by the sequencing of temperatures. Exposure of plants to inverted day/night temperature regimes, where the day temperature was lower than the night temperature, produced similar rates of leaf development to the reciprocal temperature treatments with the same mean temperature (Plate 3-3). These findings are in agreement with reports using bean (Dale, 1964), maize (Warrington and Kanemasu, 1983a,b) and Easter lily (Erwin and Heins, 1990).

The lack of data above 30 C reduces the ability to extrapolate with any confidence into this region as rapid changes in the shape of the temperature response curve may be anticipated as reported by Orchard (1976) and, Warrington and Kanemasu (1983). These changes at high temperature may be attributable to thermal inactivation of enzymes or to instability of genes (Levitt, 1972; Forward, 1960). The nature of high temperature stress is a complex process. As temperature increases, a point is reached where respiratory activity exceeds photosynthetic efficiency and growth is slowed down, finally ceasing when stored reserves are exhausted. Most mesophyllic crop plants grow and develop in the 10 to 30 C range, but are heat stressed at 35 to 45 C (Eastin and Sullivan, 1984). Although it may be useful to group plants according to their preferred growth temperature range, alone this is an inadequate classification as the upper temperature limit to growth is time dependent and related to the stage of development. High temperature damaging and stress, unlike chilling stress, varies inversely with time in an exponential manner. Young actively growing plants are more susceptible to high temperature stress than mature leaves (Alexander, 1964, 1977). Short-term thermal stress therefore would be more evident as damage or a reduction in size or development rate in new leaves formed in high temperature conditions.

At temperatures below about 10 C, rate of development would probably continue in a slightly curvilinear manner to approach the base temperature where zero development occurred. The base temperatures estimated by graphical extrapolation for Epipremnum and Fatshedera were approximately 7.6 and 9.0 C, respectively.

Chilling injury is important in plant species from the tropical regions (Wolfe, 1991). The relative sensitivity of Epipremnum and Fatshedera to chilling damage following brief exposure to low temperature is particularly significant. Breakdown of chlorophyll occurred when both species were exposed to low temperatures, and this was most severe in Epipremnum where photo-oxidative damage occurred. Environmental factors, such as chilling temperatures, will determine the appropriateness of plant production conditions and locations where either species may be produced in unprotected outdoor situations.

There was no evidence of a thermomorphogenic response, indicated by a change in development rate, that was caused by the day/night temperature differential This is in contrast to Easter lily (Erwin and Heins, 1990) and campanula (Moe and Heins, 1991) where more rapid development was claimed in specific day/night temperature treatments. There was no effect of PFD on plant development rate in Epipremnum and Fatshedera. In contrast, in chrysanthemum, development is influenced by an interaction between PFD and day/night temperature combination (Karlsson *et al.*, 1989).

The difference between the day and night temperature has been demonstrated to influence internode length and plant height, particularly in determinate crops following floral initiation. It is uncertain how the difference between the day and night temperature regulates plant growth or how applicable the principle is to vegetative plants. Internode length has been reported to increase as the differential between day and night temperature increased (Erwin *et al.*, 1989). However, in this current study and in a report by Kaczperski *et al.* (1991), no

beneficial effect of temperature differential was found on either development rate or shoot growth.

3.4.11 Summary

In summary, the present experiments have investigated the influence of temperature and PFD on the growth and development of young Epipremnum and Fatshedera plants. Clear differences in chilling sensitivity and adaptability to high temperatures were evident between the two species. Epipremnum was sensitive to chilling at 10 C and was heat tolerant at 30 C, while Fatshedera was chilling tolerant but heat intolerant to temperatures above 25 C. Relatively short periods at 10 C were responsible for reduced growth performance of Epipremnum. In both species increases in dry weight were responsive to temperature and to PFD, while morphological responses (such as leaf area and leaf development rate) were closely related to temperature effects and were largely independent of PFD. Leaf development was closely related to duration at a particular temperature and the to sum of the rates at each temperature.

CHAPTER FOUR

Effect of night temperature on vegetative growth of Epipremnum and Fatshedera

"For nature is pleased with simplicity,
and affects not the superfluous causes."

Isaac Newton
Principia, Book III.

4.1 Introduction

Plant growth and development are major determinants of yield and have been a primary focus for the attention of plant physiologists and horticulturists (Landsberg, 1977). Control of plant growth has been attributed to the influence of temperature (Post, 1939; Went, 1957; Cremer, 1976), light (Cremer, 1976; Christ, 1978; Lecharny and Jacques, 1980), leaf water status (Powell, 1976; Parrish and Wolf, 1983), photosynthate and endogenous rhythms (Lyr *et al.*, 1968) and relatively recently to hormonal control of plant growth and development (Purohit, 1985).

4.1.1 Effect of temperature variation on plant growth

The effect of temperature on plant growth has been studied for more than a century although infrequently and with widely differing results and interpretation. An exceptionally early and discerning report suggested that the growth of many crop plants occurred predominantly at night (Sachs, 1872). This suggested that night temperature could be an important factor regulating plant growth and be worthy of closer investigation. This observation is particularly relevant if the night

temperature is indeed regulating plant development through the period of maximum energy input into a heated greenhouse environment. After almost a century relatively few references are available on the effect of night temperature on plant growth. Cathey (1955), was among the first in the horticultural literature of the recent past to report development of chrysanthemum flowers was influenced more by night than by day temperature.

Few studies have investigated the effect of night temperature on foliage plant production and it is not known how these ornamental plants would respond to different night temperature regimes with the same mean. While Epipremnum is a tropical vine and Fatshedera is a relatively cool tolerant plant, both are grown for their amenity value as foliage plants. There is a dearth of literature describing their response to temperature and light, despite their popularity in ornamental horticulture.

Environmental conditions in greenhouses have been established on an empirical interpretation of ecological origins and conditions. In their natural habitats plants experience diurnal variation in temperature in all but the most unusual of habitats. Greenhouses have traditionally been programmed to maintain a warmer day than night temperature to mimic the observed temperature changes outdoors in the belief that better plant growth and development resulted (Schimper, 1898). Conservation of photosynthates produced during the light period has been offered as a physiological explanation for this management strategy (Went, 1957).

Watson (1958) contended that the formation of adequate leaf area was probably the most significant determinant of dry matter production in crop plants. While Milthorpe (1959) reported that leaf area expansion in cucumber was determined by the rate of leaf unfolding, this was regulated by temperature and the net assimilation rate of the upper leaves.

There is a widely held and popular view that diurnal temperature variation is necessary for optimal plant growth. However, in environmentally controlled facilities few experiments have demonstrated a marked benefit of a diurnal variation over constant temperature with the same mean (Robson, 1973; Friend and Helson, 1976; Warrington *et al.*, 1977; Ivory and Whiteman, 1978; Krug and Liebig, 1980; Slack and Hand, 1983). Friend and Helson (1976) found no influence of enhanced growth under a diurnal temperature fluctuation of up to 20 C when young plants were grown at a daily mean of 30 C. At mean temperatures < 30 C, the dry weight gain increased when either the day or the night temperature was increased while maintaining a common mean temperature. Increasing the day temperature was more effective than raising the night temperature.

The growth of some plants may benefit from diurnal variation in temperature and may be influenced by the particular temperature regimes experienced during the light or the dark period. A beneficial effect of diurnal temperature variation on stem growth of tomato plants was demonstrated by Went (1944, 1945) using controlled environment treatments. A change in plant growth that was related to diurnal temperature fluctuation was defined as a thermoperiodic response and has been the subject of considerable controversy in the literature (Haroon *et al.*, 1972; Friend and Helson, 1976; Warrington *et al.*, 1977). These authors could not produce an increase in fresh or dry weight required for a thermoperiodic response. Interest in thermoperiodism has been revived by recently by investigations based at Michigan State University. Shoot extension growth of many flowering plants, including Easter Lily and Companula, has been highly correlated with the day-night temperature differential (Berghage, 1989; Karlsson *et al.*, 1989; Erwin *et al.*, 1991; Moe *et al.*, 1991).

4.1.2 Respiratory losses in the dark period

The popular expectation that diurnal temperature variation would produce improved growth rates depends upon respiratory losses being reduced at low temperature during the night compared with the day. However, when respiratory losses over a diurnal cycle are compared with constant temperature treatments, the relationship between temperature and respiration is approximately linear, irrespective of the diurnal fluctuations. Reduction in respiration during the dark period would therefore be offset by a similar increase during the warmer light period. Respiratory activity is closely coupled to the rate of biomass production, and this normally increases as the temperature is raised. The efficiency of biomass production is related to the substrate available from photosynthetic activity and probably independent of the diurnal temperature cycle (Penning de Vries, 1974). When the effect of diurnal temperature variation on the carbon balance in clover plants was investigated, McCree and Amthor (1982) showed that growth at a mean of 20 C was superior to a day/night temperature of 30/10 C. This was indicative of a small negative thermoperiodic effect that was predictable from the geometric increase in maintenance respiration that occurred with increasing temperature - there was a 100% decrease in respiration from 30 to 20 C compared with a 50% decrease from 20 to 10 C.

The time courses of respiratory losses and net CO_2 production in shoots may be partitioned into three phases, each following a characteristic pattern, in a range of plants including sorghum and clover (McCree, 1974), tomato (Ludwig *et al.*, 1975) and cucumber (Challa, 1976). The initial phase shows exponential decay kinetics, while the next phase is characterised by a steady state equilibrium situation that may persist for much of the dark period in the same way that plants may adjust their light compensation point when exposed to low PFD. In the last phase, CO_2 production decreases exponentially to a new equilibrium (suggesting the uncoupling of a regulatory mechanism) before the onset of the next photoperiod.

Challa (1976) demonstrated that there was a direct relationship between sugar concentration in the leaves and CO_2 production from shoots and suggested that the time course in CO_2 production paralleled the time course in leaf sugar content.

4.1.3 Managing the greenhouse environment to control plant growth

Manipulation of the greenhouse environment to modify crop production arose before the advent of chemical growth regulators. Davidson (1960) used low night temperatures to manipulate poinsettia production and reduce internode extension. These poinsettia data may be reinterpreted as an attempt to produce plants at lower night temperatures. A constant day temperature throughout the production period in conjunction with various dark periods at lower than normal night temperature treatments were evaluated using a standardised photoperiod. Provided temperatures were high enough to allow early development of poinsettia only small production delays occurred when a mid-production night temperature was up to 11 C cooler than normal. However, if the temperature in the first 28 days was too low, development was retarded and not offset by a higher temperature treatment later in the production period. Langhans and Larsen (1960) also reported that night temperatures over the range from 10 to 21 C had more effect on poinsettia flower bud development than day temperature supporting the view that night temperatures play a very significant role in plant growth.

'Princess Anne' chrysanthemum plants were grown in a study for 0 to 9 weeks using two temperature treatments, either 6 or 17 C (Zieslin and Kohl, 1978). At intervals plants were transferred from one temperature to the another until flowering occurred. When plants were given low night temperatures (6 C) during then first 3-4 weeks or in the last 3-4 weeks of crop production, no marked delay in flowering occurred. This indicates the relative insensitivity of both the vegetative phase and the period following floral development to low temperatures.

Similar trials with chrysanthemum in England led Butters (1974) to conclude that it may be possible to alter the greenhouse temperature during the year without causing an increase in production time. During periods of high PFD in Europe (March-June) production of high quality plants and flowers occurred when day temperatures were lowered to 13 C compared with the widely used 16 C. Flower production was normally much lower during periods of low PFD experienced during the winter months. However, warmer nights had a very marked effect on improving winter production. This could be interpreted as indicating that plant growth was not only source-limited, but also limited by sink activity.

Subsequently Butters (1977) recommended that in England chrysanthemum growers could make substantial savings without cropping delays by providing the following night temperatures between March to October (13 C), November (16 C), December-January (17 C) and February (16 C). This temperature regime produced higher yields and annual heating costs were lower by about 10% compared with plants grown at 16 C all year round.

4.1.4 Development of a split-night temperature regime

Two further refinements to this heating strategy have been proposed to reduce heating costs. Firstly, thermostats could be turned down to 4 C on one night per week (which results in 10-14% saving). This is achieved at the expense of a cropping delay of 0.6-1.6 days (depending on the cultivar) for each low temperature night used per week. The second method was to examine the effect of reducing the temperature for only a proportion of the night. This heralded the introduction of a system initially called the 'Efford regime', but now more widely known as the 'split-night temperature' regime (SNT) (Butters, 1977). Trial results using the SNT temperature regimes at Efford Horticultural Research Station are difficult to obtain, but it was claimed that chrysanthemum plants grown at 16 C day and exposed to 'the Efford regime' showed little or no delay, or reduction in

modifying the night temperature regime to save energy while maintaining productivity. The SNT regime used a relatively warm period early in the night followed by a cooler period producing a similar mean night temperature over the entire night.

The investigations in England, coupled with an energy crisis, triggered a major investigation of techniques to reduce production costs while maintaining productivity and quality (primarily in the U.S.A. where there is an extensive greenhouse industry). Thorne and Jaynes (1977) have also proposed that lowering the temperature for part of the night might not limit plant development, but could result in significant energy saving. Around the same time a greenhouse grower (Loefstedt, 1977) suggested it was illogical to maintain high temperatures throughout the entire night when plants had only limited ability to produce photoassimilates in low light under winter conditions. He proposed that the metabolic processes dealing with the previous day's photosynthate would be completed in less time under low light compared with high light conditions. Using this approach Loefstedt successfully grew chrysanthemum and lily plants at 16 C until 11 pm and then at 5 C for the remainder of the night, after which the temperature was raised to 16 C for the day. Plants of an acceptable quality were produced using this approach, but it was not possible to compare production with a standard temperature regime as none was used.

Gent *et al.* (1979) also examined the effect of SNT temperatures during a North American winter on the production of tomato, tobacco and Easter lily. They reported an energy saving of 20% using SNT and no marked delay in flowering. Physiological studies conducted on tomato suggested that a warm period early in the night assisted with the processing of photosynthate and the transport of carbohydrates to fruits. The duration of the warm period would therefore depend on the quantity of assimilate processed during the previous day. Although conveying a trend, confidence in these results is reduced due to poor control of the experimental conditions.

Parups (1978) grew a large number of chrysanthemum cultivars (26) using a SNT regime of 16 C for 4 h then 10 C for 8 h in comparison with a constant 16 C night temperature. Vegetative growth was comparable with that in the control treatment and plants were taller in the SNT treatment. Flowering was delayed by 3 days without any change in quality. Similarly, little or no delay in flowering of chrysanthemum, marigold and petunia occurred using SNT. However, inconsistent results were obtained for other crops (Koths and Schneider, 1980). Part of the variation in results using SNT could be related to the effect of low temperature on leaf expansion early in the life of the crop (Milthorpe, 1959). Using chrysanthemum, Kohl and Thigpen (1979) reported that a critical leaf area was required before plants could be grown equally well at 6 or 16 C night temperature. Plant growth throughout the later part of the crop production cycle was determined during the 3 weeks prior to the start of short day treatment while plants were still vegetative. Although no differences in dry weight accumulation occurred, flowering was delayed at the lower growth temperature. Using a combination of 24 C (mean) day and 5 C from 4.30 pm till 8.30 am satisfactory growth of chrysanthemum occurred provided early growth and the start of floral initiation occurred with a night temperature of 15 C (Kohl and Mor, 1981).

Hanan (1979) reported that SNT treatments markedly delayed production of greenhouse roses and reduced flower quality during the low light conditions of winter. Also, when roses were grown at a night temperature of 12 C for 15 h instead of 17 C growth was delayed, but 6 h at 12 C (from 2 am until 8 am) following an early night temperature of 17 C did not delay flowering or reduce productivity (Osnos, 1980). In other experiments Osnos concluded that the warm period should occur in the early part of the night to minimise the delay in development. This is in accord with suggestions by Thorne and Jaynes (1977). Good growth of roses required 17 C air temperature until 2 am while satisfactory growth of chrysanthemum, hydrangea and lily occurred with 17 C until 8 pm. Shanks *et al.* (1986) used a SNT with a warm period early and cool period later in the night found that the quality of greenhouse roses was not impaired, but production was delayed and flower yield reduced. Zieslin *et al.* (1987) speculated

that the delaying aspects of SNT regimes arose from extended periods at sub-optimal temperature which would lead to an irreversible reduction in growth and development. They tested the following night temperatures treatments (1) constant 18 C, (2) constant 14 C, (3) 18 C until midnight, then 14 C until an hour before dawn and (4) 18 C alternated to 14 C every 2 h during the night. Flower production in the two partial heating treatments was similar to the constant 18 C treatment in three of the four rose cultivars examined; in the fourth, 'Golden Times' the alternating temperature treatment (4) produced 28% more flowers. The altered yield was attributed to increased carbohydrate transport capacity to the terminal buds. In an exceptional report, the relative growth rate of sweet pepper plants increased using various SNT temperature regimes (Kooistra, 1984) however, this does not appear to have been reported elsewhere.

Hurd and Enoch (1976) found little effect of night temperature on photosynthesis and transpiration of spray carnations over the range 6 to 30 C. Chrysanthemum, marigolds and petunias (Koths and Schneider ,1980) and poinsettias (Schneider and Koths, 1980) could be grown using SNT without any significant production delay. However, there have been several reports comparing yields from flowering plants produced using SNT and with warmer night temperatures treatments. Chrysanthemum development was usually slower in the cooler night temperatures used by the SNT regimes (Parups, 1978; Zieslin and Kohl, 1978; Kohl and Thigpen, 1979; Bonaminio and Larsen, 1980; Kohl and Mor, 1981). Other crops have been affected similarly. For example, development of rose flowers was delayed by low night temperature and they were of inferior quality (Hanan, 1979). Similarly, growth and development of poinsettia was impaired by low night temperatures. In a unique report (Lovelidge, 1982) poinsettia production at more than 5 C below normal night production temperatures was possible provided the humidity of the air could be maintained at a low level. More recently, White and Warrington (1984) have shown that geranium growth and development was similar in SNT and constant night temperature treatments with the same mean temperature. The comparison of environmental treatments with equivalent energy input is clearly important.

White (1981) considered several different night temperature profiles including various split night (SNT) and sliding night (SN) temperature regimes and their applicability to the greenhouse environment. The lack of standardisation of temperature conditions in the literature (Wilkins *et al.*, 1982) makes it very difficult to make meaningful comparisons between results of different workers.

Few studies have investigated the effect of SNT or night temperature on the growth and development of ornamental foliage plants (Mortensen and Larsen, 1989; Shanks, 1987; Zielsin *et al.*, 1985). Considerably more effort has been directed towards greenhouse flower and vegetable crop plants. It is recognised that the physiological changes induced by flowering and fruiting will influence plant response, and therefore caution must be exercised when translating this information back to vegetative plants. Flower development of chrysanthemum (Langhans *et al.*, 1981) and geraniums (White and Warrington, 1984a, 1988) has been related to the mean night temperature, whereas vegetative growth may be influenced more by the daily light integral (White and Warrington, 1984a,b).

4.1.5 Production delays using split night treatments

Under European winter and spring conditions Challa (1978) found cucumber plants depleted starch reserves after 12 h in the dark at 25 C. When starch was depleted, productivity was not impaired provided the air temperature was reduced to 12 C for the remainder of the dark period. When plants were grown in a constant temperature regime then development was inferior.

Production delays associated with low night temperature and SNT production schedules have been moderated using root zone heating with varying success (Shedlosky and White, 1987). When air temperatures were less than optimum some reduction of production time and other advantages are reported for a range of ornamental horticultural crops including gerbera, chrysanthemum, poinsettia,

rose and ficus where root zone heating was used. Development time were reduced by root zone heating, particularly during the vegetative phase prior to floral initiation. Fresh and dry weights of bedding plants was reduced when air temperatures were lower than 16 C using SNT, but this could be completely off-set when root zone heating at 16 or 21 C was used with SNT (Shedlosky and White, 1987). They concluded that substantial energy savings could be achieved by using root zone heating in combination with SNT regimes in many crops.

The incident light during the period when SNT treatments are in use can have a major effect on growth. Hicklenton and McRae (1984) showed that the production of chrysanthemum was not delayed in SNT treatments when PFDs were relatively high over the summer. However, in the low PFD of a Canadian winter, SNT treatments caused a substantial delay in flowering and a reduction in flower quality that could only be partially overcome with supplemental lighting.

Challa (1978) found growth of chilling-sensitive cucumber crops could be manipulated by temperature to optimise growth and development in a similar manner as reported with ornamental greenhouse flowering crops. Some plants may have critical developmental phases when vernalisation or floral induction are mediated by the thermal environment. This may prevent the lowering of temperature during the night when cropping delays become unacceptable. Following this physiologically important developmental phase it was possible to lower the night temperature with fewer adverse effects on production schedules. Zielson and Kohl (1978) and Kohl and Thigpen (1979) have also suggested that periods of low temperature early in the life of a chrysanthemum crop were more deleterious than if they occurred later in the development of the crop.

Development of Easter lilies and geranium plants in a range of temperature environments was directly correlated with the daily accumulated heat-sum (Armitage and Carlson, 1980; Wilkins *et al.*, 1980). This approach has been incorporated into the standard production schedule of these crops by many commercial producers. Instead of considering the heat-sum of the night and day

temperatures together, Langhans and Albright (1981) proposed that plants might integrate the temperatures over the day and the night independently. Growth and development of lettuce or chrysanthemum were the same in a CE study that compared the average night temperature with a similar constant night temperature. Only minor differences in plant growth were reported when comparing a constant night temperature with SNT regimes using a warm-cool or a cool-warm sequence of temperatures. Langhans and Albright concluded that plant performance depended on the mean temperature over a 24 h period. This contrasts with findings by Challa (1976) and Thorne and Jayne (1977) who suggested that during the night it was better to have a warm period before the cool period.

The effect of different temperature patterns with the same temperature integral (average) on growth and yield of tomatoes was investigated by Hurd and Graves (1984). Cucumber growth and yield has also been highly correlated with the average day and night temperature (Krug and Liebig, 1980; Slack and Hand,1983). In other crops such as chrysanthemum (Cockshull *et al.*, 1981) and rose (Van den Berg, 1987) a similar pattern has been reported indicating a general underlying response to temperature. The diurnal temperature range over which plants may effectively integrate will depend on the thermal limits of physiological processes within each plant (Wilkins *et al.*, 1982; Orchard, 1976). Langhans *et al.* (1981) using lettuce and chrysanthemum showed growth was related to the temperature integral, but this has not been evaluated further with many ornamental flowering plants (White and Warrington, 1984a) or any foliage plants. In studies using geranium, White and Warrington (1984a) reported growth and yield depended more on the average temperature than diurnal variation. In contrast, Miller and Langhans (1985) using lettuce showed that growth and productivity was influenced by both the temperature profile and the mean temperature.

4.1.6 Effect of night temperature on foliage plants

Many plants appear to act as temperature integrators and respond more to the mean daily temperature than the individual fluctuations in temperature within the physiologically active range (Liebig, 1988). Very little data are available on the response of foliage plants to night temperatures. The effect of night temperature on the growth of foliage plants has only been examined in a preliminary study by Poole and Conover (1986). Their data showed Epipremnum would tolerate one night per week at 7.2 C, whereas 3 nights per week at the same temperature caused marked loss of plant quality and plant growth. As foliage plants are sensitive to night temperatures, this study was proposed to investigate their response to different night temperatures and to different diurnal temperature regimes.

The objectives of this research were to:

(1) investigate the effect two PFD levels with a constant day (30 C) temperature and three night temperature regimes (with a daily mean of either 25 or 20 C) on growth and development.

(2) investigate the effect of temperature profile and mean night temperature on the accumulation and partitioning of dry matter and carbohydrates in vegetative growth of Fatshedera and Epipremnum.

The present study was undertaken in order to characterise the response of Epipremnum and Fatshedera plants to three different night temperature regimes so that management practices could be based on a sound knowledge of the environmental physiology of the two crops.

4.2 Materials and Methods

4.2.1 Plant material

Stock plants of *Epipremnum aureum* and *Fatshedera lizei* were grown as described in Chapter three.

4.2.2 Growth environment

Both species were grown in six walk-in controlled environment rooms at 30 ± 0.5 C during the photoperiod ('day'), whilst in the dark period ('night') temperature profiles were adjusted to give a mean night temperature of 20 or 15 ± 0.5 C. The temperatures profiles used in each treatment were achieved using programmable temperature controllers that could step through the predetermined temperature sequence (Figs. 4-1, 4-2). (Note the photoperiod in any particular treatment did not always coincide with natural day due to minimisation of peak electrical loading over the whole climate room facility. This required offsetting of the diurnal cycle in some CE rooms. Cooling in the 15 C night temperature treatments commenced slightly earlier than at 20 C due to limitations in the capacity of the air conditioning equipment.) The environmental conditions used in each CE room are summarised in Table 4-1.

A 12 h photoperiod, synchronous with the mid point of the change-over to the day temperature period, was provided by a water-screened array of four 1 Kw high pressure discharge "Metalarc" lamps and four 1 Kw tungsten halogen lamps (all supplied by GTE Sylvania, Drummondville, Que, Canada).

Table 4-1. Temperature treatments, relative humidity and mean PFD used in night temperature studies with Epipremnum and Fatshedera.

Temperature			Rel. Humidity		PFD	
Day	Night	Mean	Day	Night	High	Low
± 0.5 C			± 5% R.H.		± 5% $\mu mol \cdot m^{-2} \cdot s^{-1}$	
SN30/20 C treatments						
30[a]	20	25	70	70	314	152
30[b]	20	25	70	70	325	151
30[c]	20	25	70	70	319	119
SN30/15 C treatments						
30[d]	15	22.5	70	70	313	154
30[e]	15	22.5	70	70	326	155
30[f]	15	22.5	70	70	325	157

Superscripted letters within each mean temperature relate to particular temperature regimes; refer to schematic representation of the temperature time course in each treatment in Figs. 4-1, 4-2.

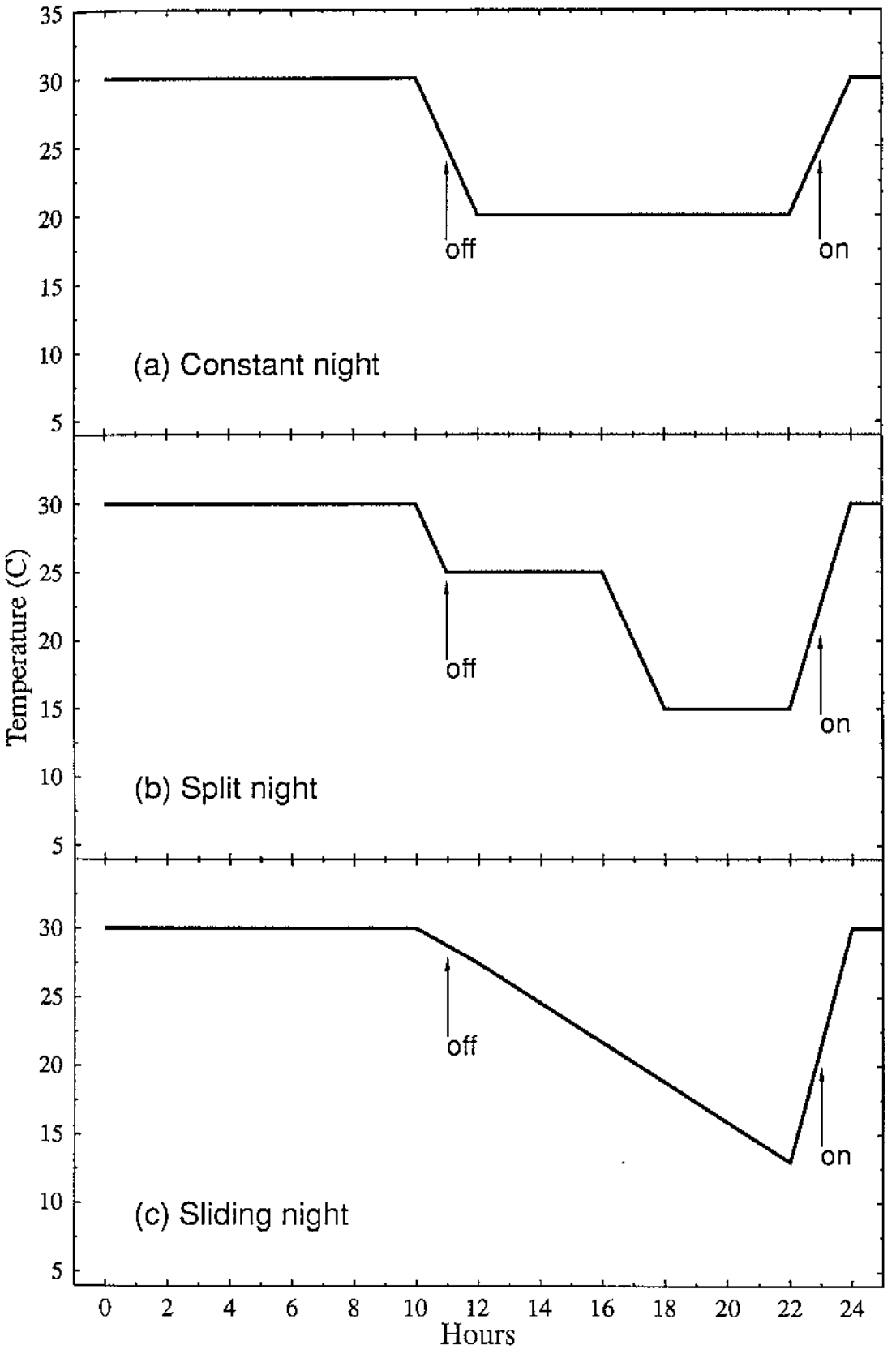


Fig. 4-1. Temperature profiles (a, b & c) used to produce 30 C day and a mean night temperature of 20 C. (on = beginning of photoperiod, off = end of photoperiod)

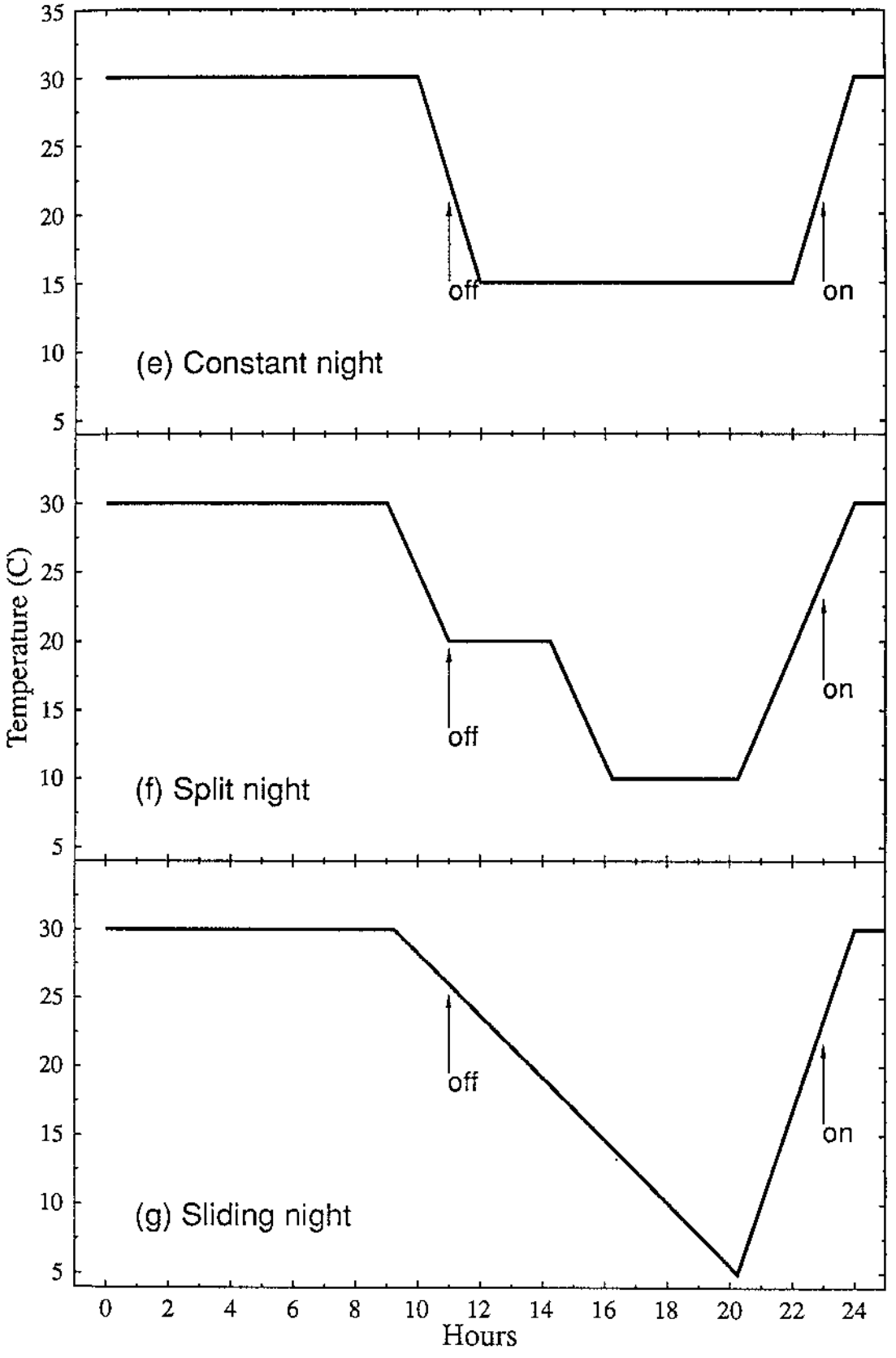


Fig. 4-2. Temperature profiles (e, f & g) used to produce 30 C day and a mean night temperature of 15 C. (on = beginning of photoperiod, off = end of photoperiod)

In each CE room plants were located on six trolleys, three being exposed to an average PFD of 320 ± 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (measured with a Li-Cor LI-185 meter and a 190S quantum sensor (Li-Cor, Lincoln, Nebraska, USA)) at the top of the plants. Low PFD treatments within each temperature treatment were achieved by screening three trolleys with green polypropylene shade cloth (Sarlon-Reid, Auckland, N.Z.) giving an average PFD of 150 ± 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the top of the plants (Warrington *et al.*, 1978; Greer and Laing, 1988a). The high and low PFD in each CE room were equivalent to a daily light integral (DLI) of 13.8 and 6.9 $mol \cdot m^{-2} \cdot day^{-1}$, respectively. Carbon dioxide was monitored continuously but not controlled during the study and ranged between 330 and 360 $\mu l\ CO_2 \cdot l^{-1}$ air. Air flow down through plants in each CE room was 0.3 - 0.5 $m \cdot s^{-1}$ measured with an Alnor Instruments thermoanemometer.

In each night temperature profile (Figs. 4-1, 4-2) 16 plants of each species were randomly assigned to each temperature x PFD treatment. In each CE room each environmental treatment was replicated producing 3 blocks. Four plants of each species from each replicate within each block were destructively harvested at 0, 15, 30 and 47 days from the beginning of the experiment in night temperature profiles a, b and c. Harvest dates in the other night temperature profiles (d, e and f) were at 0, 14, 30 and 42 days.

4.2.4 Plant Analysis

Shoot height, leaf number, leaf area, and dry weights of the leaves, stems and roots were recorded at each harvest.

Leaf area was measured with a Li-Cor model 3100 leaf area meter and samples were vacuum dried (24 h at 2 mm Hg; 40 C) to constant weight. Duplicate samples of roots, shoots and leaves from one of four plants harvested from each PFD treatment within each block were analysed for carbohydrates using the methods developed by Haslemore and Roughan (1976); Haslemore (pers. com.

1985). Total soluble sugar was determined using the phenol-sulphuric colorimetric method with a glucose standard. Starch was assessed after gelling in boiling water and hydrolysis by amyloglucosidase. The glucose released was determined colorimetrically using glucose oxidase and o-dianisidine hydrochloride with glucose standards and starch controls.

In temperature treatments with a mean night temperature of 20 C, the 2nd and 3rd harvest were conducted at the end of the photoperiod and at the end of the nyctoperiod, respectively. This pattern of harvesting was reversed in temperature treatments with a mean night temperature of 15 C and samples were first collected at the end of the nyctoperiod and then at the end of the photoperiod to allow rapid handling of plant material.

Samples of each plant part were analysed by HPLC (High Pressure Liquid Chromatography) using a modified procedure originally reported by Paull *et al.* (1984). Finely ground samples of vacuum-dried plant material were extracted in 95% ethanol on an orbital shaker for 48 h at 5 C. Samples were allowed to stand for at least 24 h at 5 C, then samples were drawn from the supernatant, filtered (0.2 µM poresize) and stored for 4 weeks at -10 C to allow separation of soluble proteins. A 1.0 ml aliquot was vacuum dried and redissolved in deionised water before autoinjection of 20 µl aliquots using a Waters 712 Wisp fitted with a Bio-Rad carbohydrate column (HPX-87, 4.5 mm x 300 mm) and an Optilab 5922 refractive index detector. The solvent (deionised water) was adjusted to a flow rate of 0.6 $ml \cdot min^{-1}$ at 85 ± 1 C. Peak heights were integrated automatically using a Waters 745 data module and compared with known standards.

4.2.5 Data Analysis.

Data for all variates were analysed using the procedures described in Chapter three.

Plate 4-1. Growth of Epipremnum (upper photo) and Fatshedera (lower photo) in day/night temperature treatments at SN30/20 C after 39 days. Treatments, (left to right) constant night, split-night and sliding night. High and low PFD treatments are in the background and foreground, respectively.

Plate 4-2. Growth of Epipremnum (upper photo) and Fatshedera (lower photo) in day/night temperature treatments at SN30/15 C after 42 days. Treatments, (left to right) constant night, split-night and sliding night. High and low PFD treatments are in the background and foreground, respectively.

4.3 Results

Data collected when each treatment was set-up, was not included in the analysis as it did not reflect the CE treatments, but rather the environment in the greenhouse prior to this study. Representative data for each factor are presented for each temperature regime with the same mean temperature, except for relative growth rate and leaf area expansion rate where the data for each treatment are presented. Photos were taken near the final harvest date (Plates 4-1, 4-2). All references to 20 C and 15 C in this chapter should be interpreted as the mean night temperature in SN30/20 C and SN30/15 C, respectively.

4.3.1 Relative growth rate

Relative growth rate was significantly ($P \leq 0.0001$) influenced by night temperature, PFD and species. There was no significant effect ($P = 0.05$) of temperature profile on RGR.

Plots of $\log_e$ total plant dry weight versus time indicate that the relative growth rate (RGR) was linear for both species over the treatment period in all treatments (Fig. 4-3). At high PFD the slopes of the lines were higher than at low PFD for Fatshedera but this was not evident in Epipremnum.

The slope of the fitted lines (and hence the RGR) for Epipremnum show a marked difference between growth at the high and at the low mean night temperature. In Epipremnum RGR was significantly higher in temperature regimes of SN30/20 C (0.032 $g \cdot g^{-1} \cdot day^{-1}$) compared with 0.012 $g \cdot g^{-1} \cdot day^{-1}$ at SN30/15 C, irrespective of the PFD (Figs. 4-3, 4-7), whereas in Fatshedera there was much less difference in the rate of growth between the high and low mean night temperatures (Figs. 4-4, 4-8). Fatshedera plants differed from Epipremnum

in their response to temperature; there was no net effect of night temperature on RGR. The mean RGR at each temperature was 0.0394 $g \cdot g^{-1} \cdot day^{-1}$ (Fig. 4-8). A consistently higher RGR of approximately 50% occurred at the higher PFD (0.0331 and 0.0458 $g \cdot g^{-1} \cdot day^{-1}$, mean values for low and high PFD, respectively) in all treatments except in profile (d) where no differences due to PFD were present.

These results are consistent with the characterisation of Epipremnum and Fatshedera (refer to Chapter three) as plants adapted to warm and cool temperatures, respectively.

The significant interaction ($P \leq 0.05$) between PFD and species was evident as a difference in the relative change in RGR of Epipremnum and Fatshedera at each PFD. The increase in RGR with higher PFD was greater in Fatshedera than Epipremnum averaged over all temperature regimes.

4.3.2 Relative leaf area expansion rate

The linear trend in $\log_e$ total leaf area over time indicated, as with RGR, that during the time course the leaf area expansion rate (LER) was linear in both species grown at night temperatures of either 20 or 15 C (Fig. 4-4).

There was no significant influence (at $P = 0.05$) of temperature profile or PFD on LER in either species (Figs. 4-7, 4-8). This indicated that LER was practically independent of the temperature profiles (Figs. 4-7, 4-8) in both species. In contrast, there were significant differences ($P \leq 0.0001$) in the response of each species to the mean temperature. At 15 C Fatshedera maintained a similar LER as at 20 C, but in Epipremnum LER was reduced to almost zero in the low night temperature treatments. In Epipremnum at 20 C and 15 C the mean LER over all profiles was 0.044 and 0.0094 $cm^2 \cdot cm^{-2} \cdot day^{-1}$, respectively (Fig. 4-7). Fatshedera LER was not markedly influenced by growth temperature and ranged

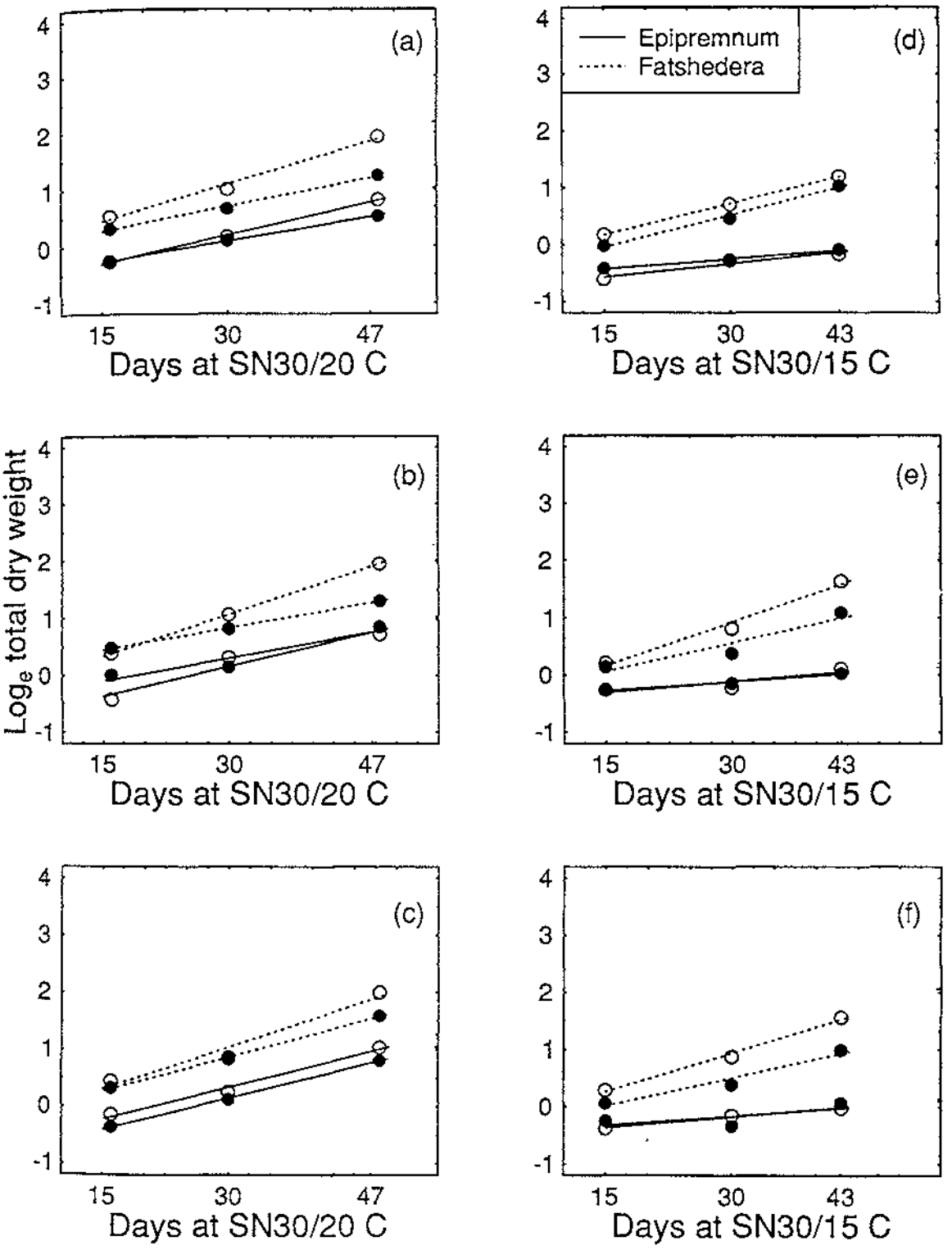


Fig. 4-3. Influence of night temperature profile (a-f) [refer to Figs. 4-1, 4-2] and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in log$_e$ of total dry weight in Epipremnum (solid line) and Fatshedera (dashed line). Each fitted line represents the functional relationship based on 36 plants and 3 harvests.

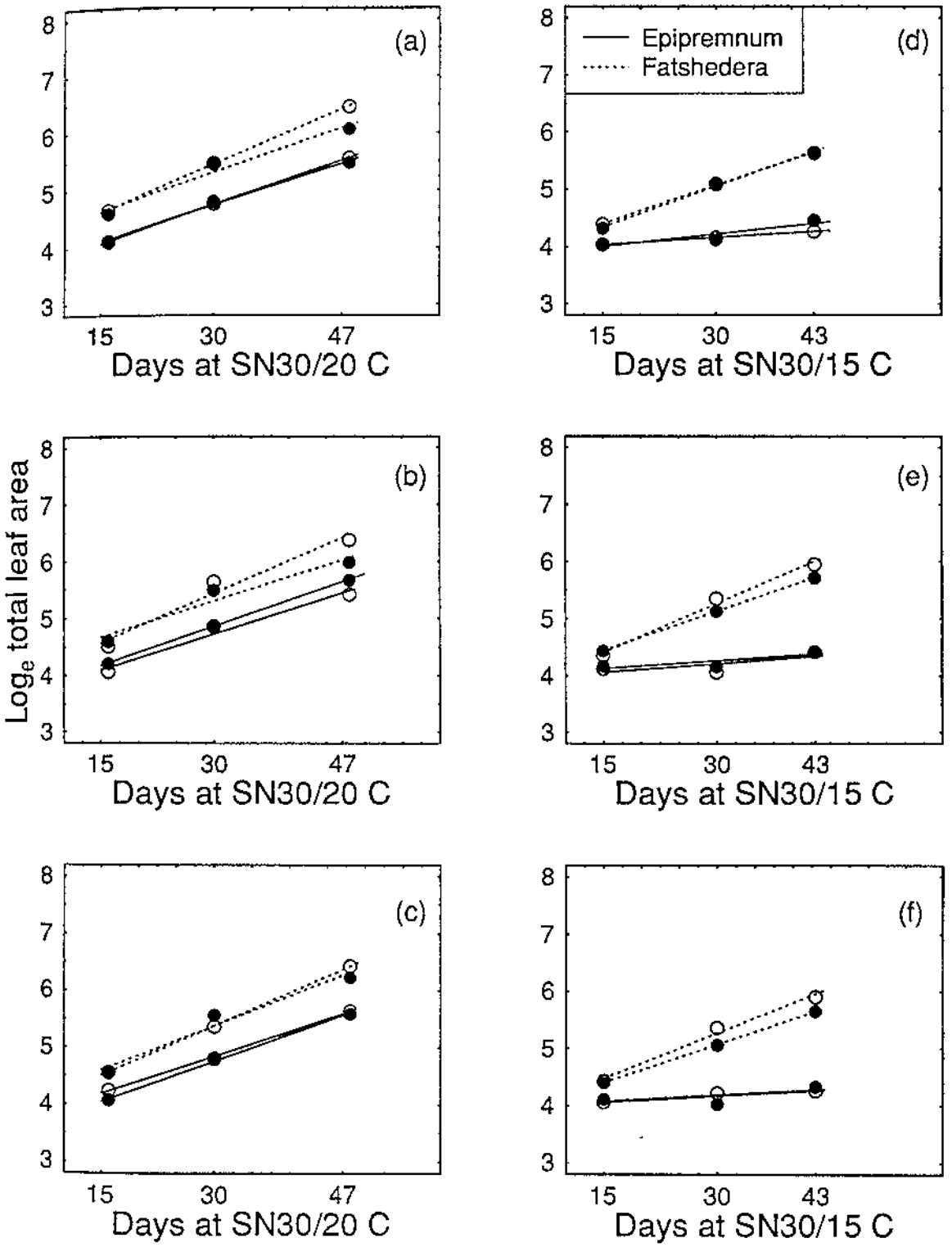


Fig. 4-4. Influence of split-night temperature profile (a-f) [refer to Figs. 4-1, 4-2] and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in log$_e$ of total leaf area in Epipremnum (solid line) and Fatshedera (dashed line). Each line represents the functional relationship based on 36 plants and 3 harvests.

between 0.04 and 0.06 $cm^2 \cdot cm^{-2} \cdot day^{-1}$ and in contrast to Epipremnum was generally higher at higher PFD (Fig. 4-8) Leaf expansion rate in Epipremnum, therefore, was more sensitive to low temperatures than Fatshedera. .

Leaf expansion rate was positively correlated with relative growth rate (RGR) with R^2 values between 0.811 and 0.935 ($P \leq 0.0001$) for both species and at each PFD. Coefficients of linear regression lines fitted to this data were not significantly different ($P \leq 0.01$) for each species and PFD suggesting a common underlying relationship between these variables applied in both species.

A significant interaction ($P \leq 0.05$) between PFD and species was evident as a difference in the relative change in LER of Epipremnum and Fatshedera at each PFD. Leaf expansion rate (like RGR) was more responsive to increased PFD in Fatshedera than in Epipremnum (Fig. 4-9).

4.3.3 Leaf area ratio

The PFD, average night temperature and species each produced significant ($P \leq 0.05$) effects on LAR, whereas the effects of the night temperature profiles were not significant at $P = 0.05$.

In night temperature profiles with a mean night temperature of 20 C, the increase in leaf area ratio (LAR) was almost linear over time at high PFD, while at low PFD the increase was slightly curvilinear (Fig. 4-5). In both species leaves tended to be thinner at low PFD as evident by higher LAR. At 15 C similar trends in LAR were evident in Fatshedera, while in Epipremnum LAR tended to decrease over time. After 30 days LAR of Epipremnum had decreased slightly from an initial value about 80 down to 75 $cm^2 \cdot g^{-1}$.

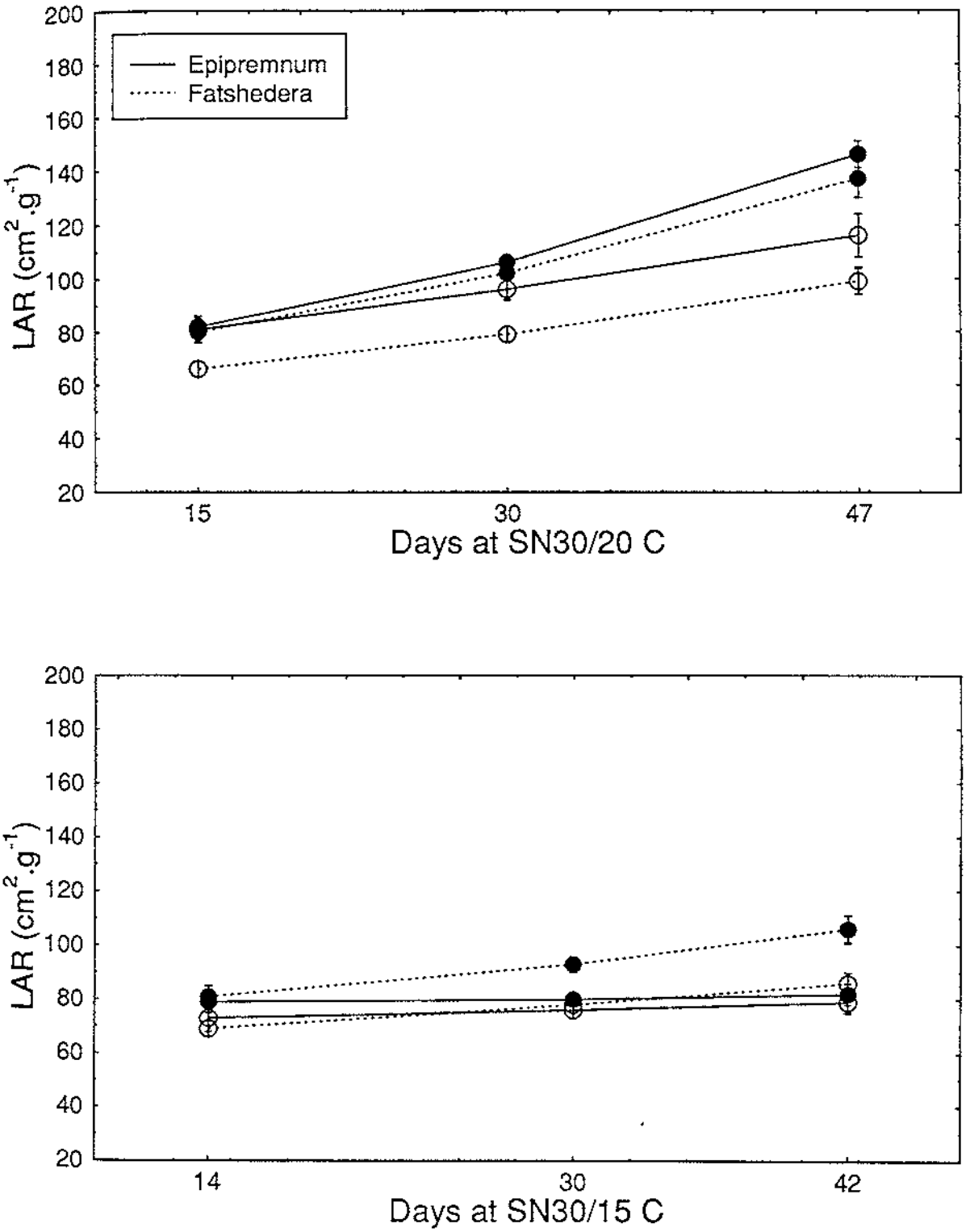


Fig. 4-5. Influence of night temperature (20 C and 15 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in leaf area ratio (cm^2.g^{-1}) in Epipremnum (solid line) and Fatshedera (dashed line). Each data point represents the mean of 12 plants. Vertical lines indicate standard error of the means.

In Epipremnum LAR was not markedly influenced by PFD, although there was a trend towards higher LAR at low PFD. Similarly, in Fatshedera leaves, LAR was significantly higher at the low PFD (94.6 $cm^2 \cdot g^{-1}$) compared with 77.7 $cm^2 \cdot g^{-1}$ at the high PFD. No effects of temperature treatment were found with LAR in Fatshedera, while LAR in Epipremnum was higher (98.0 $cm^2 \cdot g^{1}$) at 20 C than at 15 C (81.6 $cm^2 \cdot g^{-1}$).

The leaf area ratios at the second harvest (day 30) were not highly correlated (R^2 = 0.064 to 0.320 ($P \leq 0.03$)) with RGR for either species at each PFD. These factors were not coupled directly together as LAR only increased marginally with increasing RGR. Coefficients of regression lines fitted to data for each species and PFD were not significantly different ($P \leq 0.01$) suggesting a similar underlying relationship.

A highly significant interaction ($P \leq 0.001$) between PFD and species was evident as a difference in the relative change in LAR of Epipremnum and Fatshedera at each PFD (Fig. 4-9). Leaf area ratio was higher in both species at low PFD, whereas at high PFD LAR decreased more in Fatshedera than in Epipremnum (Figs. 4-7, 4-8).

4.3.4 Leaf area partitioning

No significant influence ($P = 0.05$) of temperature profile on LAP was found in this study. However, LAP was influenced significantly ($P \leq 0.01$) by the mean night temperature and PFD. Species and PFD X species interaction effects were not significant.

Leaf area partitioning in Epipremnum was markedly lower at a night temperature of 15 C (82.8 $cm^2 \cdot g^{-1}$) compared with 20 C (140.3 $cm^2 \cdot g^{-1}$). Leaf area partitioning was higher (137.7) at low than at high PFD (85.4 $cm^2 \cdot g^{-1}$).

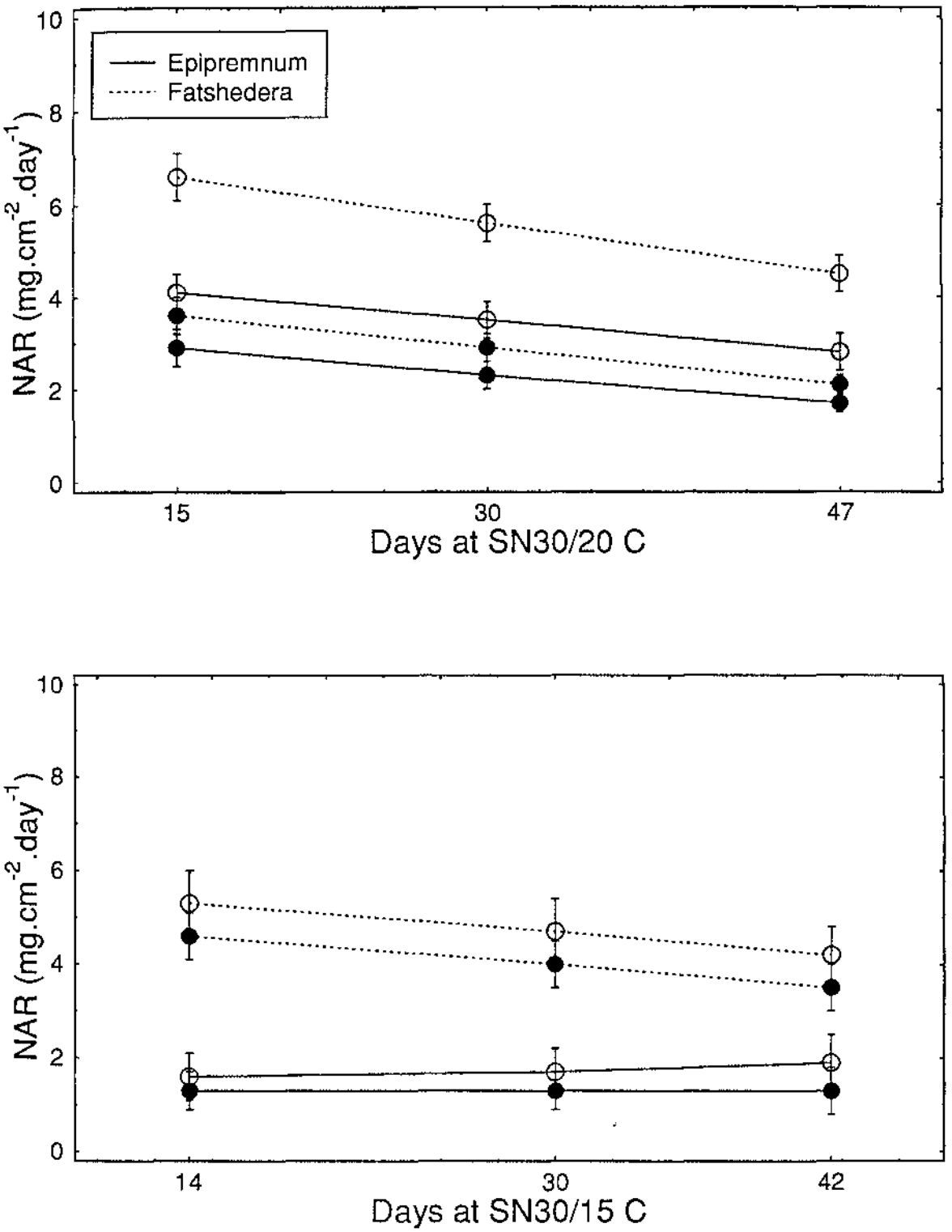


Fig. 4-6. Influence of night temperature (20 C and 15 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in net assimilation rate (mg.cm^{-2}.day^{-1}) in Epipremnum (solid line) and Fatshedera (dashed line). Each data point represents the mean of 12 plants. Vertical lines indicate standard error of the means.

Leaf area partitioning tended to be slightly lower in Fatshedera with a night temperature of 15 C (108.8 $cm^2 \cdot g^{-1}$) compared with 20 C (118.6 $cm^2 \cdot g^{-1}$). As noted in Epipremnum at the higher PFD, LAP decreased from 134.5 to 93.0 $cm^2 \cdot g^{-1}$.

The relationship between LAP and RGR was evaluated from data collected after 30 days and was not significantly correlated (at P = 0.05) suggesting that only a very weak relationship existed between the factors in both species irrespective of the PFD.

4.3.5 Net assimilation rate

There was no significant influence (P = 0.05) of night temperature profile on NAR. Average night temperature had a significant influence on NAR (Figs. 4-7, 4-8) which is consistent with the underlying temperature response of each species.

At 20 C dry matter assimilation measured as the NAR, typically decreased in a approximately linear manner over time during the treatment period in both species (Fig. 4-6). It was markedly higher at the higher PFD for both Epipremnum and Fatshedera. Net assimilation rate was always significantly higher ($P \leq 0.0001$) in Fatshedera NAR than in Epipremnum (Fig.4-6).

At 15 C NAR in Fatshedera decreased over time as at 20 C, while NAR in Epipremnum remained constant. Net assimilation rate in Epipremnum was higher at 20 C (0.27 $mg \cdot cm^{-2} \cdot day^{-1}$ than at 15 C (0.21 $mg \cdot cm^{-2} \cdot day^{-1}$) and higher under higher PFD in all temperature profiles.

Net assimilation rate in Fatshedera was higher in high PFD (0.59 $mg \cdot cm^{-2} \cdot day^{-1}$) compared with low PFD (0.35 $mg \cdot cm^{-2} \cdot day^{-1}$). The mean NAR over all

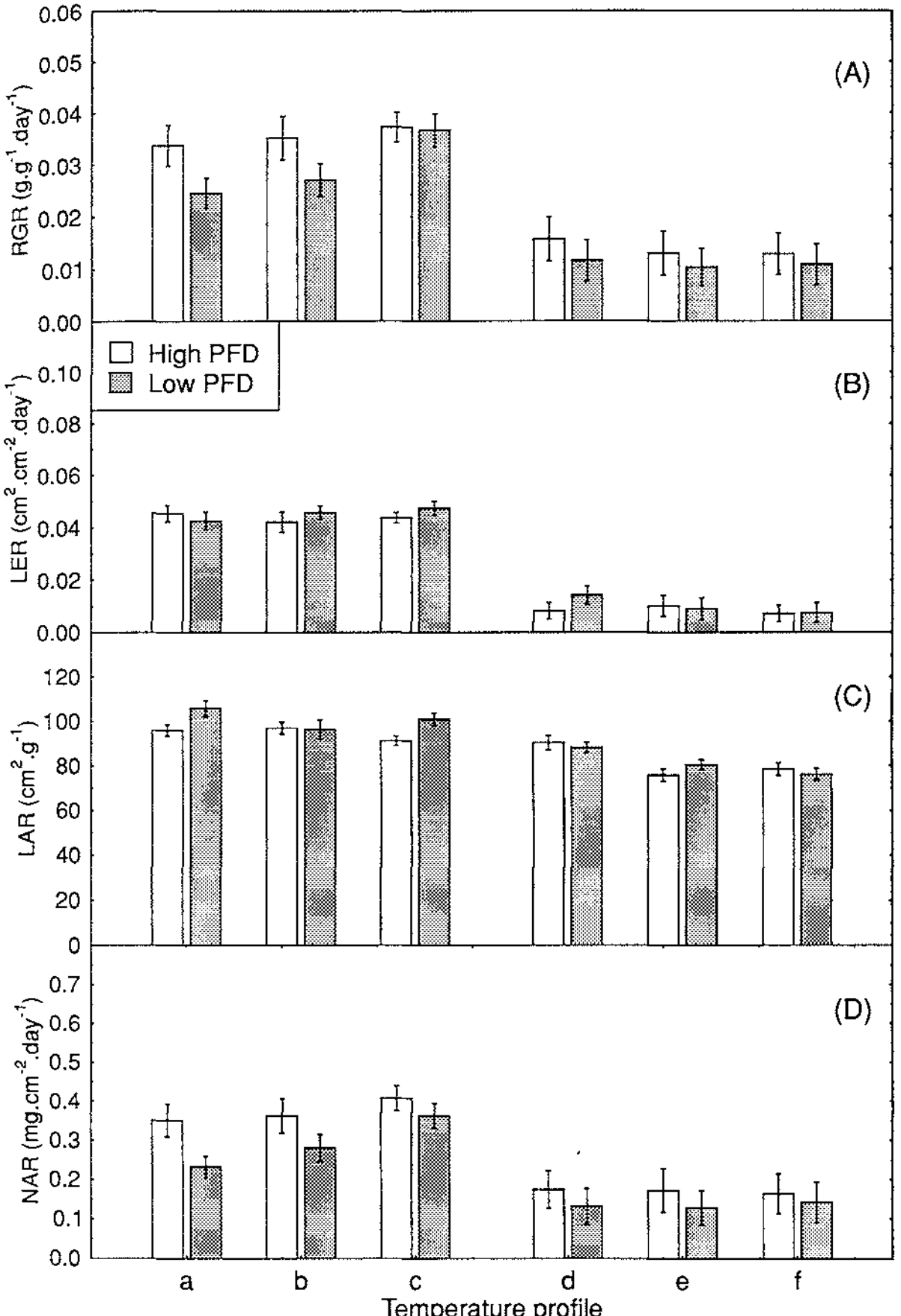


Fig. 4-7. Effect of PFD (High = 320 μmol.m^{-2}.s^{-1}, Low = 150 μmol.m^{-2}.s^{-1}) and temperature profile ([a,b,c,d,e & f] see Figs. 4-1, 4-2) on the relative growth rate of (A) dry weight and (B) leaf area expansion, (C) leaf area ratio and (D) net assimilation rate of Epipremnum leaves at day 30. Each bar represents the mean for 12 plants. Vertical lines represent the standard

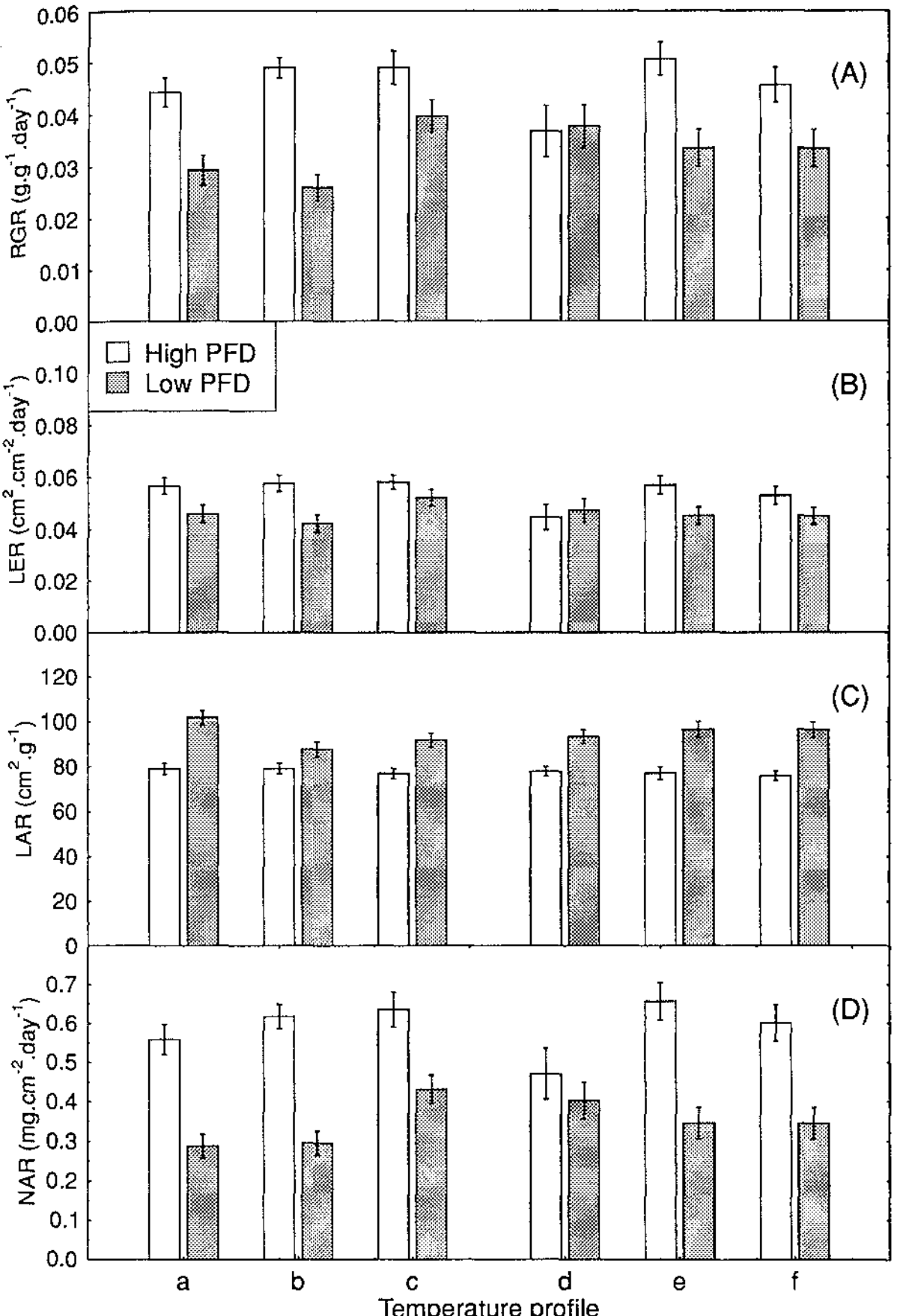


Fig. 4-8. Effect of PFD (High = 320 μmol.m^{-2}.s^{-1}, Low = 150 μmol.m^{-2}.s^{-1}) and temperature profile ([a,b,c,d,e & f] see Figs. 4-1, 4-2) on the relative growth rate of (A) dry weight and (B) leaf area expansion, (C) leaf area ratio and (D) net assimilation rate of Fatshedera leaves at day 30. Each bar represents the mean for 12 plants. Vertical lines represent the standard

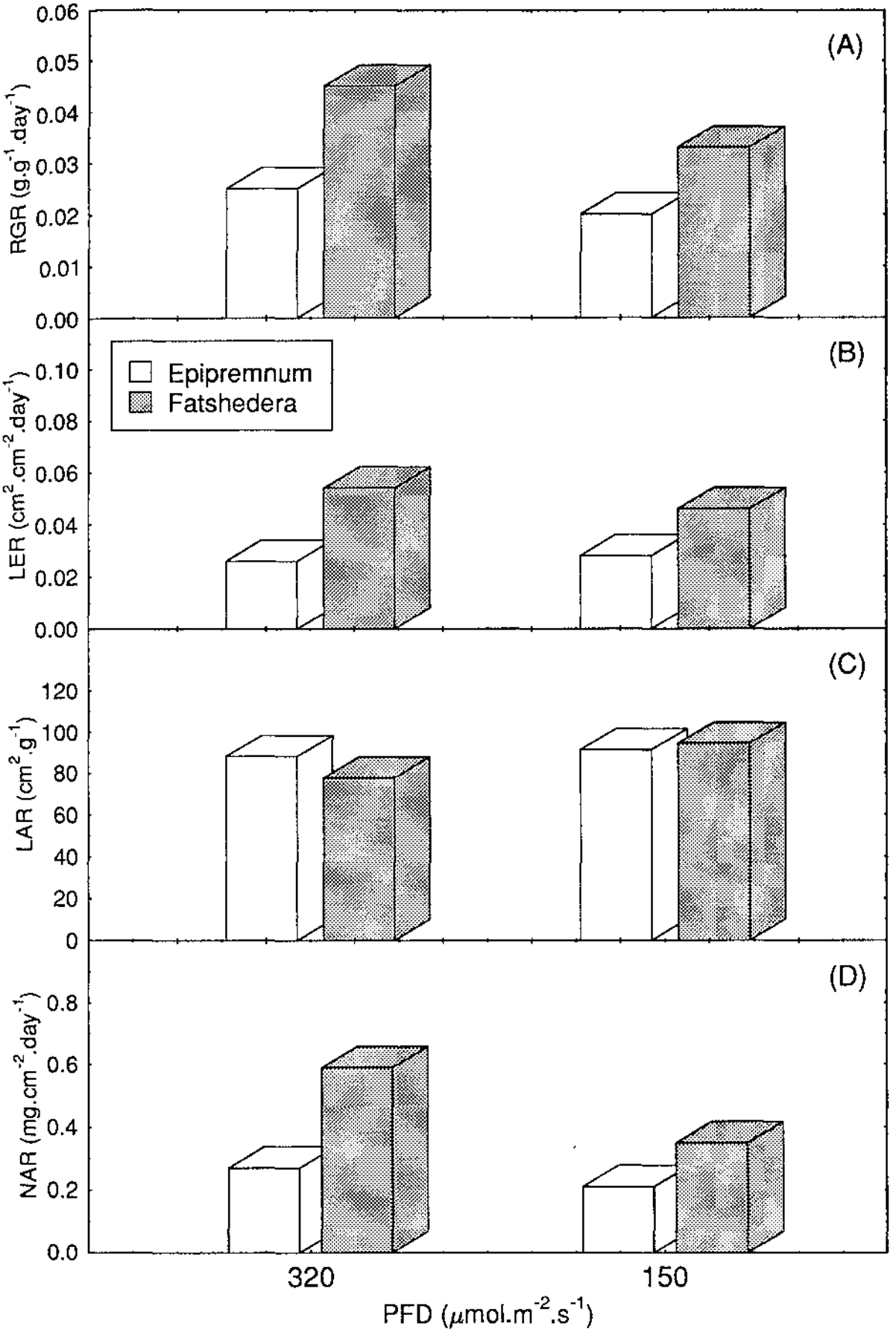


Fig. 4-9. Interaction of species (Epipremnum and Fatshedera) and PFD on (A) relative growth rate of dry weight (RGR) and (B) leaf area expansion (LER), (C) leaf area ratio (LAR) and (D) net assimilation rate (NAR) at day 30. Each bar represents the species x light interaction mean for each factor. Standard error of the means were <2% of the maximum value of each factor.

temperature profiles in Fatshedera was identical in both the high and low temperature treatments.

The interaction between PFD and species was highly significant ($P \leq 0.0001$). In Fatshedera NAR increased with increasing PFD, whereas in Epipremnum NAR increased but at a considerably reduced rate (Fig. 4-9).

Net assimilation rate at the second harvest (at day 30) was also positively correlated (R^2 values ranged between 0.849 to 0.991 ($P \leq 0.0001$)) with RGR in both species and at both PFDs. Coefficients of regression lines fitted to these data for each species and PFD were not significantly different at ($P \leq 0.01$).

4.3.6 Efficiency of dry matter production

No significant influence of temperature profile ($P = 0.05$) was found, but there were highly significant effects of both temperature and PFD on the utilisation of incident light for dry matter production. When dry weight accumulation is expressed on the basis of the total light integral during the experiment it was clear that significantly more dry weight was produced in both species per unit of incident PAR at low PFD, than at high PFD.

In Epipremnum at 20 C and under low PFD between 6.6 and 6.8 $mg[dw] \cdot mol[photon]^{-1} \cdot m^{-2}$ were produced, whereas at high PFD between 3.0 and 3.3 $mg[dw] \cdot mol[photon]^{-1} \cdot m^{-2}$ were produced (Fig. 4-10). At 15 C and under low PFD the productive efficiency was lower than at 20 C where rates between 4.2 to 5.0 $mg[dw] \cdot mol[photon]^{-1} \cdot m^{-2}$ were found, while at high PFD values were between 2.0 and 2.1 $mg[dw] \cdot mol[photon]^{-1} \cdot m^{-2}$.

In contrast to Epipremnum, in Fatshedera the dry matter production per unit of light integral was less consistent across all temperature treatments (Fig. 4-10). At 20 C and under low PFD between 11.8 and 13.4 $mg[dw] \cdot mol[photon]^{-1} \cdot m^{-2}$

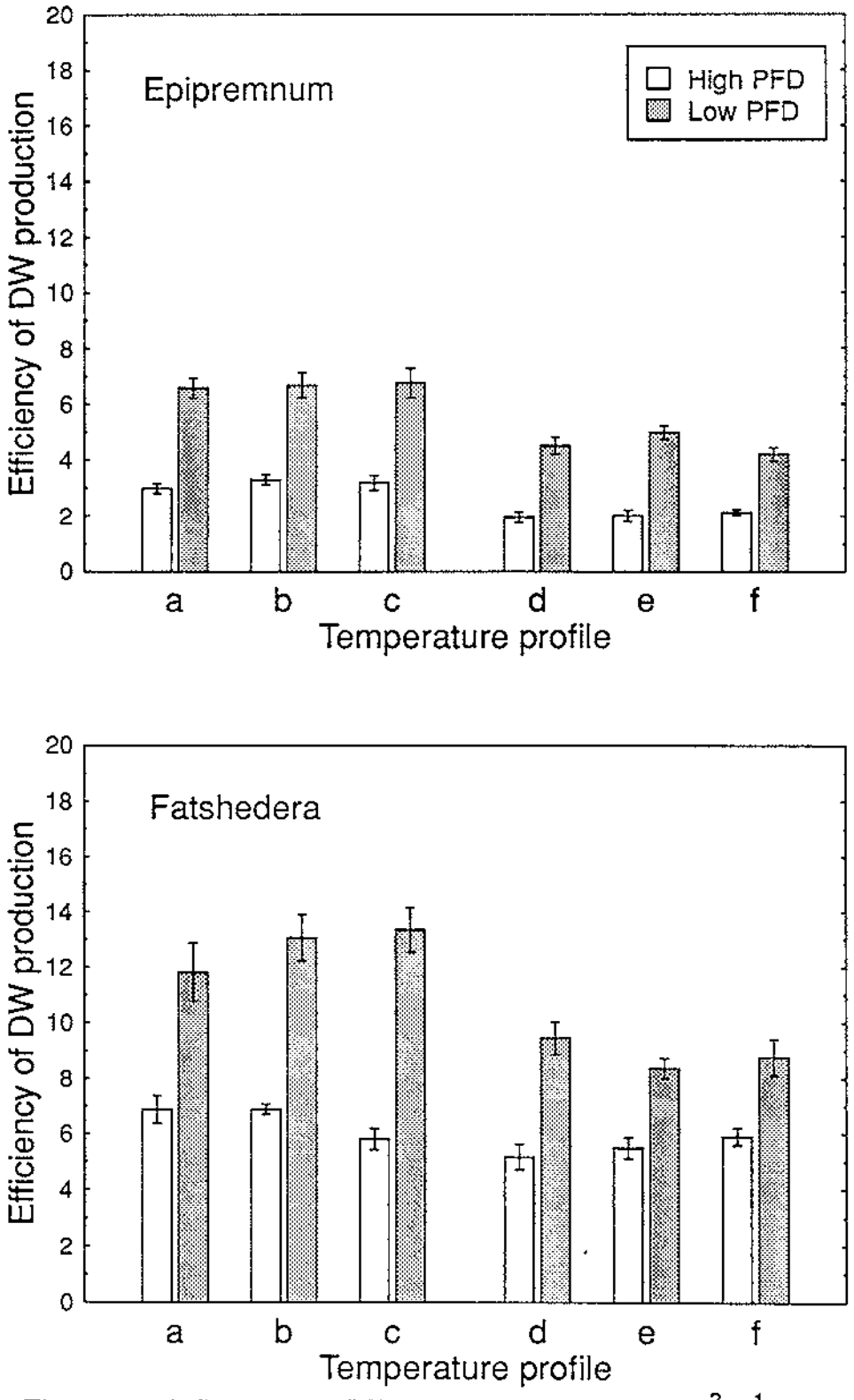


Fig. 4-10. Influence of PFD (High = 320 μmol.m^{-2}.s^{-1}, Low = 150 μmol.m^{-2}.s^{-1}) and temperature profile ([a,b,c,d,e & f] Figs. 4-1, 4-2) on relative efficiency of incident light on dry matter production (mg[dw].mol[photons]$^{-1}$.m^{-2}) at 30 days. Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

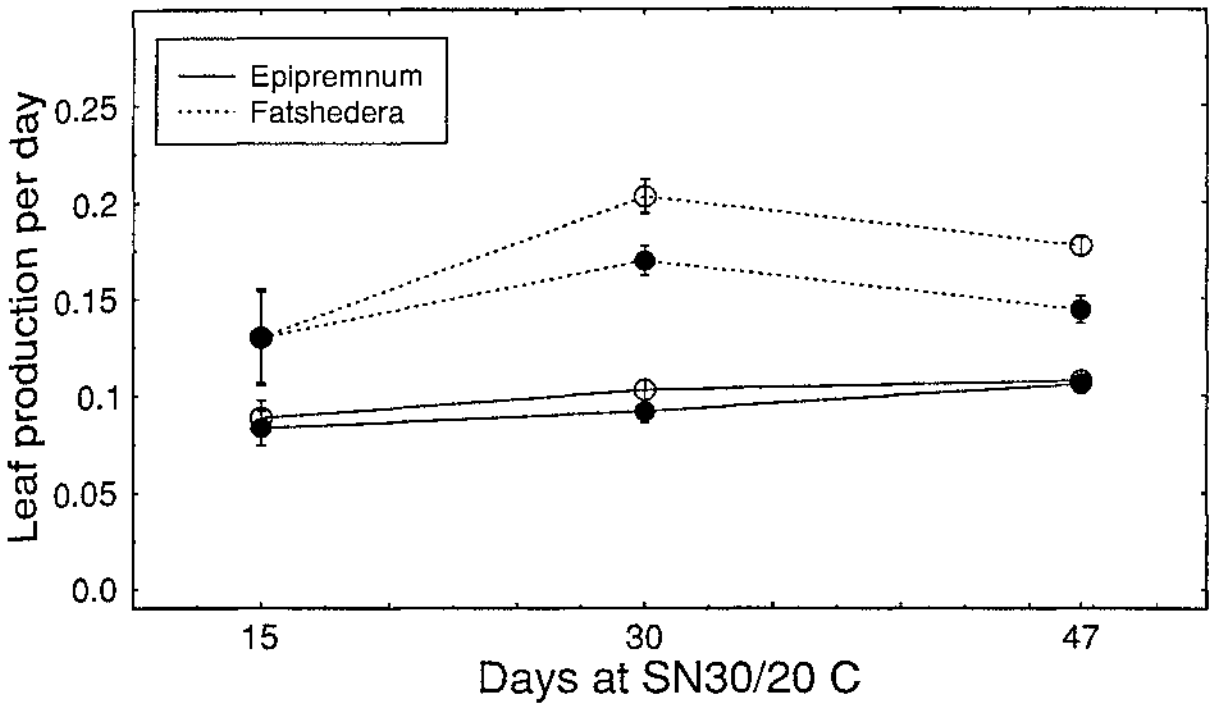
were produced and at high PFD productivity decreased to values between 5.8 and 6.7 mg[dw]·mol[photon]$^{-1}$·m^{-2}. Like Epipremnum, at 15 C the efficiency of light utilisation decreased compared with that at 20 C -at low PFD between 8.4 and 9.5 mg[dw]·mol[photon]$^{-1}$·m^{-2} were produced while at high PFD the relative efficiency was reduced to rates between 5.2 and 5.9 mg[dw]·mol[photon]$^{-1}$·m^{-2}.

4.3.7 Leaf production rate

There was no significant influence (at P ≈ 0.01) of temperature profile on leaf production rate (LFP). Typical LFP plots over time reveal that in Epipremnum at 20 C, LFP increased linearly to a maximum of 0.1 leaves·day^{-1}, whereas in Fatshedera LFP increased to 0.2 leaves·day^{-1} and then decreased (Fig. 4-11). At 15 C LFP decreased markedly in Fatshedera while there was a much smaller reduction in Epipremnum during the treatment period. The LFP was influenced significantly (P≤0.0001) by mean temperature, species and harvest. Overall, there was a trend towards higher LFP at higher PFD in Fatshedera but that trend was less evident in Epipremnum (Fig.4-11). Leaf production rate in Epipremnum after 30 days growth was similar in all night temperature treatments at 20 C, whereas the rate was approximately halved at the lower growth temperature (Fig. 4-12). In contrast, LFP of Fatshedera was almost double the rate of Epipremnum at 20 C, and almost four times that at 15 C indicating that LFP was much more temperature dependent in Epipremnum than in Fatshedera.

4.3.8 Mean leaf area per leaf

The mean leaf area per leaf (MLA) was not significantly influenced by the night temperature profile, species or PFD (P = 0.05). However, the MLA was significantly (P≤0.0001) influenced by the mean night temperature treatments, overall.



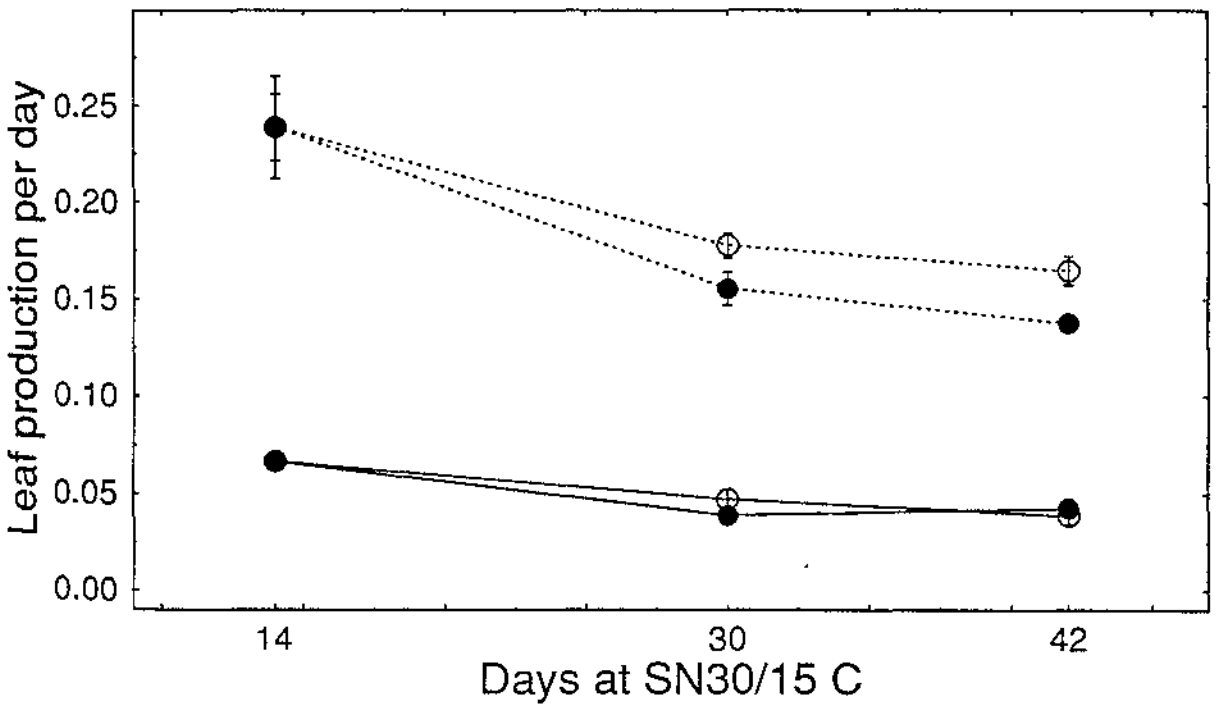


Fig. 4-11. Influence of night temperature (20 C and 15 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in mean rate of leaf production (leaves.day^{-1}) in Epipremnum (solid line) and Fatshedera (dashed line). Each data point represents the mean of 12 plants. Vertical lines indicate standard error of the means.

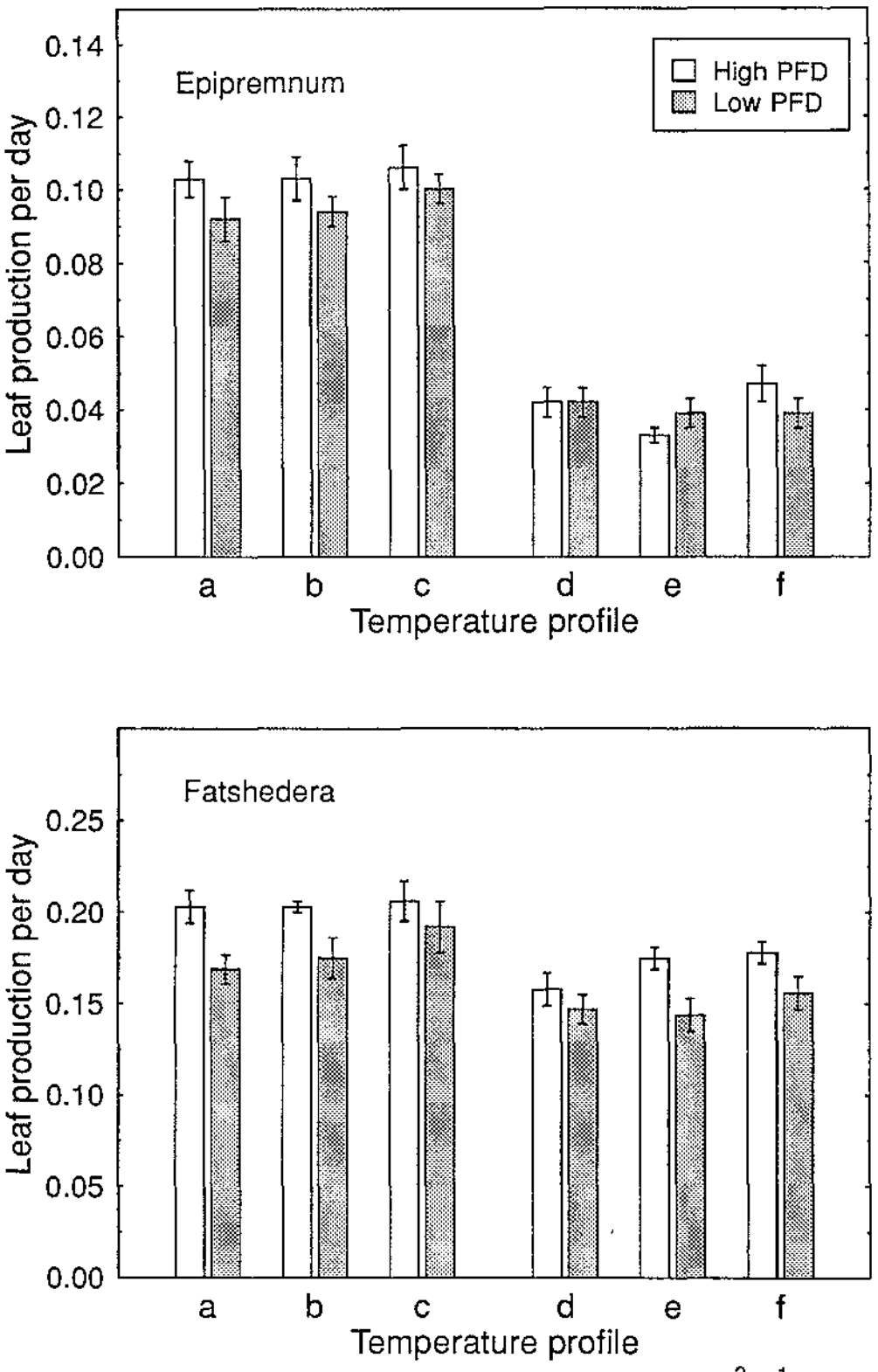


Fig. 4-12. Influence of PFD (High = 320 μmol.m^{-2}.s^{-1}, Low = 150 μmol.m^{-2}.s^{-1}) and temperature profile ([a,b,c,d,e & f] Figs.4-1, 4-2) on leaf production rate in (A) Epipremnum and (B) Fatshedera at day 30. Each bar represents the mean of 12 leaves. Vertical lines indicate the standard error of the mean. (Note difference in scales for each species)

At 20 C MLA of Epipremnum was relatively constant at approx. 45-50 cm and influenced by PFD. In contrast, in Fatshedera MLA tended to be slightly higher at high PFD. The initial MLA was approx. 65 cm^2 and tended to decrease after 30 days to about 45-50 cm^2 followed by a return to the initial MLA at the final harvest. This result caused a significant interaction between species and harvest ($P<0.0001$). At 15 C there were marked differences in the response of each species; in Epipremnum MLA decreased during the time course while in Fatshedera MLA increased. At the end of the experiment MLA in both species was approx. 50 cm^2.

4.3.9 Specific leaf area

The main effects of night temperature profile, mean temperature, PFD, species and harvest were all highly significant ($P\leq0.0001$) for SLA. Interspecific differences accounted for 45% of the total sum of squares due to treatment effects.

The SLA was significantly higher ($P\leq0.01$) in the constant night temperature (CNT) than in the SN or SNT temperature regimes. Specific leaf area was significantly higher ($P\leq0.0001$) at the higher night temperature. During a typical time course at SN 30/20 C in Epipremnum, SLA was always markedly higher than Fatshedera and increased from about 180 to 200 $cm^2 \cdot g^{-1}$ at high PFD and to 220 $cm^2 \cdot g^{-1}$ at low PFD (Fig. 4-13). Specific leaf area in Fatshedera plants increased from about 90 $cm^2 \cdot g^{-1}$ to a plateaux after 30 days of 120 and 150 $cm^2 \cdot g^{-1}$ at high and low PFD, respectively.

At SN30/15 C SLA in Epipremnum decreased slowly during the time course from 150 to 140 $cm^2 \cdot g^{-1}$, but there was no evidence for an influence of PFD (Fig. 4-13). In Fatshedera the pattern of change in SLA during the time course was similar to that at the higher temperature with values increasing to a maximum of

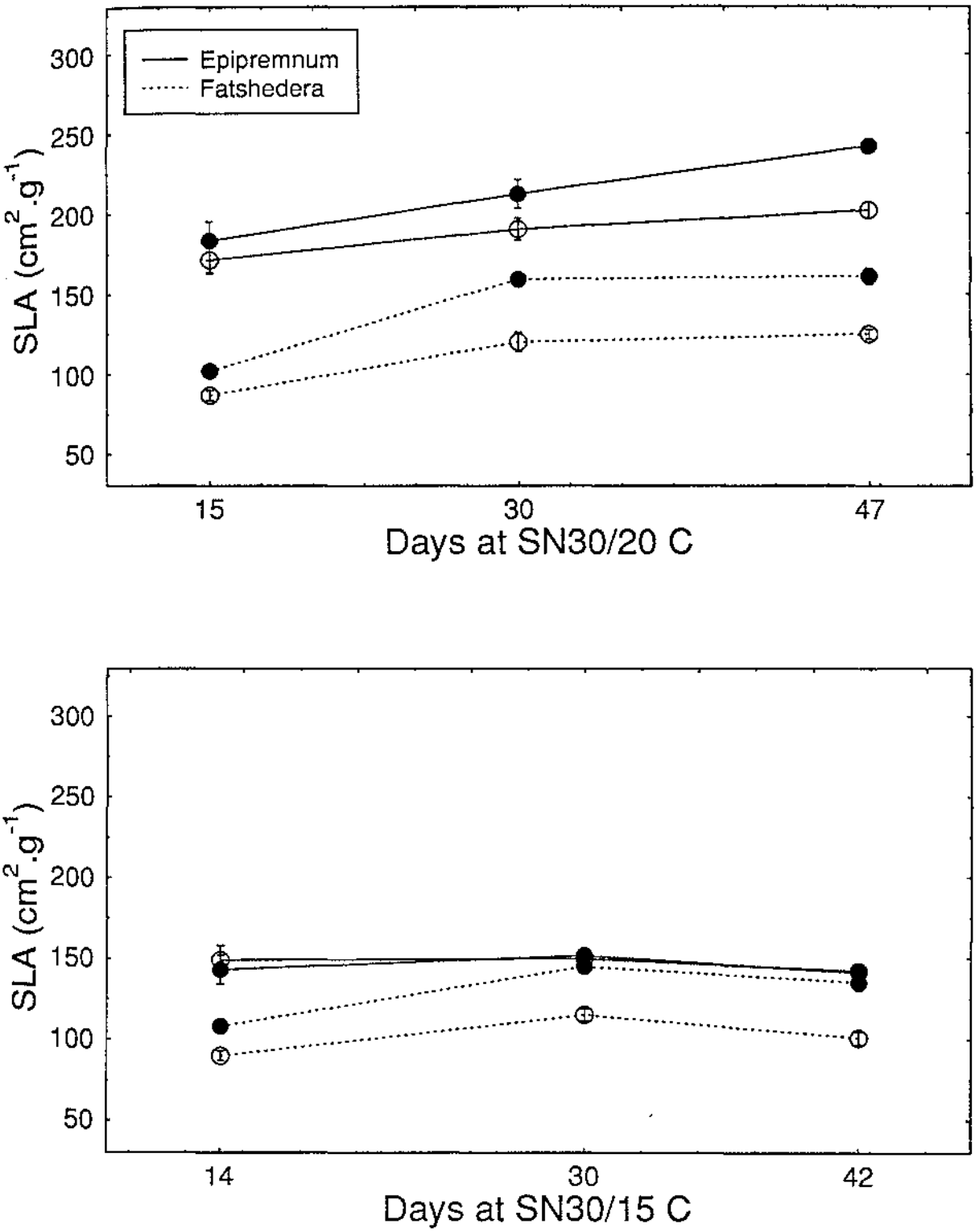


Fig. 4-13. Influence of night temperature (20 C and 15 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in specific leaf area (cm^2.g^{-1}) in Epipremnum (solid line) and Fatshedera (dashed line). Each data point represents the mean of 12 plants. Vertical lines indicate standard error of the means.

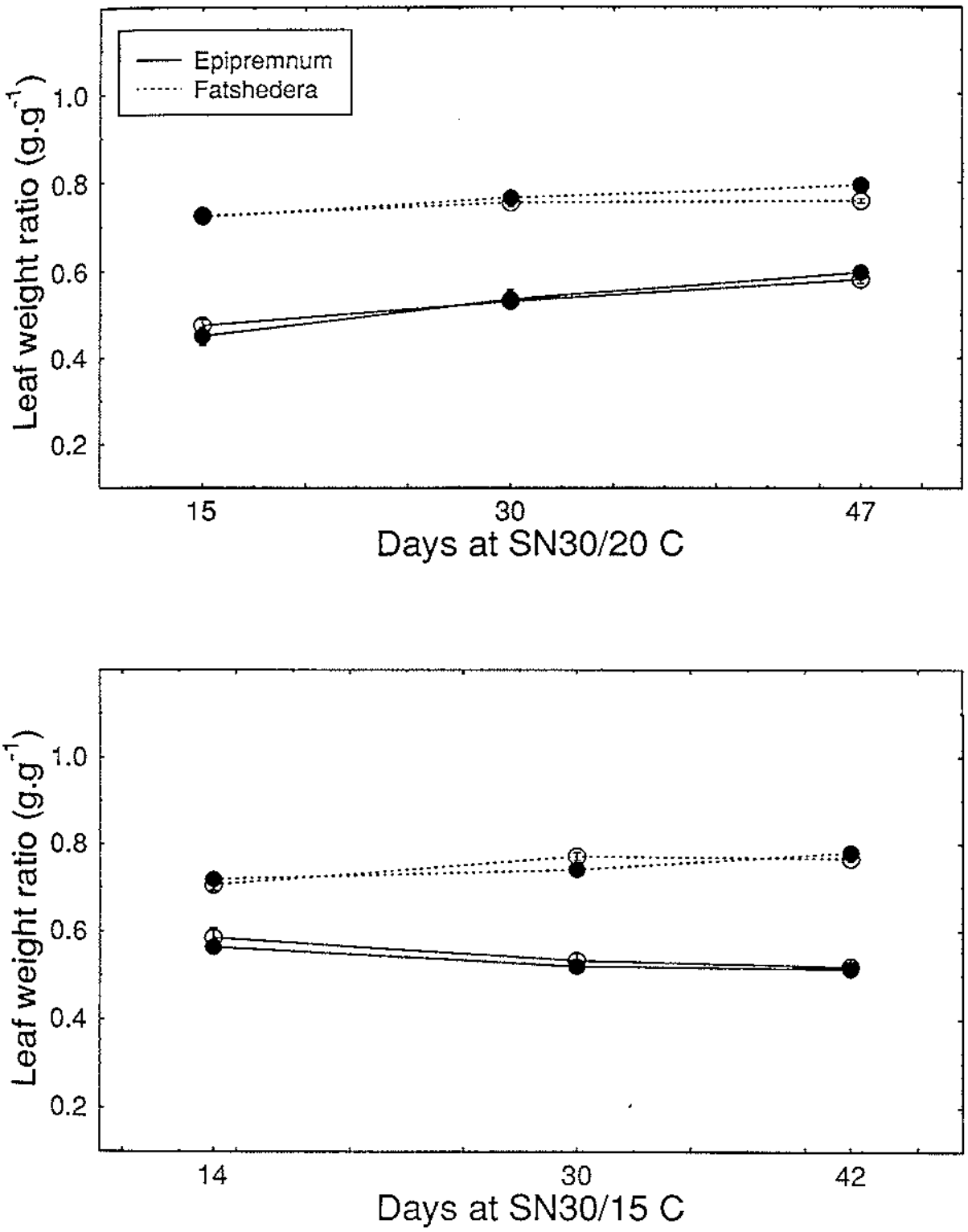


Fig. 4-14. Influence of night temperature (20 C and 15 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in leaf weight ratio in Epipremnum (solid line) and Fatshedera (dashed line). Each data point represents the mean of 12 plants. Vertical lines indicate standard error of the means.

100 and 140 $cm^2 \cdot g^{-1}$ at high and low PFD, respectively after 30 days, and then decreasing marginally by the final harvest.

4.3.10 Leaf weight ratio

There was no significant influence (P = 0.05) of temperature profile or mean night temperature on LWR in either species. In Epipremnum (at night temperature of 20 C) LWR increased from approx. 0.45 to 0.6 between the first and last harvest. Over the same period, the LWR for Fatshedera increased from approx. 0.7 to 0.8 (Fig. 4-14). At 15 C LWR of Epipremnum decreased slightly over time from 0.6 to 0.5 and in Fatshedera LWR increased slightly from approx. 0.7 to 0.8 (Fig. 4-19). The differences in variance between species and harvests were each highly significant (P<0.0001) while differences between temperature and PFD treatments were each not significant. These results indicate that during these experiments the proportion of total plant dry matter of Fatshedera leaves increased slightly at each growth temperature. A similar trend occurred in Epipremnum at 20 C, whereas at 15 C the proportion of dry matter as leaves in Epipremnum decreased slowly over time.

4.3.11 Total shoot length

Shoot length (SHL) was influenced by all treatment effects and their interactions. The most important highly significant effects were temperature and harvest (P≤0.0001) collectively accounting for more than 59% of the total variance. At 20 C SHL in both species increased concomitantly, and was higher at the higher PFD. During the time course SHL increased curvilinearly from 50 mm to at least 200 mm in both Epipremnum and Fatshedera (Fig. 4-15).

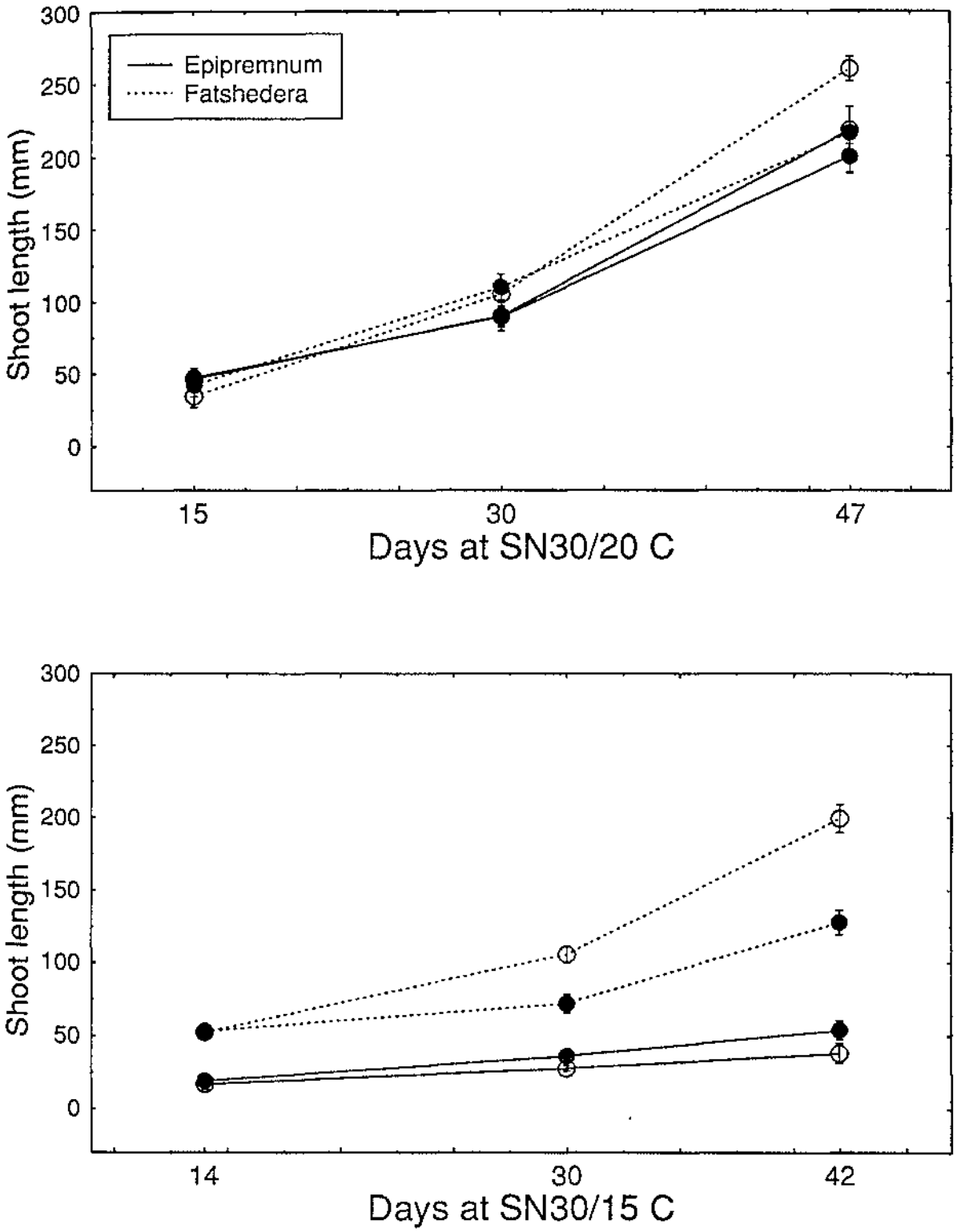


Fig. 4-15. Influence of night temperature (20 C and 15 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in shoot length (mm) in Epipremnum (solid line) and Fatshedera (dashed line). Each data point represents the mean of 12 plants. Vertical lines indicate standard error of the means.

At 15 C Fatshedera SHL increased as at 20 C, but at a slower rate particularly at the lower PFD, and when the treatments were terminated SHL in the high and low PFD treatments were approx. 200 and 125 mm, respectively. Epipremnum shoot extension growth was nearly linear at 15 C and proceeded very slowly compared with Fatshedera (Fig. 4-15). In contrast to Fatshedera, SHL in Epipremnum in the lower night temperature treatments were higher at low PFD.

4.3.12 Average shoot growth

The average shoot growth (SHG) was significantly ($P \leq 0.01$) influenced by night temperature profile, mean temperature treatment, species and harvest (compare plates 4-1 and 4-2).

Average shoot growth at the mean temperature of 20 C was 118.0 mm, whereas at the lower mean of 15 C plant height only 60.1 mm. The SHG was significantly higher in the SNT than the CNT, while the SN was not significantly different ($P=0.01$) from the other night temperature profiles. Shoot growth rate increased in a nearly linear manner from 3 to 4 $mm \cdot day^{-1}$ during the experiment at 20 C in both species, except where Fatshedera was exposed to high PFD a more rapid increase in SGR up to 5.5 $mm \cdot day^{-1}$ occurred. At 15 C night temperature, SHG was essentially constant at 1.2 and 2.8 $mm \cdot day^{-1}$ in Epipremnum and Fatshedera, respectively.

4.3.13 Mean node length

Node length (NOL) was significantly ($P \leq 0.0001$) influenced by mean temperature, species and harvest effects. Whereas the night temperature profiles were without effect on NOL at 20 C the NOL of 27.6 mm (over all treatments and species) was markedly higher than that at the mean night temperature of 15 C (20.2 mm).

Node length in Epipremnum grown in 20 C night treatments increased from 30 to 37 mm during the time course, while in Fatshedera NOL increased from 20 to 25 mm.

At 15 C Fatshedera NOL increased from about 18 to 22 mm at low PFD and to 28 mm at high PFD, whereas node length in Epipremnum was more variable and showed no consistent pattern during the time course. The reduction in node length of Epipremnum in 15 C nights when exposed to high PFD during the day corresponded with similar reductions in shoot growth rate and shoot length (Fig. 4-15).

4.3.14 Shoot/root ratio

Shoot/root ratio (SHR) was significantly influenced ($P \leq 0.05$) by the mean night temperature, species and harvest, whereas no significant effect of temperature profile was found. Furthermore, the interactions between harvest and PFD or species were highly significant and accounted for >31% of the treatment variance.

Allometric relationships were evaluated by regressing $\log_e$ shoot dry weight against $\log_e$ root dry weight. Highly significant ($P \leq 0.0001$) regressions were obtained for each species and each night temperature treatment. The slopes of each regression line for each species were significantly different ($P \leq 0.01$) from one another. A significant difference ($P \leq 0.01$) in the allometric ratios for Epipremnum occurred at each temperature, whereas no differences were found in Fatshedera.

In the temperature profiles at 20 C SHR did not vary during the time course. At low PFD, SHR was higher in both species, the larger difference occurring in Fatshedera (Fig. 4-16). The mean SHR at 20 C for Epipremnum and Fatshedera was 5.4 and 15.5, respectively.

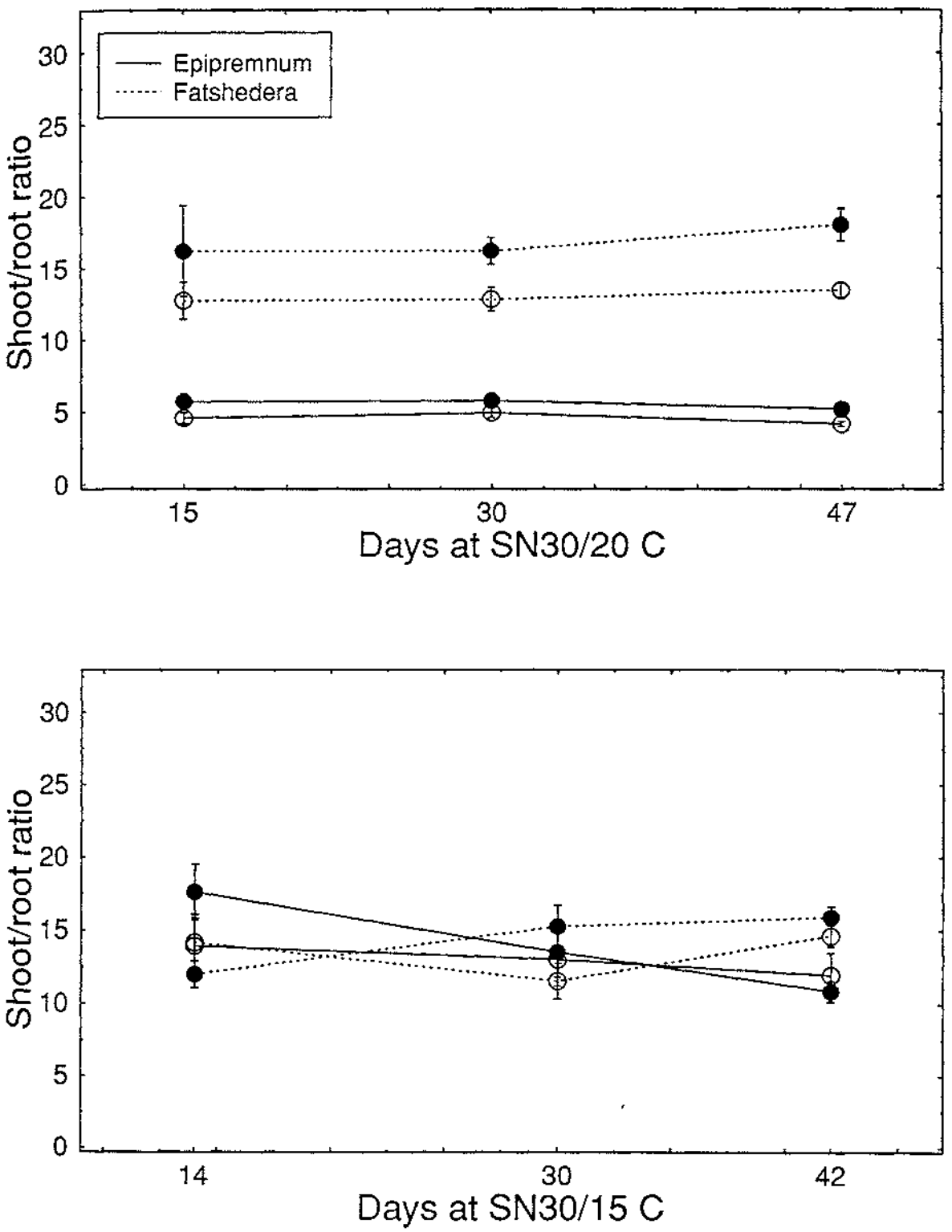


Fig. 4-16. Influence of night temperature (20 C and 15 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in shoot/root ratio in Epipremnum (solid line) and Fatshedera (dashed line). Each data point represents the mean of 12 plants. Vertical lines indicate standard error of the means.

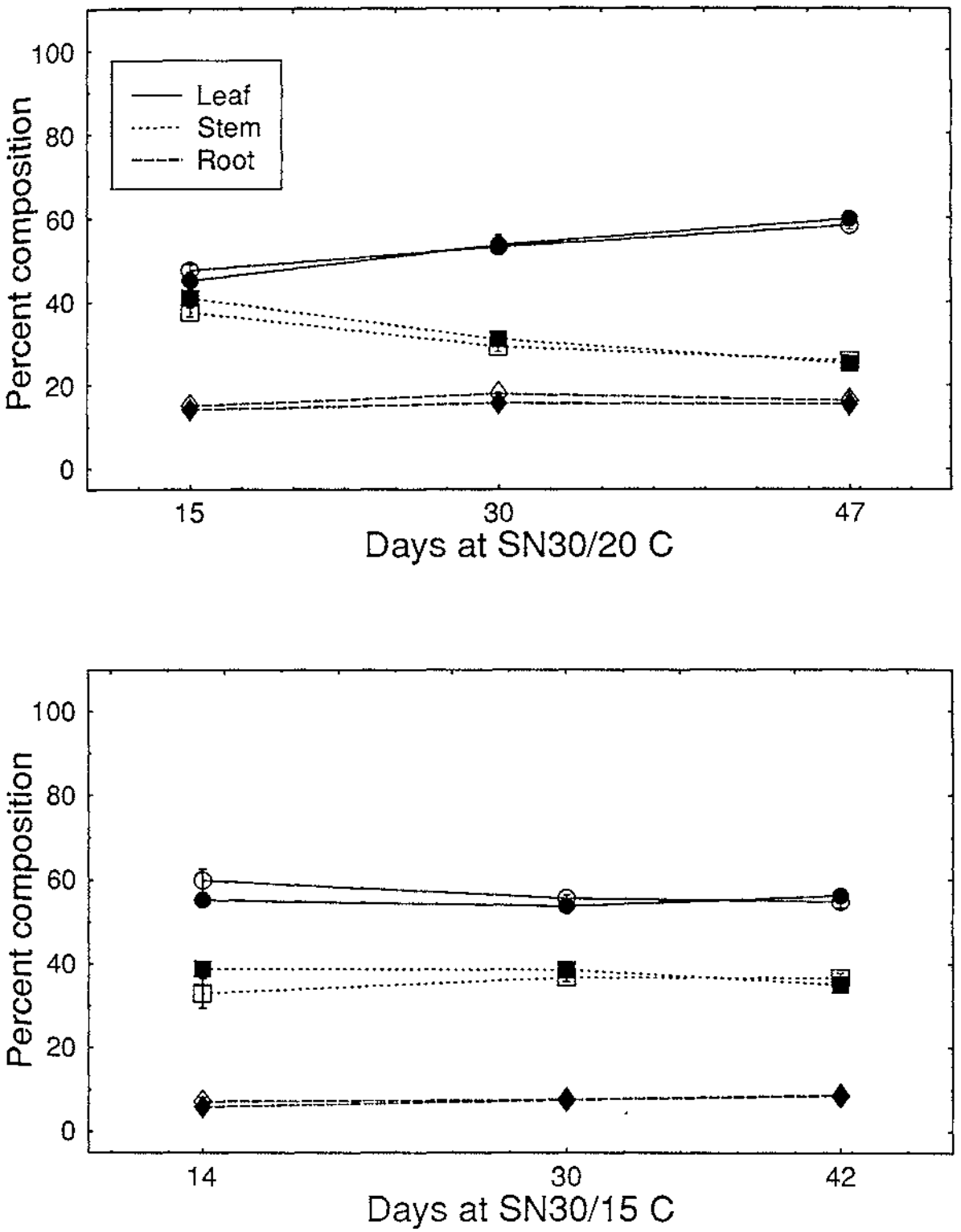


Fig. 4-17. Influence of night temperature (20 C and 15 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in partitioning between leaf, stem and roots in Epipremnum. Each data point represents the mean of 12 plants. Vertical lines indicate standard error of the means.

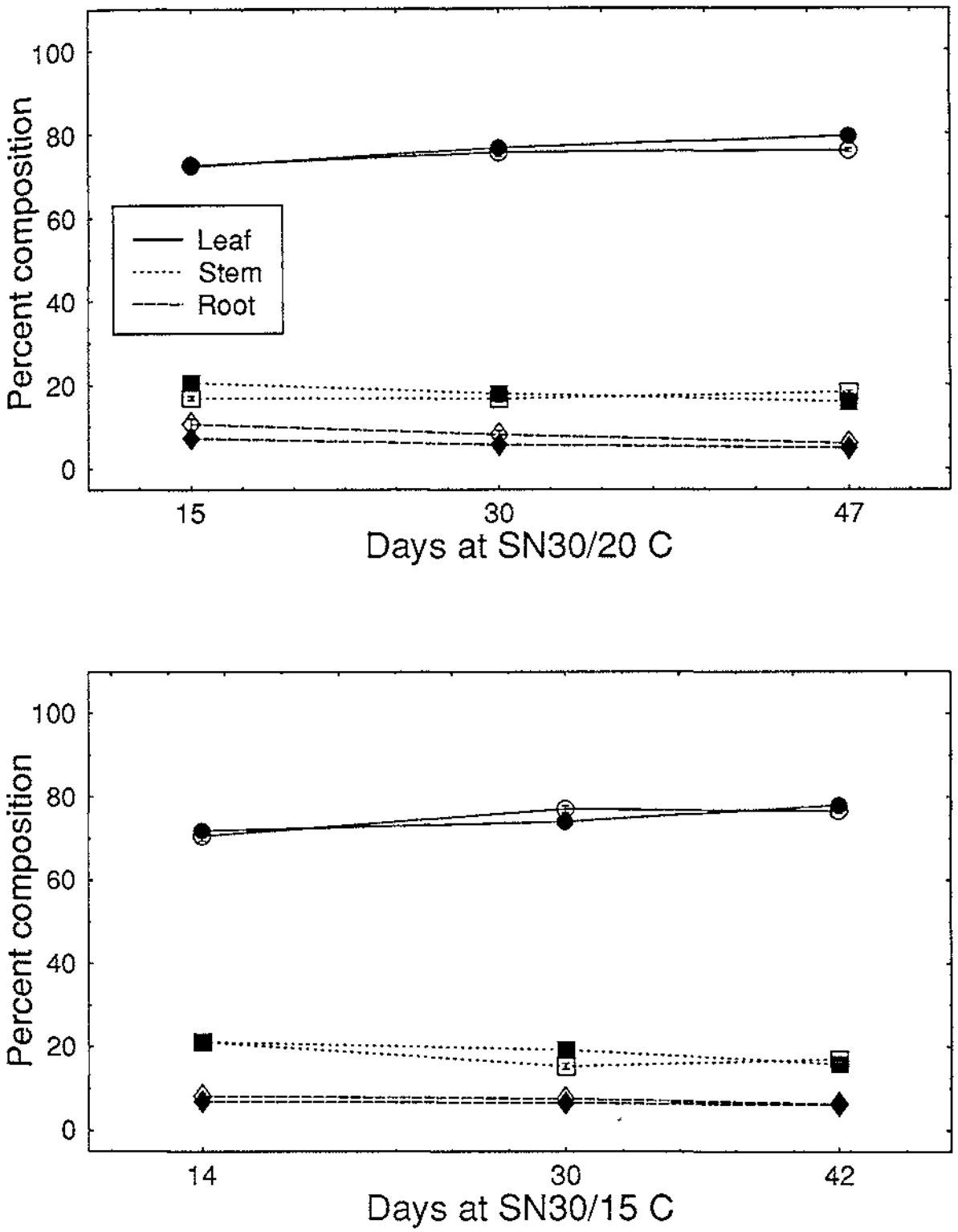


Fig. 4-18. Influence of night temperature (20 C and 15 C) and PFD (open symbols = 320 μmol.m^{-2}.s^{-1}, closed symbols = 150 μmol.m^{-2}.s^{-1}) on time course of change in partitioning between leaf, stem and roots in Fatshedera plants. Each data point represents the mean of 12 plants. Vertical lines indicate standard error of the means.

The mean SHR at 15 C for Epipremnum and Fatshedera was 17.8 and 14.3 respectively, indicating that a lower proportion of dry matter was allocated to roots of Epipremnum in temperature profiles at the lower mean temperature (Fig. 4-16). Interaction between harvest and PFD or species was evident in the 15 C temperature profiles where SHR in Epipremnum the decrease over time was PFD-dependent. In Fatshedera SHR increased slowly overall, but was also dependent on both PFD and harvest.

4.3.15 Partitioning to leaf, stem and roots

Significant differences ($P \geq 0.0001$) in dry matter partitioning occurred between Epipremnum and Fatshedera and partitioning was also influenced by the temperature treatment and harvest time, whereas PFD had no significant effect (Figs. 4-17, 4-18). A large proportion of the variance (between 74% in the leaves and 17% in the roots) was attributable to differences between the two species.

In Epipremnum the proportion of dry matter in the leaves and roots increased over time at 20 C while the proportion of stem dry matter decreased. At 15 C the proportions comprising leaf, stem and root remained almost constant (Fig. 4-17).

Dry matter in Fatshedera leaves increased in all temperature treatments over time. Over the treatment period the proportion of dry matter allocated to stem and roots decreased slightly, except at 15 C where the proportion of roots remained essentially constant (Fig. 4-18).

The influence of night temperature profiles on partitioning of dry matter is summarised in Figure 4-19. No consistent effect due to the night temperature profiles occurred in these experiments. The proportion of dry matter partitioned to leaves in Epipremnum varied between 50-56%. Similarly, the proportion of stem and roots relative to the leaves was approximately constant across all experiments. However, the mean night temperature influenced the partitioning

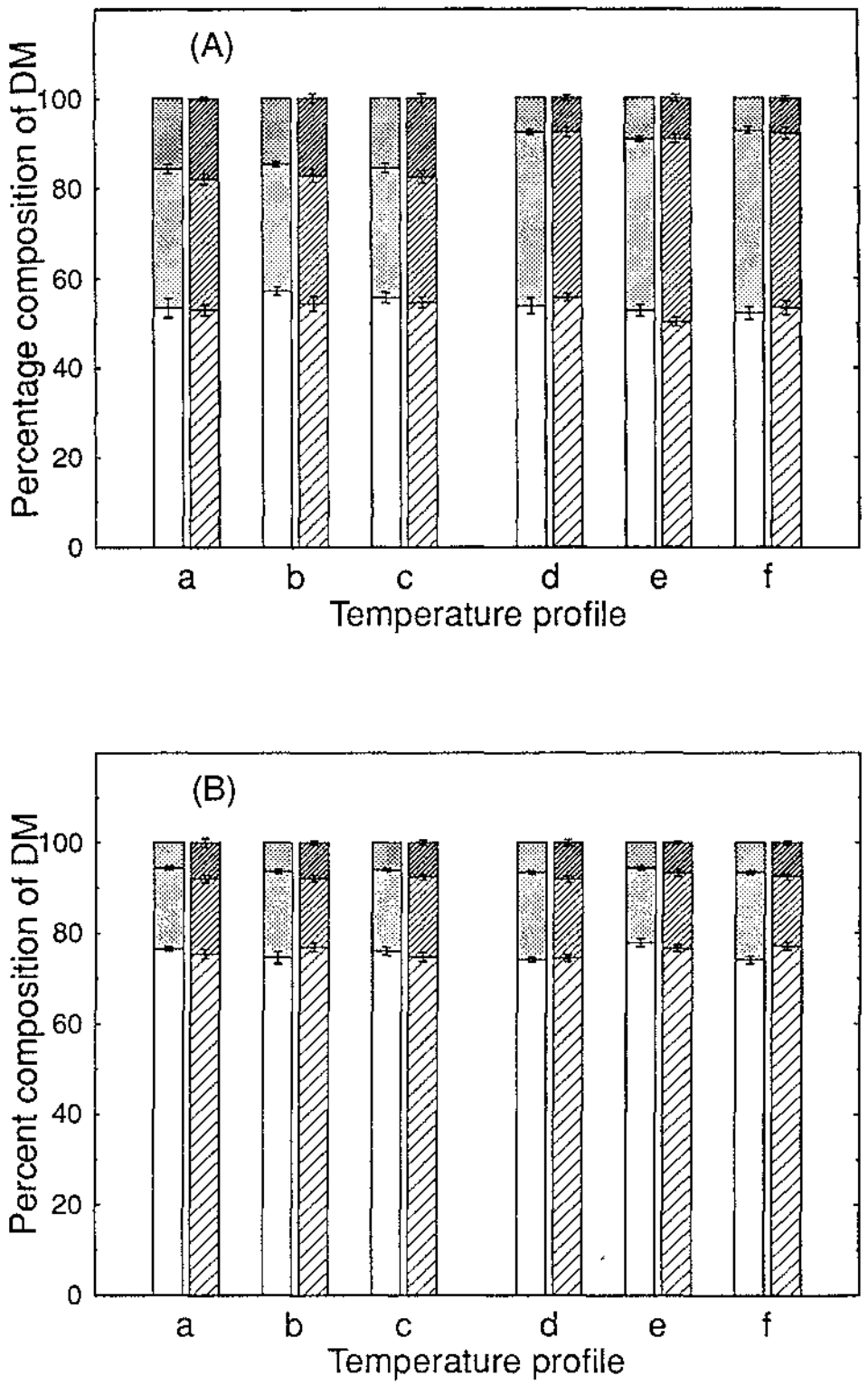


Fig. 4-19. Effect of PFD and temperature profile ([a,b,c,d,e,f] see Figs. 4-1, 4-2) on the dry matter partitioning between leaves, shoots and roots (base, middle and upper section of each bar) on (A) Epipremnum and (B) Fatshedera after growth for 30 days. (Light shading = 320 μmol.m^{-2}.s^{-1}, diagonal lines = 150 μmol.m^{-2}.s^{-1}.) Each bar represents the mean of 12 plants. Vertical lines indicate the standard error of the mean.

between the root and stem. At 20 C, between 28-30% and 17-18% of total plant dry matter were allocated to stem and roots, respectively, whereas, at 15 C approximately 40% and 10% of total plant dry matter was allocated to stem and roots, respectively. The PFD did not markedly influence the allocation of dry matter between the plant components.

In contrast, to Epipremnum the partitioning of dry matter between the leaves, stem and roots of Fatshedera varied only slightly for each component in each temperature profile. The proportion of the dry matter allocated to leaves (75-77%), stem (15-17%) and roots (7-8%) were similar in each treatment irrespective of the mean temperature or the temperature profile used during the night. As with Epipremnum, the PFD did not influence the partitioning of dry matter.

4.3.16 Carbohydrate accumulation and distribution

Carbohydrate accumulation was measured as the soluble sugar and starch concentration in leaf, stem and roots. The night temperature profiles, harvest time, PFD and species all resulted in highly significant effects ($P \geq 0.0001$) for soluble sugar, starch and total carbohydrate concentrations.

In the 20 C CNT temperature profile, soluble sugars were slightly higher and starch concentration was markedly higher in all Epipremnum tissues at the end of the photoperiod than at the end of the dark period (Fig. 4-20). A similar pattern of carbohydrate distribution was found in leaves grown at low and high PFD. Soluble sugar concentration in leaves and stems averaged 3.5 - 4%, whereas roots contained only a third as much. Stems tended to have higher concentrations of starch (14%) than leaves (5%) or roots (0.8%). In the SNT and SN temperature profiles a similar pattern of carbohydrate distribution was maintained irrespective of the harvest time or the PFD, except in the SN profile where significantly higher starch was present at high PFD (Fig. 4-20).

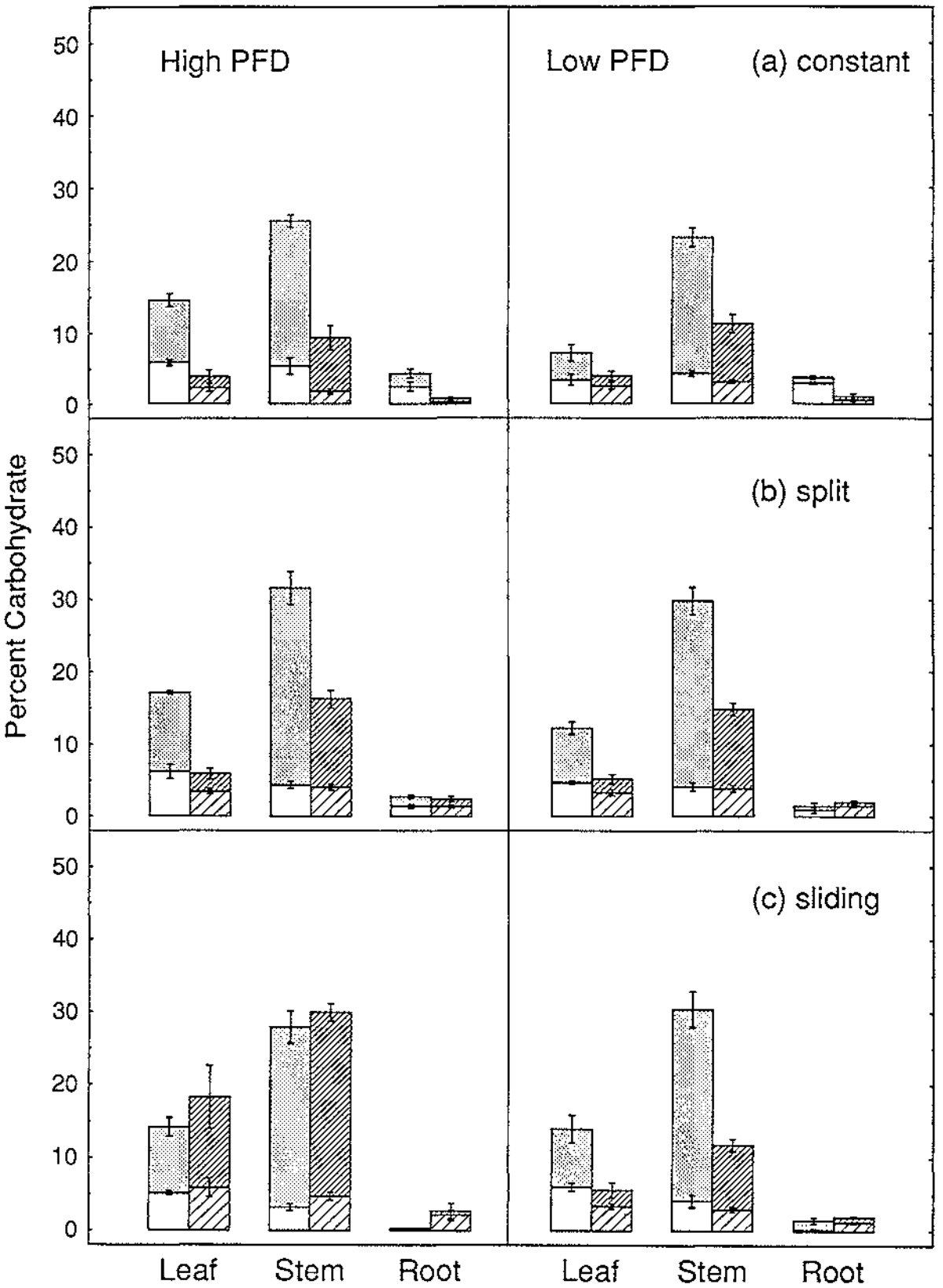


Fig. 4-20. Effect of temperature profile SN30/20C (see Fig. 4-1) and PFD (high = 320 μmol.m^{-2}.s^{-1}, low = 150 μmol.m^{-2}.s^{-1}) on the distribution of soluble sugar (base of bar) and starch (top of bar) in Epipremnum leaf, stem and root tissues at the end of the photoperiod (light shading) and the dark period (diagonal shading). Each bar represents the mean of 3 leaves. Vertical lines indicate standard error of the means.

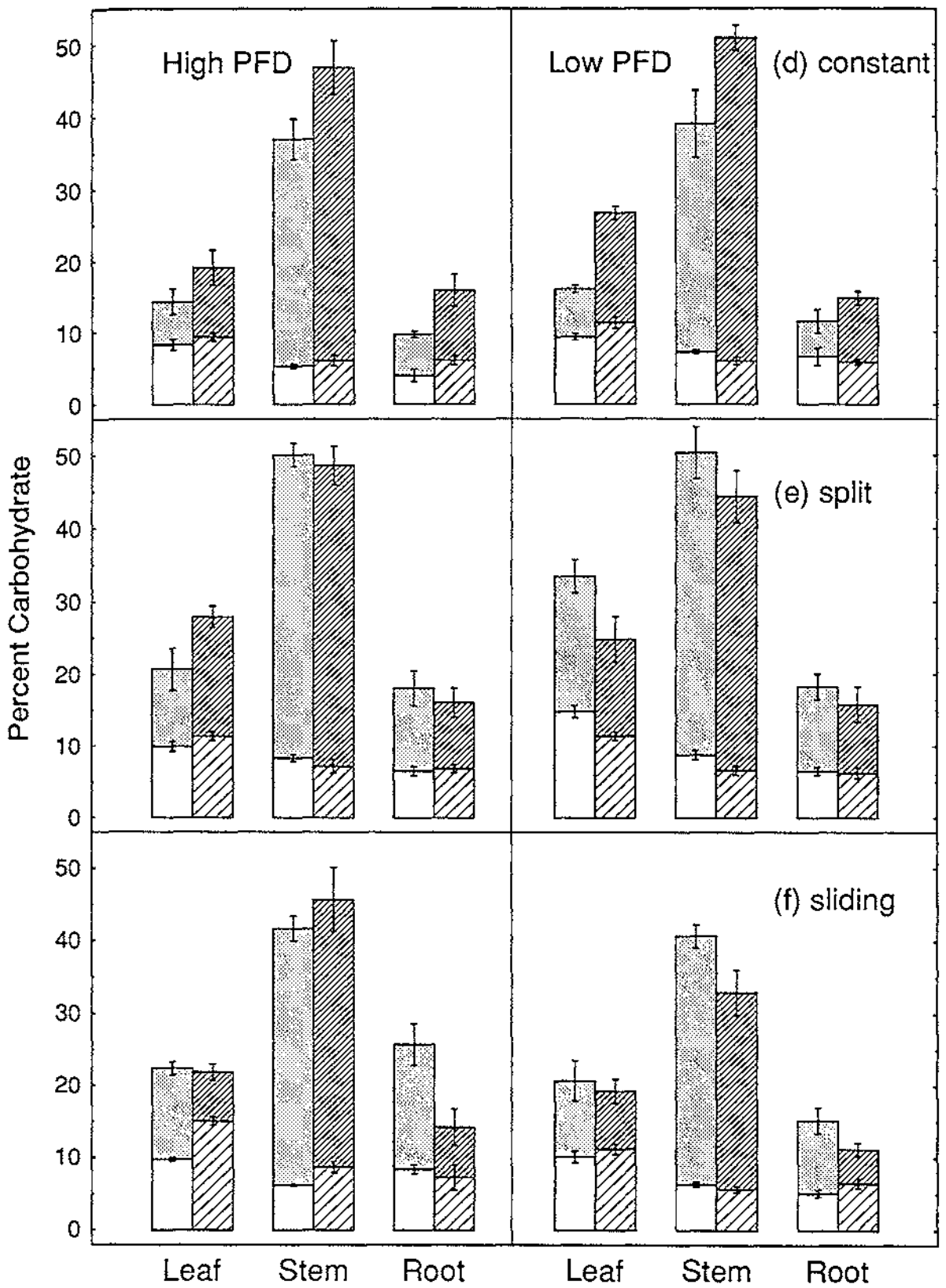


Fig. 4-21. Effect of temperature profile SN30/15C (see Fig. 4-2) and PFD (high = 320 μmol.m^{-2}.s^{-1}, low = 150 μmol.m^{-2}.s^{-1}) on the distribution of soluble sugar (base of bar) and starch (top of bar) in Epipremnum leaf, stem and root tissues at the end of the photoperiod (light shading) and the dark period (diagonal shading). Each bar represents the mean of 3 leaves. Vertical lines indicate standard error of the means.

Soluble sugar and starch concentrations in Epipremnum in all the 15 C night temperature profiles were markedly higher than those at the higher night temperature (compare Figs. 4-20, 4-21). The mean soluble sugar concentrations of leaf, stem and root tissue were 9, 6.5 and 5%, respectively and the average starch concentrations were 8, 36 and 8%, respectively (Fig. 4-21).

The type and distribution of carbohydrates in Fatshedera were markedly different from those in Epipremnum. At 15 C mean night temperature the soluble sugars comprised more than 75% of the total carbohydrate. Leaf tissue usually had more soluble sugar and starch than either stem or roots and was markedly higher at the end of the photoperiod than at the end of the dark period (Fig. 4-22). At the end of the dark period starch concentrations had diminished suggesting it had been respired during the dark period. A similar pattern of carbohydrate partitioning was found in leaves grown at low and high PFD. Soluble sugar concentrations averaged 13% in leaves, 8.5% in stems and 3% in roots. Relatively low starch concentrations were measured in leaves (2.5%), stems (0.7%) and roots (0.3%) (Fig. 4-22).

In the lower night temperature profile at 15 C the soluble sugar and starch concentrations were markedly higher than in the warmer night temperature profiles (Fig. 4-23). In the CNT treatment the soluble sugar concentrations of leaf, stem and root tissue were 20, 9.5 and 7%, respectively. Starch concentrations were 8, 1.3 and 0.4%, respectively (Fig. 4-23). Similar concentrations were found in the SNT and SN temperature regimes. While carbohydrate concentrations were generally higher in the lower night temperature profiles than in the warmer profiles, the distinction between starch and soluble sugar and between leaves, stem and roots were generally similar to night temperature profiles at 20 C where carbohydrates decreased during the dark period, except there was a tendency for soluble sugar to accumulate in the roots at the lower night temperature.

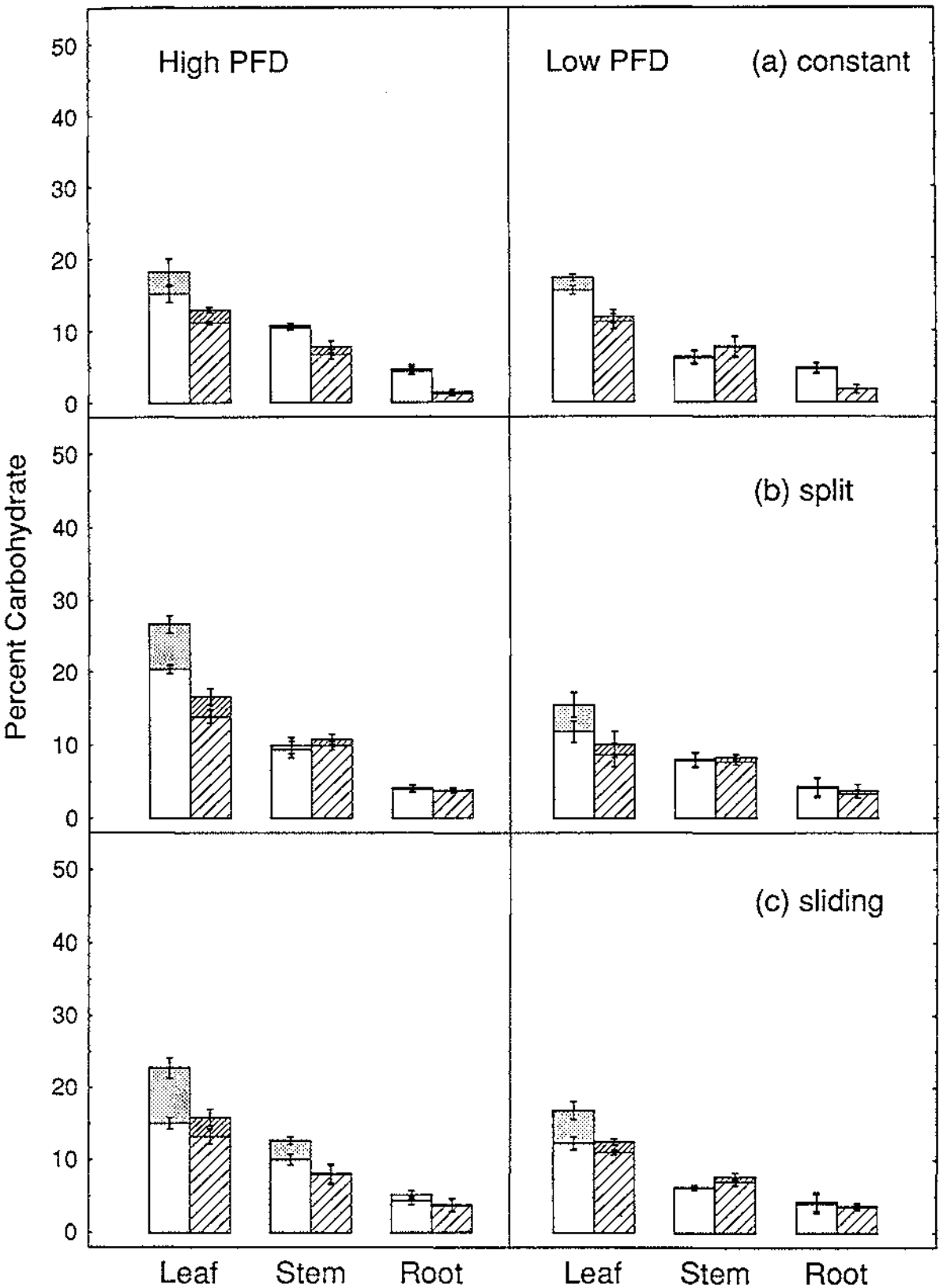


Fig. 4-22 Effect of temperature profile SN30/20C (see Fig. 4-1) and PFD (high = 320 μmol.m^{-2}.s^{-1}, low = 150 μmol.m^{-2}.s^{-1}) on the distribution of soluble sugar (base of bar) and starch (top of bar) in Fatshedera leaf, stem and root tissues at the end of the photoperiod (light shading) and the dark period (diagonal shading). Each bar represents the mean of 3 leaves. Vertical lines indicate standard error of the means.

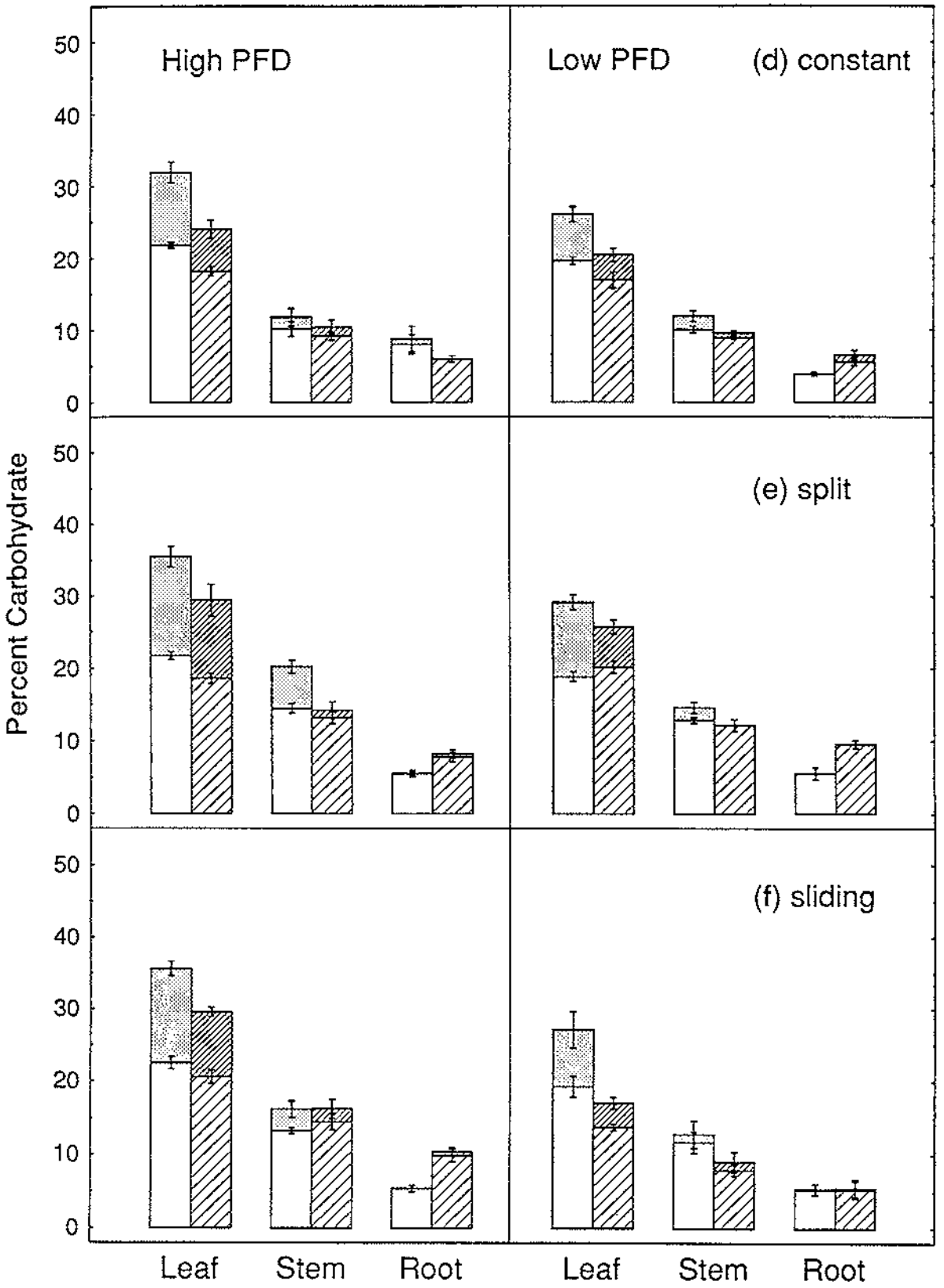


Fig. 4-23. Effect of temperature profile SN30/20C (see Fig. 4-2) and PFD (high = 320 μmol.m^{-2}.s^{-1}, low = 150 μmol.m^{-2}.s^{-1}) on the distribution of soluble sugar (base of bar) and starch (top of bar) in Fatshedera leaf, stem and root tissues at the end of the photoperiod (light shading) and the dark period (diagonal shading). Each bar represents the mean of 3 leaves. Vertical lines indicate standard error of the means.

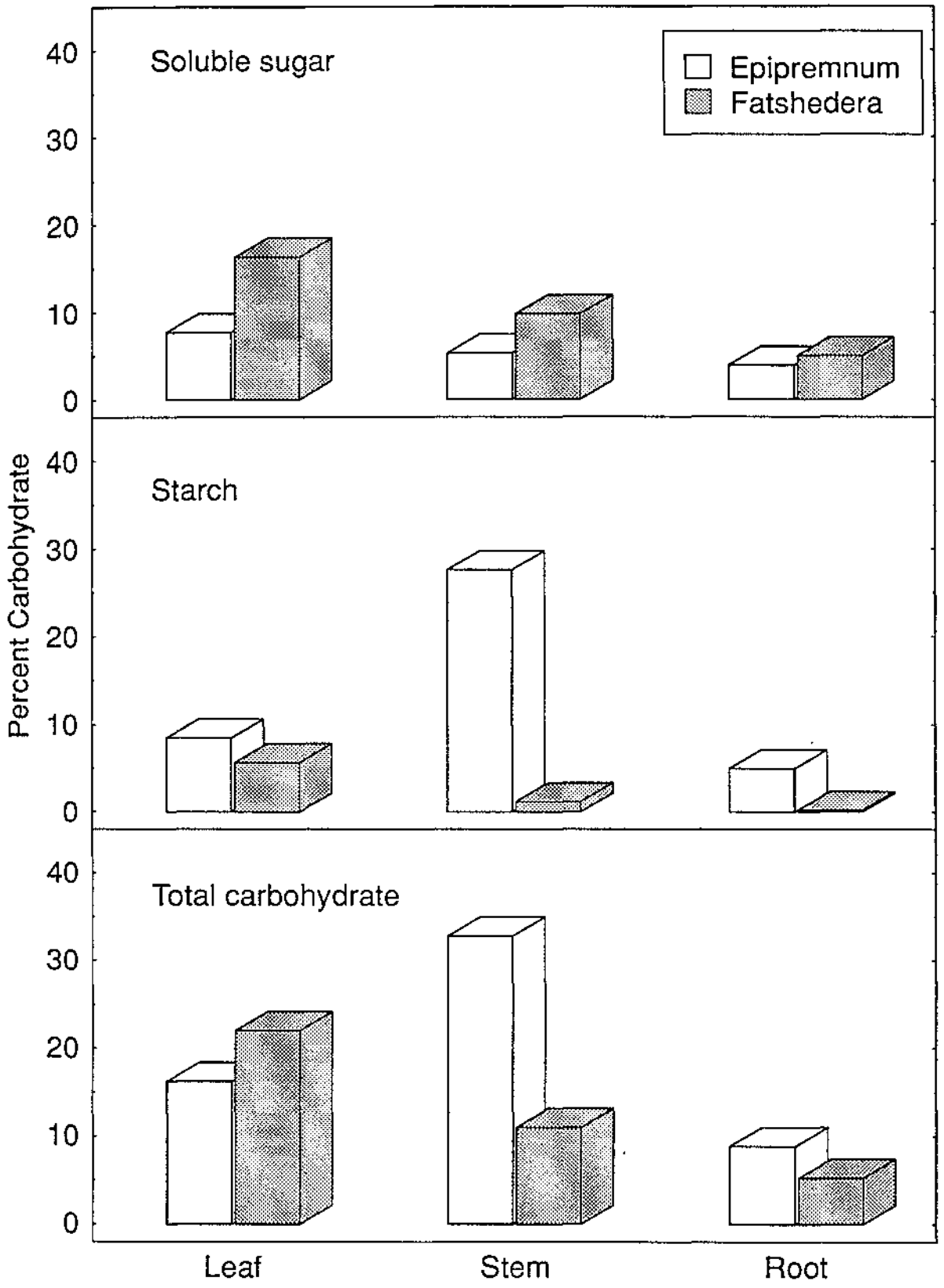


Fig. 4-24. Interaction of species (Epipremnum and Fatshedera) and plant part (leaf, stem and root) on soluble sugar, starch and total carbohydrate content. Each bar represents the species x plant part interaction mean. Standard error of the means were <2% of the maximum value of each parameter.

Interactions between treatments were often statistically significant, the species x plant part interaction contributed substantially more to the variance than any other interaction and was comparable with the main effects in importance. The interaction means (Fig. 4-24) showed that carbohydrate concentration in a particular plant part was dependent on the species and on the form of the carbohydrate. Almost twice the soluble sugar concentration was found in Fatshedera leaf and stem tissues than in Epipremnum, while concentrations were comparable in the roots. Starch concentration was comparable in Epipremnum and Fatshedera leaves, but an order of magnitude higher in stem and roots of Epipremnum than in Fatshedera.

The principal soluble carbohydrate (80%) in Epipremnum was fructose, and the balance was 7% sucrose and 13% glucose on a molar basis. In Fatshedera, sucrose represented 25% of the soluble sugar and the balance was equal proportions of glucose and fructose. The proportions of these sugars did not vary markedly with any diurnal changes in PFD or temperature (data not presented).

4.4 Discussion

This study has shown that for most growth parameters Epipremnum and Fatshedera integrated temperature over the diurnal cycle for the range of temperatures investigated. The individual temperature profiles **per se** exerted only a very limited effect on the growth and development of each species. The major differences in plant growth of Epipremnum and Fatshedera arose from their contrasting response to the low night temperature.

4.4.1 Effect of night temperature profiles on plant growth parameters

The results from this study showed that growth of Epipremnum and Fatshedera depended on the mean night temperature with only minimal differences occurring between night temperature profiles. Similar results have been established by White and Warrington (1984) with geranium and Langhans *et al.* (1981) using lettuce and chrysanthemum.

Many studies have examined the effect of variable night temperature on plant growth and reported cropping delays at reduced night temperature, but have neglected to use treatments that were equivalent in the comparative studies (Thorne and Jaynes, 1977; Tsujita and Craig, 1980; White, 1981; Shanks, 1987; Shedlosky and White, 1987). Differences in environmental conditions make comparisons within investigations and between investigators difficult when treatments were not equivalent in their energy inputs from light and temperature.

Growth and productivity of a range of greenhouse crops such as chrysanthemum (Cockshull *et al.*, 1981), tomato (Koning, 1988), cucumber (Krug and Liebig, 1980), kohlrabi (Liebig, 1988) and rose (Van den Berg, 1987) have been reported to be dependent on the mean daily temperature. Similar findings have been reported in other crops (Armitage and Carlson, 1980; Langhans and Albright, 1981; Wilkins *et al.*, 1980; Miller and Langhans, 1985). The only instances where

comparable growth has been obtained in SNT or SN have occurred where treatments with equivalent daily temperature integrals have been compared (Langhans (*et al.*, 1981; White and Warrington 1984; Miller and Langhans, 1985). These publications contrast with a report that RGR in sweet pepper was increased using a SNT temperature regime (Kooistra, 1984).

Relative growth rate and LER increased concomitantly with increasing temperature. Similar results have been presented by Warren Wilson (1966). This is not surprising as the leaf dry weight comprised between 55 and 75 % of the total dry weight in Epipremnum and Fatshedera, respectively. The primary effect of radiation appeared in the rate of growth and not in the pattern of growth. At the higher PFD, Epipremnum and Fatshedera grew more rapidly presumably because of the direct effect on photosynthesis, where increased light produced more assimilates that could be used for growth. However, the overall response to high PFD was actually typical of shade plants (Boardman, 1977). Most efficient utilisation of the incident light for dry matter production occurred in the low PFD treatment, with a marked reduction in efficiency occurring at the higher PFD (Fig. 4-10).

The NAR expresses the dry weight gain of the whole plant on a leaf area basis and also represents the photosynthetic efficiency of both species. In this study RGR was highly correlated with NAR. There were marked differences in the influence of night temperature on RGR of Epipremnum and Fatshedera. These differences may have arisen from the large effect of temperature on NAR and LER that occurred in the temperature profiles of the SN30/20 C treatments compared with those at SN30/15 C. The general sensitivity of NAR to temperature has been reported in other crops like rape, sunflower and maize (Warren Wilson, 1966). This contrasts with the findings of Potter and Jones (1977) who reported that, for a range of species, NAR was not particularly temperature sensitive, but this result may have been related to the low level of photosynthetically active radiation (100 $W \cdot m^{-2}$) used in their studies.

In the current study plant growth rate depended on both the efficiency of the leaves as producers of photo-assimilates and upon the relative leafiness of the plant. The RGR in both species was highly correlated with LER and NAR indicating a tight coupling between leaf area, the rate of photosynthesis and dry matter accumulation. This contrasts with the findings of Potter and Jones (1977).

The LER in Epipremnum, unlike Fatshedera, was dependent on the mean night temperature. This response pattern may have arisen because the mean night temperature may have been substantially different to the optimum temperature for growth. From results in Chapter three it is evident that at the mean temperatures used in this study Fatshedera was very close the temperature optima whereas Epipremnum was considerably removed from it.

This investigation did not establish the same correlation between RGR and LAP reported by Potter and Jones (1977) with seven of the nine agronomic species investigated. Presumably the limited change in LAR seen over time in this study offset any relationship between RGR and LAP as LAP is defined as the daily change in LAR. Net assimilation rate and RGR were highly correlated in this work and the response is similar to the relationships between carbon fixation and NAR found with wheat (Friend and Helson, 1976).

In a general, leaf area ratio reflects the ratio of photosynthetic to respiratory tissue in the plant. In the CE temperature treatments, LAR increased with increasing time and contrasts with the decrease in LAR found in field-grown cowpeas (Fernandez and Miller, 1987). Leaf area ratio also increased with increasing temperature, similar to findings of Warren Wilson (1966). Leaf area ratio in both Epipremnum and Fatshedera was higher at low PFD as also reported in sugar beet (Terry, 1968). As RGR was constant over the time course it follows that any ontogenetic drift in LAR must have been matched by an equivalent increase in NAR. (Assuming at any point in time, RGR = LAR x NAR). However, plants did not exhibit the typical shade-adapted response, as leaves produced at low PFD were not significantly thinner or larger than at high PFD

(Boardman, 1977). This suggests that Epipremnum and Fatshedera were better adapted to the lower fluence rate at low PFD than at high PFD as is also evident from the relative efficiency of dry weight production (Fig. 4-10). In each species LAR was similar in treatments with the same mean temperature corroborating similar findings by Dale (1964) using bean plants.

The downward ontogenetic drift in NAR in Epipremnum and Fatshedera observed in this study has been reported in other species including, for example, barley (Thorne, 1961), strawberry (Olsen *et al.*, 1985), muskmelon (Acock et al., 1990) and recently in photinia (Norcini *et al.*, 1991). Thorne (1961) showed the downward movement in NAR over time was attributable to deterioration of the growth conditions in the field. This explanation is not valid in CE studies where normally environmental conditions are defined and may be held constant. However, the reduction in NAR may arise from mutual shading of leaves or could reflect some incipient stress or senescence. The net effect of reduced NAR was that, as the plant enlarges during growth, the maintenance requirement for an increasing quantity of structural material increases, which results in the apparent photosynthetic efficiency decreasing. Epipremnum and Fatshedera accumulated more dry weight at the higher DLI as reported by Gislerod *et al.*, (1989), Mortensen and Grimstad (1990), Lieth *et al.* (1991) and Warrington and Norton (1991).

Net assimilation rate in the chilling-insensitive Fatshedera was relatively insensitive to change in the mean temperature and is in agreement with results based on other plants (Warren Wilson, 1966; Heuvelink, 1989). However, chilling-sensitive Epipremnum plants grown at the lower night temperature had significantly lower NAR than at higher temperature irrespective of the temperature profile. A similar response in another chilling sensitive plant (bean) was reported by Dale (1964). The reduction in photosynthetic efficiency at the lower temperature suggests that gas exchange rates may have been reduced or

alternatively light harvesting efficiency was impaired by chilling injury in the chloroplast (Wise *et al.*, 1983) without being visibly obvious.

Specific leaf area increased with temperature indicating a reduction in the relative thickness of the leaves. This pattern of response has been observed in diverse crops such as rape, sunflower (Warren Wilson, 1966) and macadamia (Trochoulias and Lahav, 1983). Increased SLA in low PFD treatments indicated compensatory growth was directed towards improving light interception. The altered SLA would partially counter the observed reduction in NAR. Impatiens plants responded similarly in classical studies by Hughes and Evans (1962). A relationship between SLA or SLW (SLA = SLW^{-1}) and daily light integral (DLI) has been demonstrated by Björkman *et al.* (1972); Chabot *et al.* (1979); Bunce (1983) and Warrington and Norton (1991). The relationship between PFD and SLA was also dependent on the influence of temperature, particularly in the way LER was affected (Figs. 4-7, 4-8). Hunt (1982) reported that ontogenetic drift of SLA depended on the temperature, which concurs with results found with Epipremnum and Fatshedera; at the higher temperature SLA increased over time whereas at the lower temperature SLA decreased. Plant growth and development in the variable night temperature profiles (SN and SNT) were generally not significantly different to the CNT treatment. However, SLA was significantly lower in SN and SNT compared with CNT treatments. This suggests that some aspects of leaf expansion and development are dependent upon steady state temperature conditions to maximise SLA. Similar results have been established using geranium plants (White and Warrington, 1984).

Evidence obtained in this study using Epipremnum and Fatshedera demonstrated the limited capacity of LWR to discriminate between environmental influences and ontogenetic drift compared with SLA. This suggests that each plant partitions a relatively constant proportion of the total plant dry weight into leaves regardless of the environmental conditions experienced. This confirms findings by other researchers including Warren Wilson (1966), Evans (1972), Harssema (1977) and Hunt (1982).

4.2 Effect of night temperature profiles on plant development

Rate of leaf appearance in both species was not altered by the night temperature profiles or by the PFD, but was strongly influenced by the mean temperature. Similar findings have been reported by Karlsson *et al.* (1989) with chrysanthemum. The lack of response to PFD observed in this study contrasts with that reported by Meyling (1973) using maize. This disparity could probably be due to the adaptation of Epipremnum and Fatshedera to low PFD as shade plants. This was evident by the apparent photoinhibition of photosynthesis occurring at 320 $\mu mol \cdot m^{-2} \cdot s^{-1}$ causing a marked reduction in the conversion efficiency of incident light into plant dry weight (Fig. 4-10). It appears that conditioning during the dark period in the low night temperature profiles predisposed Epipremnum in particular, to reduction in photosynthetic efficiency when exposed subsequently to high PFD. Presumably in the dark period only limited restoration of any light harvesting sites occurred following impairment during earlier exposure to bright light (Greer, 1990). An alternative hypothesis to explain chilling-impaired photosynthesis has been developed by Brüggemann *et al.* (1992) based on the efficiency of ribulose-1,5-biphosphate carboxylase/oxygenase. The temperature response of each species confirms the earlier characterisation of Epipremnum as a warm temperature requiring species and Fatshedera as a cooler temperature tolerant species.

Rate of leaf appearance in Epipremnum was linear over time as reported in sunflower (Rawson *et al.*, 1980) and increased with temperature as reported in many other plants including poinsettia (Berghage *et al.*, 1990), Easter lily (Karlsson *et al.*, 1988), hibiscus (Karlsson *et al.*, 1991), pigeon pea (McPherson *et al.*, 1985), maize (Tollenaar *et al.*, 1979; Warrington and Kanemasu, 1983). In Epipremnum LFP at SN30/15 C was very slow and decreased with time indicating minimal capacity to adapt to low temperature. In contrast, in Fatshedera LFP was less affected by the change from high to low night

temperature indicating that the optimum temperature for leaf production was probably close to mean of the higher night temperature treatment.

Node length tended to increase with increasing positive DIF (day - night temperature). This contrasts with flowering plants with a determinate habit where internodal length increased with increasing positive temperature differential (Berghage, 1989; Karlsson *et al.*, 1989; Erwin *et al.*, 1991; Moe, 1990). The relative consistency of node size over time indicated that for each species, in the temperature treatments investigated, leaves were unfolding regularly and that all plants would have a compact leafy appearance (Plates 4-1, 4-2).

Shoot growth in Epipremnum and Fatshedera was directly related to LER and RGR. Increased temperature and PFD increased vegetative growth, in agreement with results from other ornamental plants and represents a typical plant response (Armitage *et al.*, 1990; Berghage and Heins, 1991; Gislerod *et al.*, 1989; Mortensen and Grimstad, 1990; Mortensen and Larsen, 1989). Shoot growth response of these plants may have been anticipated from earlier evidence (Chapter three) of Epipremnum as a chilling-sensitive plant and Fatshedera as a chilling-tolerant plant (Raison and Lyons, 1986). Reduction in shoot growth and plant quality of Epipremnum after exposure to chilling temperatures has also been reported by Poole and Conover (1986).

4.4.3 Effect of night temperature profiles on partitioning and carbohydrates

Eco-physiologists have examined the kinetics of CO_2 fixation and attempted to relate this to differences in biomass production in different species with variation in RGR (Poorter and Bergkotte, 1992). However, CO_2 fixation is only the first part of a complex series of biochemical reactions that lead to the construction of new dry matter and plant growth. Plants function as a collection of integrated sources and sinks that are maintained in a stable equilibrium during growth, while the

factors determining the balance between each sink are poorly understood (Daie, 1985).

Dry matter distribution between leaves, stems and roots in Fatshedera was remarkably constant in all SN30/20 C and SN30/15 C temperature profiles. A similar consistency was noted in the proportion of dry matter in the leaves of Epipremnum, but the proportion partitioned to the roots decreased and that to the stems increased in all low temperature profiles. The higher proportion of dry matter partitioned to the stem at low temperature indicates a reduction in root sink strength (and hence increased shoot/root ratio) at low temperature. Sink strength in the stems would be maintained by the demand for photosynthates in the buds. In other plants, including potato and passionfruit, increased gibberellin activity occurs in buds at higher temperatures (Menzel, 1983) creating increased demand for assimilates (Ginzburg, 1974). As the mean temperature increased in Epipremnum there was no change in the proportion of dry matter in the leaves, but assimilates were allocated to the roots at the expense of the stem. In contrast, Menzel and Paxton (1985) showed that, as temperature increased, lychee plants allocated dry matter to leaves at the expense of the roots while the proportion of stem remained constant.

The ratio between the shoot size and root size is subject simultaneously to genetic, environmental and ontogenetic influences (Ledig and Perry, 1965). In this study the allometric relationship determined between shoots and roots indicated that Epipremnum plants allocated less resources to the roots when growing at temperatures further away from the optimum. Although the slopes of these regressions for Fatshedera were significantly different and higher in plants grown in the SN30/15 C than at SN30/20 C at final harvest, plants were not different after 30 days growth. Hunt and Nichols (1986) showed that stress would alter distribution of reserves and proposed that plants would attempt some compensatory growth in the organ most influenced by any environmental factor. Data for Epipremnum confirms this hypothesis -as previously described leaf growth was repressed in all low night temperature treatments and this resulted

in an increase in shoot weight relative to root weight. While it is less clear in Fatshedera, the allometric relationships indicated a small reduction in the proportion of shoots with increasing temperature. This confirms earlier findings (Chapter three) that the optimum temperature for vegetative growth was < 25 C.

There were marked differences in the carbohydrate composition in each species and also in the extent of carbohydrate accumulation. In Epipremnum the proportion of soluble sugars (predominately fructose) remained relatively constant at both warm and cool night temperature treatments and did not show much diurnal variation compared with the starch concentrations. In contrast, in Fatshedera the soluble sugar concentrations fluctuated markedly, reflecting a basic physiological difference between the two species in their mode of carbohydrate storage and utilisation.

Regulation of starch biosynthesis is known to occur at the level of ADP-glucose phosphorylase (Preiss and Levi, 1979). This enzyme is regulated with allosteric activation by 3-phosphoglyceric acid (PGA), an intermediate of the reductive pentose pathway and repressed by inorganic phosphate (Pi). Starch synthesis may not occur in chloroplasts (and amyloplasts) until the export of triose phosphate to the cytoplasm for sucrose synthesis has reached saturation in the cytosol. In Epipremnum plants relatively little sucrose was found in the soluble sugar while starch levels were much higher. The sucrose pool in the cytosol may accumulate to a high level before redistribution to active sinks as noted in cucumber (Toki *et al.*, 1978). However, in Epipremnum the soluble sugar concentration in the entire leaf was relatively low. A high soluble sugar concentration adjacent to specific enzymes may provide the necessary stimulus for starch synthesis by activation of ADP-glucose phosphorylase. Low immediate demand for carbohydrates (particularly at low temperature) or slow dispersal elsewhere within the plant might be responsible for the marked accumulation of starch. Furthermore, Herbert and Bickett (1984) reported that high concentrations of fructose in spinach leaves caused a reduction in sucrose synthesis while

enhancing starch production. The concentration of fructose, compared with other soluble carbohydrates, suggests that it may be used preferentially or that there could be a selective feedback mechanism preventing conversion of fructose to glucose. However, from the evidence available, it is not possible to decide which process predominates.

In Fatshedera it may be possible that rapid transport of monosaccharides and other soluble sugars from the site of synthesis to sinks in other parts of the plant occurs concurrently with synthesis (as reported in tomato Gent *et al.*, 1979 and Toki *et al.*, 1978), thereby accounting for the high concentrations of soluble carbohydrates and relatively low concentrations of starch found throughout the plant. This would prevent the activation of ADP-glucose phosphorylase required for starch formation. When transport is reduced by environmental factors like low temperature or the supply increased by high PFD, then starch accumulation occurs.

Thorne and Koller (1974) found higher concentrations of Pi in heavily shaded leaves and argued that starch concentrations would be lowered because Pi concomitantly stimulates degradation of starch by starch phosphorylase and inhibits the synthesis of further starch. The results of this study at low PFD contrast with their findings. The reason could be related to starch accumulation not being regulated in Epipremnum by low activity of ADP-glucose phosphorylase. In Fatshedera this enzyme, although present, it may not be particularly active.

In each species carbohydrates tended to accumulate more in leaves, stems and roots at the lower night temperature and this was probably related to reduced metabolic activity. Similar findings have been reported by Warren Wilson (1966); Chatterton *et al.* (1972) and Forde *et al.* (1975). Accumulation of carbohydrates may have arisen through reduced respiratory activity, but probably more importantly, temperature was limiting utilisation and organ expansion before moderating carbohydrate production. Temperature influences the mobilisation of

carbohydrates (Porvin *et al.*, 1984), utilisation in leaf expansion (Hesketh and Baker, 1969) and in other metabolic processes (Went, 1958), and development of other organs (Hall and Brady, 1977).

Reduction in photosynthetic activity such as occurred in Epipremnum and Fatshedera following reduced night temperatures, has also been reported in tomatoes (Vallejos and Björkman ,1983; Yakir *et al.*, 1986; Brüggemann *et al.*, 1992) and may be associated with accumulation of sugar and starch (Warren Wilson, 1966; Warrington *et al.*, 1977) or reduced gas exchange as reported in cucumber (Peeler and Naylor, 1988). Carbohydrate accumulation under conditions that reduce photosynthesis may be attributable to slow translocation of assimilates from the source (Chatterton, 1973). The magnitude of the changes in the concentrations of carbohydrates in all plant parts at the end of the dark period, compared with those at the end of the light period, suggests that rather less was carbohydrate was metabolised in the lower night temperature treatments than in the higher temperature treatments as proposed by Went (1944).

Carbohydrates tended to accumulate during the photoperiod in all temperature treatments and were mobilised during the dark period (Fondy and Geiger, 1982; Sicher *et al.*, 1984). The evidence presented in this study does not support the hypothesis that warm temperatures are required during the early part of the dark period to allow translocation and metabolism of photosynthates before the next photoperiod (Thorne and Jaynes, 1977; Gent *et al.*, 1979; White, 1981) or that depletion of carbohydrates could be avoided by lowering the temperature in the latter part of the night. In the current study, depletion of carbohydrate reserves to limiting levels during the dark period did not occur in either species. This contrasts with Challa's (1978) findings using cucumber plants but similar results were reported with geranium (White and Warrington, 1984). The carbohydrate concentrations in both Epipremnum and Fatshedera indicated their functioning as biological temperature integrators in an inverse manner. Plant physiological behaviour and hence carbohydrate metabolism of each species was determined by the mean daily temperature, rather than by responding to perturbations about

the mean temperature. Similar findings have been reported using geranium, Easter lily, rose and chrysanthemum (Armitage and Carlson, 1980; Langhans and Albright, 1981; Wilkins *et al.*, 1980).

Soluble carbohydrates and starch accumulated in all plant parts (leaf, stem and roots) during exposure to light. Presumably this happened because carbohydrate synthesis and transport from the leaves occurred simultaneously. These results show that in Epipremnum and Fatshedera all plant parts contained higher carbohydrate concentrations when grown at high PFD. This would be a direct consequence of higher rates of photosynthesis at high PFD producing carbohydrate in excess of that required for immediate use. Earlier studies with Easter lily also reported that the highest concentrations of carbohydrates in leaves occurred in treatments exposed to high PFD and is agreement with trends reported by Miller and Langhans (1989a,b) and by White and Warrington (1984, 1988).

The question arises as to whether limitations in carbohydrate supply actually cause a reduction in growth. Poorter and Bergkotte (1992) suggest that the cost of producing new biomass in both slow and fast growing plants is remarkably similar and is not a significant factor that would account for differences in RGR between species. The presence of substantial carbohydrate reserves in tissues of both species at the end of the dark period suggests that carbohydrate supply was exceeding the demand for growth and maintenance. This is probably due to a sink limitation imposed by the low night temperature. Most plants probably accumulate soluble sugar and starch because temperature was limiting LER and not NAR. This is supported by a reduction in the carbohydrate pool at the higher growth temperature which is indicative of a better balance between demand and supply of assimilates.

In this study the changes in the diurnal composition of the soluble sugars over a complete day/night cycle and the influence of night temperature profiles were not examined. Evidence from other investigators using a range of species,

suggests that significant diurnal changes in the composition of carbohydrates might be anticipated in Epipremnum and Fatshedera (Lechtenberg *et al.*, 1971; Sicher *et al.*, 1984; Karlsen, 1989; Davis and Loescher, 1991).

Growers could manage diurnal temperature fluctuations to optimise crop production and economic return by reducing energy consumption during production. Provided an appropriate daily mean and minimum temperature for each crop was maintained, then day temperature could be allowed to increase and offset a lowering of the night temperature. Temperature control in a greenhouse could be optimised using electronic temperature integrators linked to a programmable controller.

Another benefit to growers arises from increased carbohydrate accumulation using lowered night temperature. Where plants require transport over extended long distances in the dark, pre-dispatch hardening at low night temperatures would improve plant quality by increasing the carbohydrate reserves at the start of transportation.

4.4.4 Conclusion

This study evaluated the hypothesis that two vegetative ornamental plants differed in their response to low temperatures experienced in SN temperature profiles with a common mean temperature. Experience has show that Epipremnum and Fatshedera acted as daily temperature integrators. For all parameters investigated, Epipremnum and Fatshedera responded to the mean temperature rather than to a range night of temperatures that fluctuated about a common mean. Although differences in metabolism may occur, the net effect of the night temperature treatments with a common mean was equivalent vegetative growth. The contrasting growth responses between Epipremnum and Fatshedera were explained by their interaction with both temperature and PFD.

These experiments demonstrated the remarkable capacity of foliage plants to adapt to a range of light and temperature conditions producing equivalent growth for equivalent energy input. The overall response to temperature confirmed the relative chilling sensitivity of Epipremnum and Fatshedera determined in Chapter three.

CHAPTER FIVE

Photoinhibition and recovery

"Although all life depends directly or indirectly on photosynthesis the chemical nature of this remarkable process is not well understood... The reason for our for ignorance is not so much due to lack of scientific effort as to the inherent complexity of the system."

'The search for understanding'.
French, 1967.

5.1 Introduction

5.1.1 Light and Photosynthesis

Plant growth, development and photosynthetic performance are inextricably linked to the light environment (Monteith and Elston, 1983). Photosynthesis in leaves of higher plants depends on the adsorption of light at wavelengths between about 350 and 700 nm where approximately 56% of the incoming solar radiation occurs. Leaves absorb 70-80% of the incident radiation, but only about 2% is finally converted into chemical energy and stored by plants (Sauer, 1986). Light entering plant tissue is attenuated by both absorption and scattering. This creates a light gradient within the leaf so that cells deeper inside the leaf experience considerably reduced PFD and will contribute less to the net energy trapping and carbon fixation. Depending on leaf structure, it is possible for multiple internal reflections to concentrate the PFD so that the internal fluence rates may be several times higher than the incident PFD (Vogelmann, 1989). Relatively small changes in the refractive index of surface waxes and cuticle may also lead to significant differences in the light trapping capacity of leaves (Kaufmann and Hartmann, 1988). This may be further intensified up to 20 times when focused by epidermal cells (Bone, 1985). These factors will influence the fluence rate within leaves, in addition to variation in incident PFD.

Plant growth is a function of the net photosynthetic activity of all the chloroplasts exposed to light. Near the adaxial leaf surface chloroplasts not only experience a higher PFD than chloroplasts further from the adaxial surface, but also experience a different spectral quality due to selective absorption of red and blue wavelengths (Terashima *et al.*, 1986). Some chloroplasts are adapted to a high-light environment within focal spots in palisade tissue (Martin *et al.*, 1989) and may be able to withstand prolonged exposure to high PFD without impairment (Greer *et al.*, 1991). However, most chloroplasts within the leaf do not appear to have the capacity to function efficiently in this manner.

5.1.2 Utilisation of absorbed light

The trapping and utilisation of light in photosynthetic carbon fixation is a complex biochemical process described by the overall equation (Clayton, 1980; Fork, 1986):

$$\text{Light} + nH_2O + nCO_2 \rightarrow (CH_2O)_n + nO_2 \qquad [5.1]$$

Photochemistry takes place in the chloroplast where it is catalysed first by components located in the thylakoid membranes (grana), and then in the clear phase (stroma) where stromal enzymes using 2 moles of NADPH and 3 moles of ATP produced in the grana fix and convert 1 mole CO_2 into carbohydrates (Krause, 1988).

The chloroplast membranes contain many closely linked sites designed to operate as a pair known as photosystem I and II (PS I and PS II) (Fig. 5-1). Associated with the lipoprotein membrane complexes are essential pigments and cofactors such as chlorophyll, pheophytin and quinones. The whole complex moderates the photochemical electron transport to the plastoquinone pool of the noncyclic electron transport chain (Arntzen and Pakrasi, 1986). This ischeme

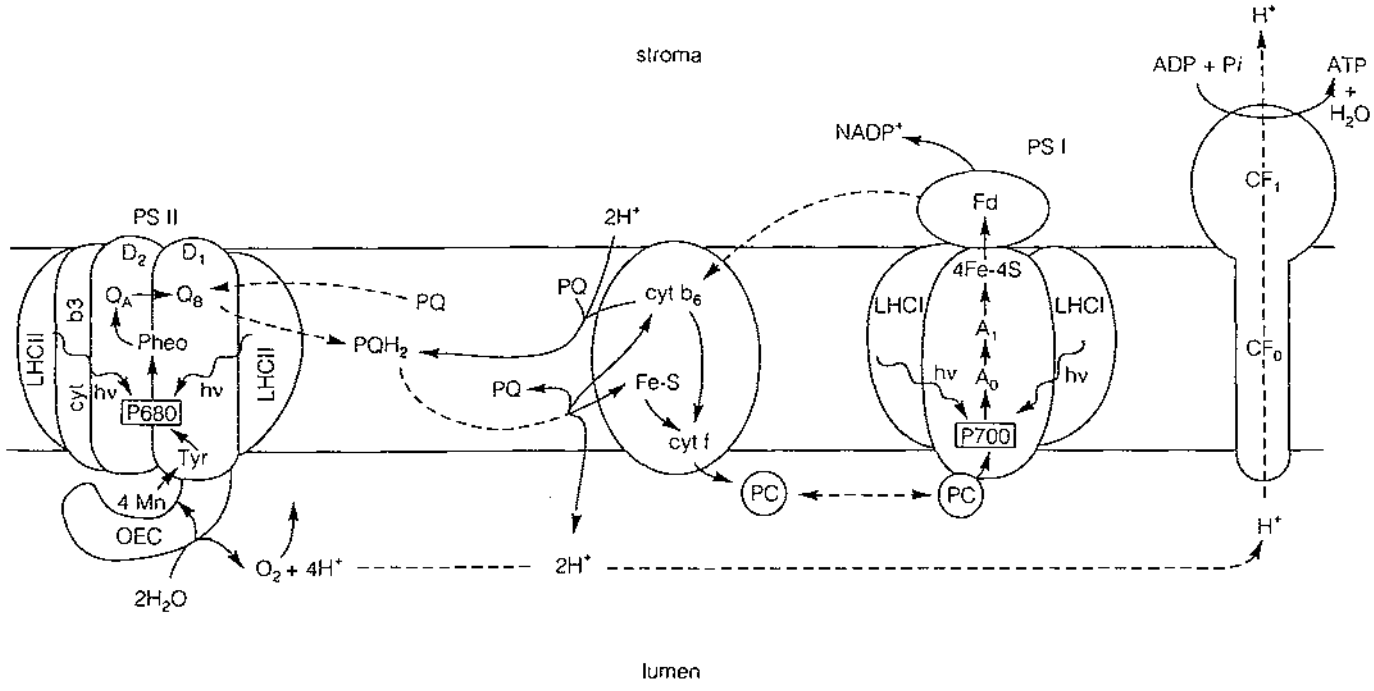


Fig. 5-1: The location of electron transport and Photosystems I and II in the thylakoid membrane. When light energy is trapped by the light harvesting centers in each photosystem electrons, produced in the oxygen evolving complex (OEC) from water and pass through PS II (left), the cytb_6-f complex and PS I (right) in the lumen across the thylakoid membrane to $NADP^+$ in the stroma. These complexes also cooperate to transfer H^+ from the stroma to the lumen. ATP-synthetase (far right, shown as CF_0 and CF_1) transports H^+ back from the lumen to the stroma and converts ADP and P_i to ATP and H_2O. Membrane lipids and most of the polypeptides in each of the major complexes have been omitted to facilitate interpretation. Plastiquinones (PQ), plastocyanin (PC) and ferrodoxin (Fd) are mobile and transport electrons as represented by the dashed lines. The function of cytb_3 in PS II is not clear. Adapted from Salisbury and Ross (1991).

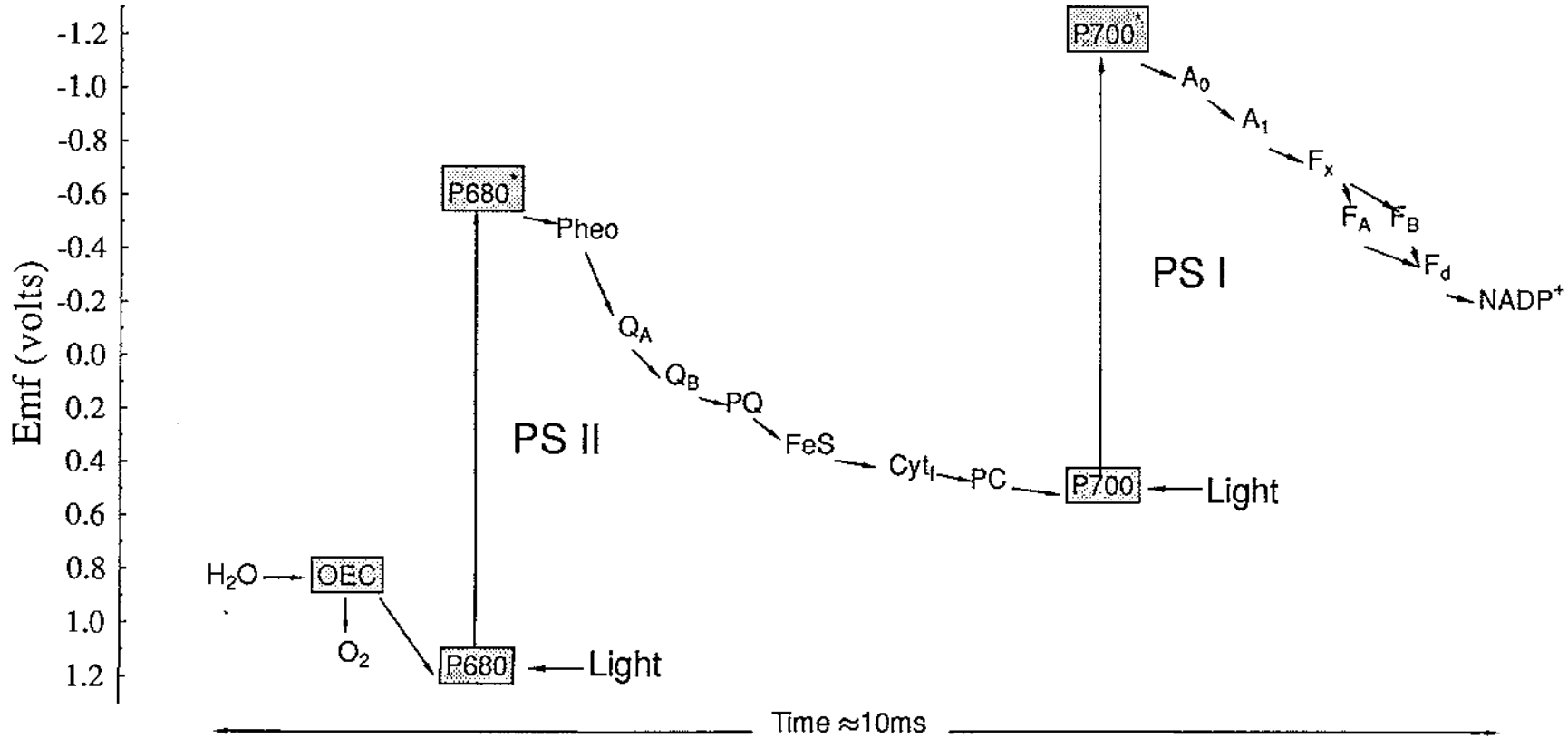


Fig. 5-2. The Z-scheme: pathway of non-cyclic electron transport in chloroplasts. The vertical ordinate represents the standard redox potential of the intermediates as electron flow is from left to right. (Adapted from Govindgee and Eaton-Rye (1986).

represented diagrammatically (and in a more simplified form) in the Z-soriginating from Hill and Bendall (1960) (Fig. 5-2). Each photosystem presents a large number of pigment-rich photon trapping antennae containing approximately 200-400 P-700 chlorophyll molecules. Absorption of a photon in the antennae protein-chlorophyll complex raises a chlorophyll molecule to an excited state (Fig. 5-3). It may dissipate this energy by photochemistry and radiation-less transition (as heat) back to the ground state, or by discharge of the energy as chlorophyll fluorescence. The photon emitted is of a longer wavelength (hence lower energy) than the photon originally absorbed. Photochemistry occurs by the very rapid propagation of photons between adjacent pigment molecules towards a reaction centre where a receptor pigment is reduced, the whole process occurring in less than a nanosecond. Each reaction centre consists of a small number of specialised chlorophyll proteins embedded in the thylakoid membrane and is designed to transfer photons to a primary electron donor (P680). The dimer protein-chlorophyll complex in PS II transfers energy via the electron transport chain to P700, a monomeric protein-chlorophyll complex in PS I. The primary function of PS II is to transfer the electron released in the reaction centre through pheophytin a to the secondary electron plastoquinone (PQ) acceptor (Q_A) through to PS I and also to produce sufficient oxidising power to drive the water oxidation complex. Photosystem II is functioning as a light-driven plastoquinone reductase and may be considered as that part of oxygenic photosynthesis which catalyses the photoinduced transfer of electrons from water to plastoquinione (Hansson and Wydrzynski, 1990). The reducing power is derived from the oxidation of water to molecular oxygen and hydrogen ions. This may be represented in the following reaction:

$$\text{Light(2 photons)} + H_2O + PQ + 2H^+ \rightarrow O_2 + 2H^+ + PQH_2 \quad [5.2]$$

Rapid reduction of the primary electron donor by other components in the reaction centre prevents reversal of this process (Marder and Barber, 1989).

5.1.3 Photoinhibition of photosynthesis

Photoinhibition is characterised by a reduction in the light-saturated rate of photosynthesis in a wide range of plants (Ludlow and Björkman, 1984; Ögren and Öquist, 1984; Öquist, 1986; Demmig and Björkman, 1987; Smillie *et al.*, 1988; Greer, 1990; Greer *et al.*, 1991).

When plants are maintained in an environment favourable to photosynthesis, but with low oxygen and CO_2, the interception of light continues unabated. This results in photoinhibition of photosynthesis similar to a low PFD-adapted plant exposed to high PFD and normal CO_2 (Powles and Critchley, 1981). When carbon fixation is limited the thylakoid membranes are more sensitive to damage by light (Powles and Thorne, 1981). Photoinhibition of photosynthesis is either exacerbated by or coincides with the release of abscisic acid (ABA) from within the chloroplast membrane causing closure of the stomates (Milborrow, 1979). Assimilation of CO_2 is then further restricted by reduced CO_2 and increasing Ph in the stroma is induced by exposure to high light. This is thought to restrict the production of ATP for the fixation of CO_2 (Giersch and Robinson, 1987). Catalase activity is depressed by high PFD which may increase the damaging effects of reactive oxygen species and free radicals produced during photoinhibition (Feierabend and Engel, 1986). When carbon fixation is operating inefficiently, then the normal pathway for energy utilisation will also be impaired.

Photosynthetically competent leaves absorb a high proportion of the incident light to drive the oxygenic photosynthetic electron transport system. Theoretically, eight photons are required to assimilate one CO_2 molecule into carbohydrate (Fork, 1986; Krause, 1988). This theoretical limit is approached at low PFD where the rate of photosynthesis is light-limited and photorespiration is suppressed. Björkman and Demmig (1987) reported average photon yields of 0.106 ± 0.001 O_2.photon^{-1} for a wide range of plants; this corresponds with a requirement of 9.4 moles of photons per mole of CO_2 fixed. As light levels increase, energy transfer from the reaction centres to the site of carbon metabolism continues until the

carbon reduction cycle is operating to maximum capacity and becomes unable to keep pace with the rate of photosynthesis, then oxygen evolution and CO_2 fixation are reduced (Stitt, 1986). Photoinhibition of photosynthesis occurs when an excess of photons over and above that required for light-saturated photosynthesis persists for a prolonged period. The excess in excitation energy depresses photosynthetic electron transport (Powles and Critchley, 1980) and depresses the photon yield of oxygen evolution (Powles *et al.*, 1983; Powles, 1984). Critchley and Smillie (1981) used chlorophyll fluorescence as an indicator of high light stress in cucumber leaves and concluded that the dominant effect was the inactivation of the PS II reaction centre. Using oleander leaves, Powles and Björkman (1982) demonstrated that photoinhibition was caused by inactivation of the photochemistry of PS II with negligible effect on PS I. Ohad *et al.* (1984) showed that *Chlamydomonas* spp. had a light intensity dependent turnover of the 32 kDa Q_B apoprotein and concluded that light causes damage to the Q_B apoprotein. More recently, Jegerschöld *et al.* (1990) suggested that the inactivation of the water-splitting enzyme complex by high light promotes the degradation of the D1 protein in PS II. Ohad *et al.* (1990) reported that the initial steps in photoinhibition could be described as a reversible conformational change in the PS II reaction centre directly affecting the Q_B binding site. This is correlated with reduced electron transport and variable fluorescence and is followed by a second step in which the D1 protein is irreversibly damaged.

Prolonged exposure to excess radiation can produce irreversible damage to the reaction centre and cause pigment degradation. Bleaching of plant pigments may occur by photo-oxidation of carotenoids, chlorophyll (van Hasselt, 1972) and lipids (Wise and Naylor, 1987). Ultra-structural changes may also occur following severe inactivation of the reaction centres (Taylor and Craig, 1971; Wise and Naylor, 1987).

5.1.4 Chlorophyll fluorescence

Energy transferred to the PS II reaction centre may be dissipated in several ways as the excited chlorophyll (P680) returns to the ground state. In relatively low light

and thermal conditions that favour photosynthesis, the majority of the absorbed energy will be utilised for photochemistry and transferred to PS I. As much as 1-3% of the absorbed light energy may be emitted as chlorophyll fluorescence (Schäfer and Björkman, 1989). The minimum or instantaneous fluorescence (Fo), a transitory condition, occurs when the primary electron acceptor in PS II is completely oxidised and optimum electron transport can take place. The fluorescence yield immediately after exposure to light is determined primarily by the redox condition of the primary electron acceptor (Duysens and Sweers, 1963). The maximum fluorescence (Fm) can be determined by blocking electron transport between PS II and PS I with chemical inhibitors (eg DCMU) or by low temperature (77 K) which restricts electron transport, but does not interfere with the primary photochemistry.

The correlation between chlorophyll fluorescence and assimilation was recognised by Müller as early as 1874, but a systematic study of this relationship has only been possible since the development of sensitive light detection equipment (Schreiber, 1983). The characteristic emission of light from dark-adapted leaves at 692 nm when illuminated with a flash of light is known as the Kautsky effect (Kautsky and Hirsch, 1931). The initial or minimum fluorescence (Fo) represents the fluorescence emitted from the bulk chlorophyll when all the reaction centres are active and in an open state. The maximum fluorescence (Fm) is the fluorescence emission that occurs when all the reaction centres are closed. The majority of the fluorescence emission at 692 nm emanates from PS II. The variable fluorescence, Fv, emission does not represent an independent fluorescence component, but rather describes the difference between two states defined for Fo and Fm where Fv = Fm - Fo (Butler and Kitajima, 1975). In isolated chloroplasts the quantity of the energy dissipated as chlorophyll fluorescence was directly related to the photoinhibition. Using the relatively simple low temperature (77 K) fluorescence emission kinetics they proposed that the ratio of variable fluorescence to maximum fluorescence (Fv/Fm) would serve as a valuable estimate of how the photochemistry of the photosystem II reaction centre responded to any stresses imposed on the plant. The ratio Fv/Fm has

become an easily measured and reliable index of the photochemical efficiency of photosystem II in intact leaves. In unstressed leaves the fluorescence ratio (Fv/Fm) is remarkably stable at 0.832 ± 0.004 in a wide range of species (Björkman and Demmig, 1987).

The measurement of fluorescent yield in leaves frozen at 77 K has been the standard method used in chlorophyll fluorescence studies as the primary photochemistry can take place unhindered with relatively simple kinetics, while other biochemical processes (such as electron transport and photosynthesis) are suspended. The measurement of chlorophyll fluorescence at 77 K has been the standard method used in chlorophyll fluorescence studies until the advent of equipment that could resolve the kinetics of fluorescence emission at room temperature (Schreiber *et al.*, 1986).

Chlorophyll fluorescence is now widely recognised as an intrinsic probe of photosynthesis that is useful in the diagnosis and assessment of environmental stress on leaves in photoinhibition studies (Critchley and Smillie, 1981; Fork *et al.*, 1981; Powles and Björkman, 1981). These investigations have been followed by other related reports that demonstrated the effect of high light stress on chlorophyll fluorescence (Powles, 1984; Ludlow and Björkman, 1984; Ögren and Öquist, 1984; Greer *et al.*, 1986; Greer and Laing, 1988 a, b).

In many plants quenching of chlorophyll fluorescence occurs during exposure to high PFD or other environmental stress. This bipartite process has been described by Butler and Kitajima (1975) and Björkman (1987).

Two separate concurrent processes have been identified as taking place, one causing a rise in the instantaneous fluorescence (Fo) and the other causing a general quenching of maximum fluorescence (Fm) (Demmig and Björkman, 1987). The changes in chlorophyll fluorescence taking place may be described in terms of several first-order reactions describing the deactivation of excited

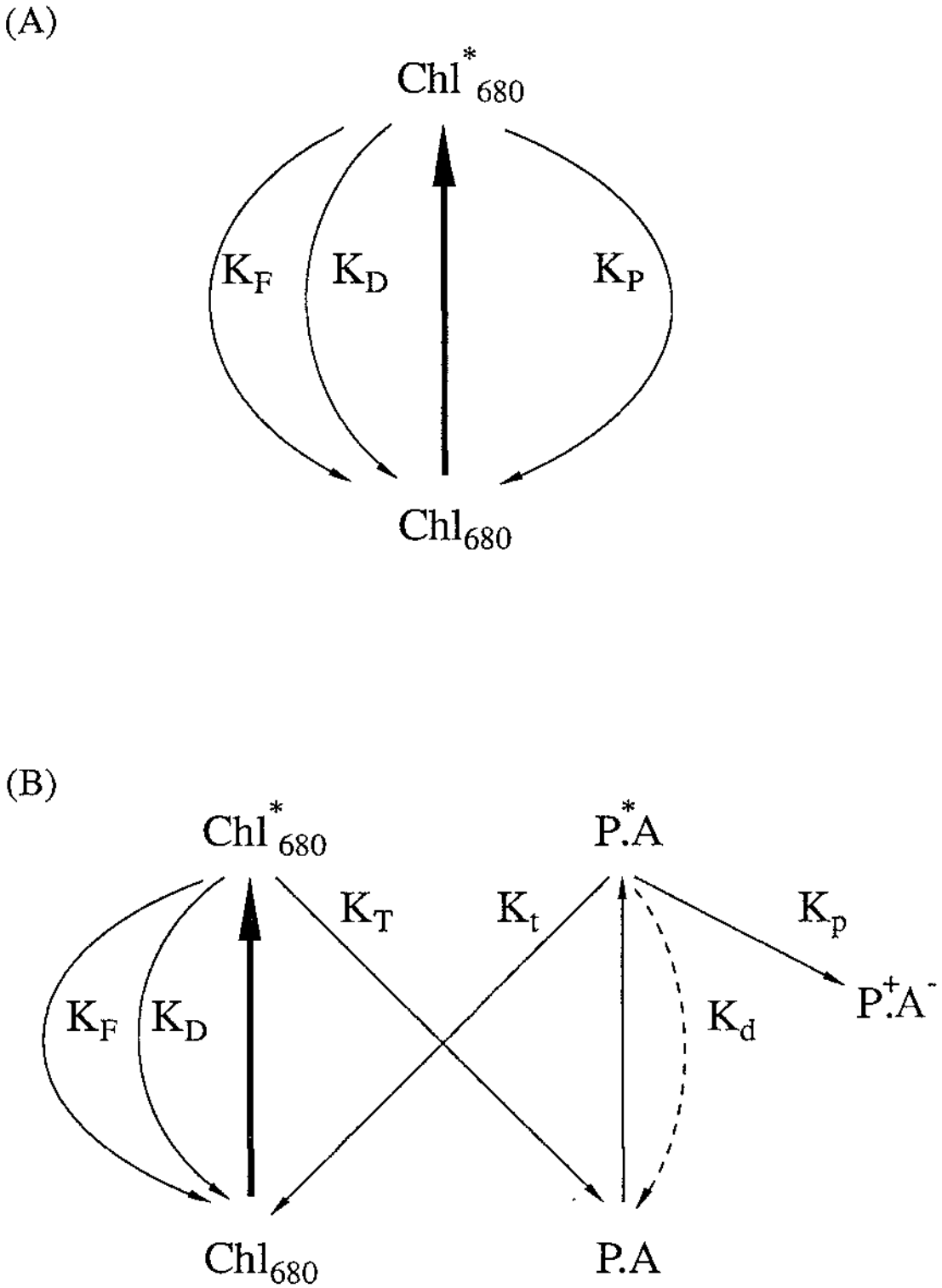


Fig. 5-3. Chlorophyll excitation and rate constants for energy dissipation within the PS II reaction centre, (A) transfer back to the ground state, and (B) transfer to the primary electron acceptor.

chlorophyll and their corresponding rate constants. The fluorescence yield (ϕF) from PS II reaction centres is described by the equation:

$$\phi_F = F/J = K_F \cdot A/(K_F + K_D + K_T + K_P) + K_F \cdot (1-A)/(K_F + K_D + K_T) \qquad [5.3]$$

where F is the emitted fluorescence, J the absorbed photon flux in actinic light and A the fraction of open reaction centre traps. K_F is the rate constant for fluorescence, K_D is the rate constant for non-radiative (thermal) dissipation in the pigment bed. The rate constant K_T represents the rate constant for direct transfer of excitation energy from PS II to PS I, K_P is the rate constant for photochemistry describing electron transport to PS II via Q_A to PS I, and A is the proportion of open reaction centres.

Therefore, at the Fo level where all the reaction centres are open (A=1)

$$\phi_{Fo} = Fo/J = K_F \cdot A/(K_F + K_D + K_T + K_P) \qquad [5.4]$$

and at the Fm level where all the reaction centres are closed (A=0)

$$\phi_{Fm} = Fm/J = K_F/(K_F + K_D + K_T) \qquad [5.5]$$

As the reaction centres are closed then Q_A is reduced and $K_P \rightarrow 0$. The efficiency of the photochemical reactions emanating from PS II (ϕ_{Pc}) is represented by

$$\phi_{Pc} = K_P/(K_F + K_D + K_T + K_P) \qquad [5.6]$$

By rearrangement of Eqns. 5.3, 5.4 and 5.5 it follows that

$$\phi_{Pc} = (\phi_{Fm} - \phi_{Fm})/\phi_{Fm} = Fv/Fm \qquad [5.7]$$

Inactivation of the primary photochemistry in PS II will cause a reduction in the photochemistry rate constant (K_P) and be observed as a minimal effect on Fm, but Fo will increase while exposed to high PFD resulting in a net decrease in

Fv/Fm. Evidence that increased non-radiative dissipation (NRD) was occurring during treatment with high PFD would be reflected in increased K_D with a concurrent reduction in both Fo and Fm (Björkman, 1987; Demmig and Björkman, 1987).

The sensitivity of plants to photoinhibition can depend on their previous history, but is probably most heavily influenced by the current environmental conditions (Greer and Laing, 1989). The effect of growth temperature and growth PFD on photoinhibition have sometimes been confounded (Seemann *et al.*, 1987; and Smillie *et al.*, 1988). This confusing situation prompted Greer and Laing (1987, 1988, 1989; Greer *et al.*, 1988; Greer, 1990) to clarify the effect of environmental factors using a systematic approach.

The interaction between bright light and chilling temperature on the inhibition of photosynthesis has also been investigated in chilling-sensitive (Powles *et al.*, 1983; Greer *et al.*, 1986) and chilling resistant plants (Greer *et al.*, 1991; Strand and Öquist, 1985a,b), but few reports have compared the effect of environment on both chilling-sensitive and chilling-resistant plants simultaneously (Smillie *et al.*, 1988; Hetherington *et al.*, 1989).

5.1.5 Photon yield as an estimate of photoinhibition

Björkman (1987) considered the light-saturated rate of photosynthesis (P_S) and the light-limited rate of photosynthesis (photon yield of oxygen evolution) as a basis for quantification of photoinhibition. The estimates of P_S were highly variable and dependent on other factors such as the previous history of the leaves. In contrast, the photon yield (ϕ_i) determined as the slope of oxygen evolution as a function of incident PFD is highly consistent among a large number of C_3 plants across a wide range of growth environments (Björkman and Demmig, 1987). A modified Clark electrode is used to determine the photon yield of oxygen evolution. Measurements are now routinely performed in a leaf disc-electrode

(LD-2; Hansatech) or similar apparatus (Björkman and Demmig, 1987) using a closely regulated temperature and CO_2-saturated atmosphere to minimise variation between samples and eliminate stomatal limitations that would otherwise lower the estimate of ϕ_i (Delieu and Walker, 1981, 1983).

Björkman and Demmig (1987) demonstrated a linear relationship between photon yield of oxygen evolution and Fv/Fm and its widespread validity across many different genera. This provided a quantitative assessment of the extent of photoinhibition that occurs when plants were subject to higher photon fluxes than could be utilised by photosynthesis. This relationship may not be very robust in some situations and an improved linear relationship has been reported between ϕ_i and Fv (Greer *et al.*, 1988). This may occur where photoinhibition is influencing the primary photochemistry and some step in the electron transport chain (Björkman, 1987). Both Fv and Fv/Fm have been used to estimate the photochemical efficiency of plants when exposed to environmental stress.

5.1.6 Photoinhibition: damage and protection

During prolonged exposure to high PFD's electron transport to PS I and carbon fixation can become progressively impaired. However, photon absorption by the antennae and energy transfer to the reaction centre continues unabated. When PS II is unable to discharge its energy in a productive manner then protective mechanisms that are either regulatory or adaptive must be activated to avoid photoinhibitory inactivation of the primary photochemistry of PS II (Krause, 1988).

Initially, all photoinhibition of photosynthesis was thought to cause some damage within the chloroplasts (Powles and Björkman, 1984). More recent views (Krause, 1988; Gillies and Vidaver, 1990) recognise the importance of protective mechanisms and the reversible nature of the processes originally postulated by Steeman-Nielsen (1949, 1962).

In a review article on photoinhibition of photosynthesis, Krause (1988) reported that the extent of photoinhibition depended upon:

> (1) the physiological condition of the plant linked with the protective and repair mechanisms it possesses to minimise photosynthetic impairment (Greer *et al.*, 1986; Guenther and Melis, 1990).
>
> (2) The current and previous environmental conditions such as PFD, duration and temperature (Greer *et al.* 1988, Greer and Laing, 1988, 1989).

A protective mechanism has been reported depending on non-radiative dissipation (NRD) of energy from PS II as heat in the pigment bed (Björkman and Demmig, 1987). This process may be mediated by the conversion of violaxanthin to zeaxanthin in the xanthophyll cycle (Demmig *et al.*, 1987, 1988; Thayer and Björkman, 1990; Bilger and Björkman, 1990).

5.1.7 Recovery from photoinhibition

The Q_B protein is damaged during the normal course of photosynthesis and must be either repaired or replaced for the reaction centre to remain functional. Light-induced damage to the Q_B protein results in removal from the PS II complex in the thylakoid membrane by a highly efficient membrane-bound protease (Ohad *et al.*, 1985). Guenther and Melis (1990) have postulated the existence of a repair cycle that is consistent with these findings. Recovery from photoinhibition required chloroplast encoded protein synthesis in *Chlamydomonas* sp. More recently the requirement for protein synthesis in higher plants during recovery has been identified in isolated pea chloroplasts (Ohad *et al.*, 1985) and in intact leaves of bean and barley plants (Greer *et al.*, 1986, 1991). The Q_B protein is turned over up to eighty times faster than any other protein in the chloroplast and is proportional to the light intensity (Mattoo *et al.*, 1984). In high light, a large proportion of thylakoid protein synthesis is dedicated to formation of the Q_B protein (Anderson, 1986) and this is reflected in the high level of mRNA transcripts coding for this protein indicating advance preparation for rapid *de novo*

protein synthesis (Arntzen and Pakrasi, 1986). Photoinhibition is occurring when the rate of inactivation of the Q_B protein and removal of the damaged protein exceeds the rate of resynthesis or recovery (Kyle and Ohad, 1986). When the rate of photoinhibition is balanced by the rate of recovery, the breakdown, the *de novo* synthesis of the D1 protein, and the functional restoration of PS II to perform photochemistry are in equilibrium (Ohad *et al.*, 1984; Guenther and Melis, 1990).

Normally the reduction in photochemical efficiency is not permanent, and recovery from photoinhibition will occur rapidly following removal from high light to favourable environmental conditions (Greer and Laing, 1988b).

The recovery process is dependent on both the light and temperature conditions. Recovery proceeds very slowly in the dark (Greer *et al.*, 1986; Le Gouallec *et al.*, 1991), and is light dependent for maximal recovery. Recovery from photoinhibition saturates at a very low PFD between 3.5 - 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and may be completely inhibited at $\geq$ 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Le Gouallec *et al.*, 1991) in a shade-adapted plant and in sun-adapted leaves was very slow at PFD of a 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Greer and Laing, 1988).

The extent of recovery, and the time taken, depend on the extent of photoinhibition and the recovery conditions, in particular temperature (Peeler and Naylor, 1988; Falk *et al.*, 1990). Leaf temperature must be high enough to permit the necessary protein synthesis to take place. Negligible recovery occurs at temperatures below 20 C (Greer, 1988), and the process proceeds more quickly with increasing temperature up to a maximum value near the thermal limit of growth (Burke, 1990).

5.1.8 The effect of temperature on the susceptibility of chilling-sensitive and chilling-resistant plants to photoinhibition.

Plants originating from warm temperate and tropical regions of the world may develop chilling injury when exposed to low temperatures between 10 and 15 C (Smillie *et al.*, 1988). Prolonged exposure to chilling stress results in reduced plant growth (Lyons, 1973). This is reflected in metabolic impairment often caused by the altered stability of cell membranes (Musser *et al.*, 1984). However, the interaction of light and temperature on the growth of chilling-sensitive plants is recognised as a more important source of injury than chilling in the dark, and is manifested as a low temperature-induced light impairment of the primary photochemistry of PS II (Greer, 1990; Smillie *et al.*, 1988). Any damage that results from chilling stress may be reversible if the stress is relieved soon enough. However, if the stress is prolonged, then severe and irreversible photoinhibition will usually result in photo-oxidative destruction of chlorophyll and plant organelles (Taylor and Craig, 1971; van Hasselt and van Berlo, 1980; Bongi and Long, 1987).

The interaction between chilling and photoinhibition of photosynthesis in bright light has been examined in many plants known to be intolerant to chilling stress. In contrast, there have been limited photoinhibition studies of chilling-tolerant plants or comparisons between chilling-sensitive and chilling-intolerant plants (Hetherington *et al.*, 1989).

Furthermore, many environmental factors including temperature and light interact to exacerbate photoinhibition. Surprisingly, Powles (1984) in his review commented on the effect of current leaf temperature on photoinhibition of photosynthesis, without considering the historical effect of temperature on photoinhibition. Nevertheless, there is a growing body of evidence indicating that low growth temperature for spinach (Garber, 1977), kiwifruit (Greer and Laing, 1989), maize (Greer and Hardacre, 1989), green algae (Falk *et al.*, 1990) and in

a range of other species (Smillie *et al.*, 1988) reduced the predisposition of these plants to photoinhibition.

Despite the numerous research that has been conducted to study the effect of growth temperature and light on plants there is still a lack of information on this subject.

This study was therefore designed to investigate the effects of growth temperature and leaf temperature on the sensitivity of Epipremnum (chilling-sensitive) and Fatshedera (chilling-resistant) plants to bright light and subsequent recovery from photoinhibition.

5.2 Materials and Methods

5.2.1 Plant material

Stock plants of *Epipremnum aureum* and X *Fatshedera lizei* were greenhouse-grown and propagated as described in the Materials and Methods section of Chapter three.

5.2.2 Growth environment

Both species were grown in two CE rooms at 20 ± 0.5 C and 30 ± 0.5 C constant temperature. The respective water vapour pressure deficits (VPD) in each room were 5.0 and 5.1 ± 0.5 kPa. Lighting was provided by a water screened array of four 1 Kw high pressure discharge "Metalarc" lamps and four 1 Kw tungsten halogen lamps (GTE Sylvania, Drummondville, Que, Canada). A 12 h photoperiod with an average PFD of 370 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the top of the Fatshedera plants was used in each CE room. Epipremnum plants in each temperature treatment were screened by a green polypropylene shade cloth (Sarlon-Reid, Auckland, N.Z.) to reduce the PFD to an average of 136 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the top

of the plants. A lower PFD was used for Epipremnum because earlier tests had shown that at higher PFDs Epipremnum developed chlorophyll bleaching and phot-oxidative damage in the variegated leaves. To facilitate sampling, the photoperiod in both CE rooms was extended by 2 h with six 150 W incandescent lamps (GTE Sylvania, Drummondville, Que, Canada) that preceded the use of the high PFD lamps each day (Warrington *et al.*, 1978; Greer and Laing, 1988a).

Only fully-expanded leaves that had developed in the CE rooms were used for experimental studies. Leaves developed approximately normal to the incident light. The temperature and light treatments investigated with Epipremnum and Fatshedera in this chapter are represented schematically (Fig. 5-4).

5.2.3 Photoinhibition treatments

Photoinhibitory treatments were applied to attached fully-expanded leaves (usually the fourth to sixth visible leaf from the apex) sealed in a 240 mm diam. temperature regulated gas-exchange chamber as described by Greer *et al.*, (1988) and exposed to a PFD of ≈1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from a 1 Kw high pressure discharge "Metalarc" lamp (Plate 5-1). Leaf temperature was maintained constant at 10, 15, 20, 25 and 30 ± 0.5 C within the leaf chamber (Plate 5-2).

Additional experiments investigated the effects of chilling at 10 C in the dark, of PFD and the effects of leaf age on chlorophyll fluorescence.

The CO_2 partial pressure was monitored (but not controlled), using an infra-red gas analyser (Binos; Leybold Heraeus, G.m.b.H., Hanau, Germany.) in an open gas-exchange system and was 395 ± 7 Kpa. The O_2 partial pressure and VPD were approximately 21 Kpa and 9.2 ± 1.0 Kpa, respectively. The VPD was monitored by a dew-point hygrometer (110DP; General Eastern, Watertown, Mass., USA.) During photosynthetic measurements, the remainder of the plant was at ≈25 C and a PFD of ≈100 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

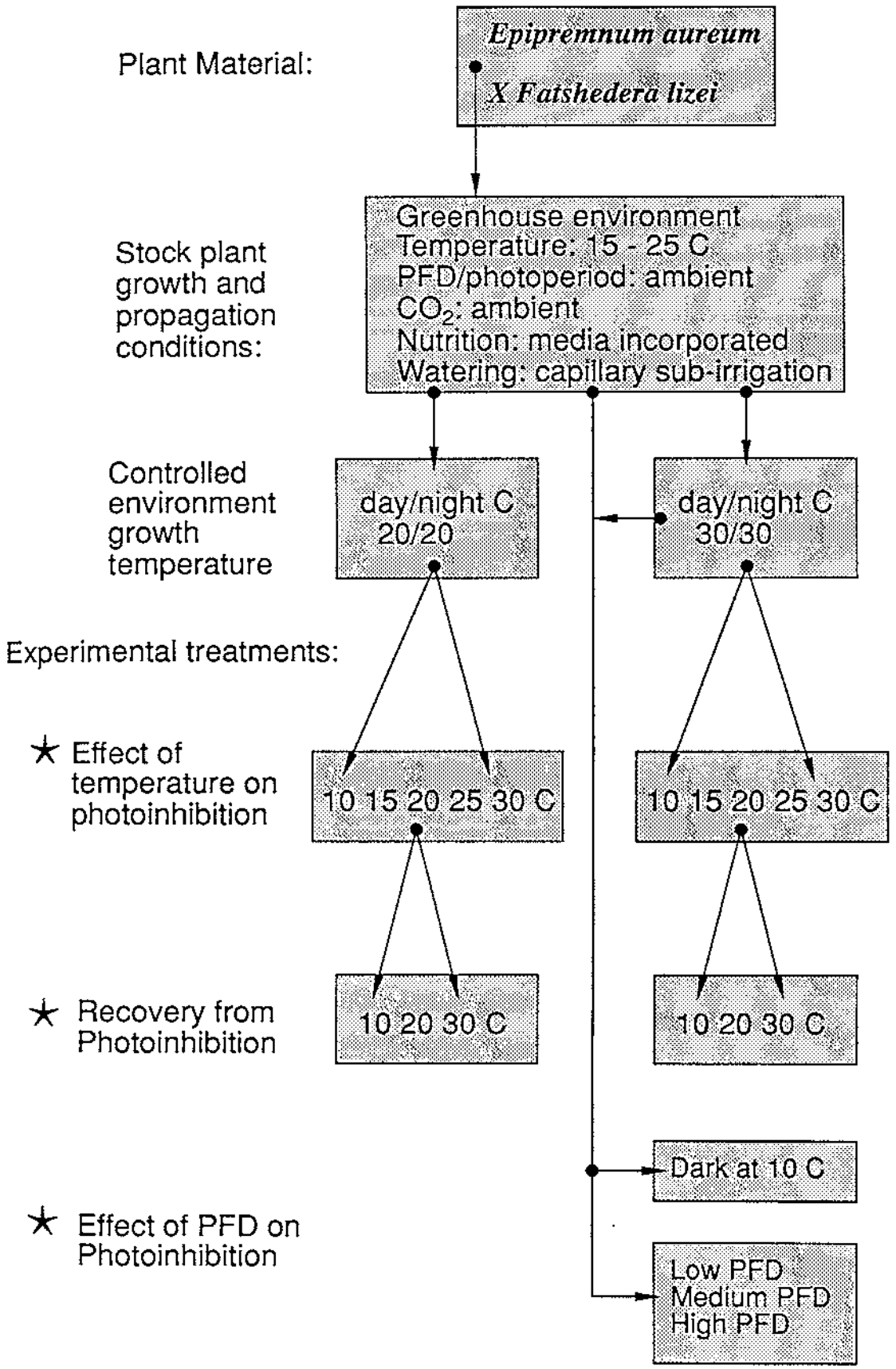


Fig. 5-4. Schematic representation of photoinhibition and recovery treatments used in Chapter five.

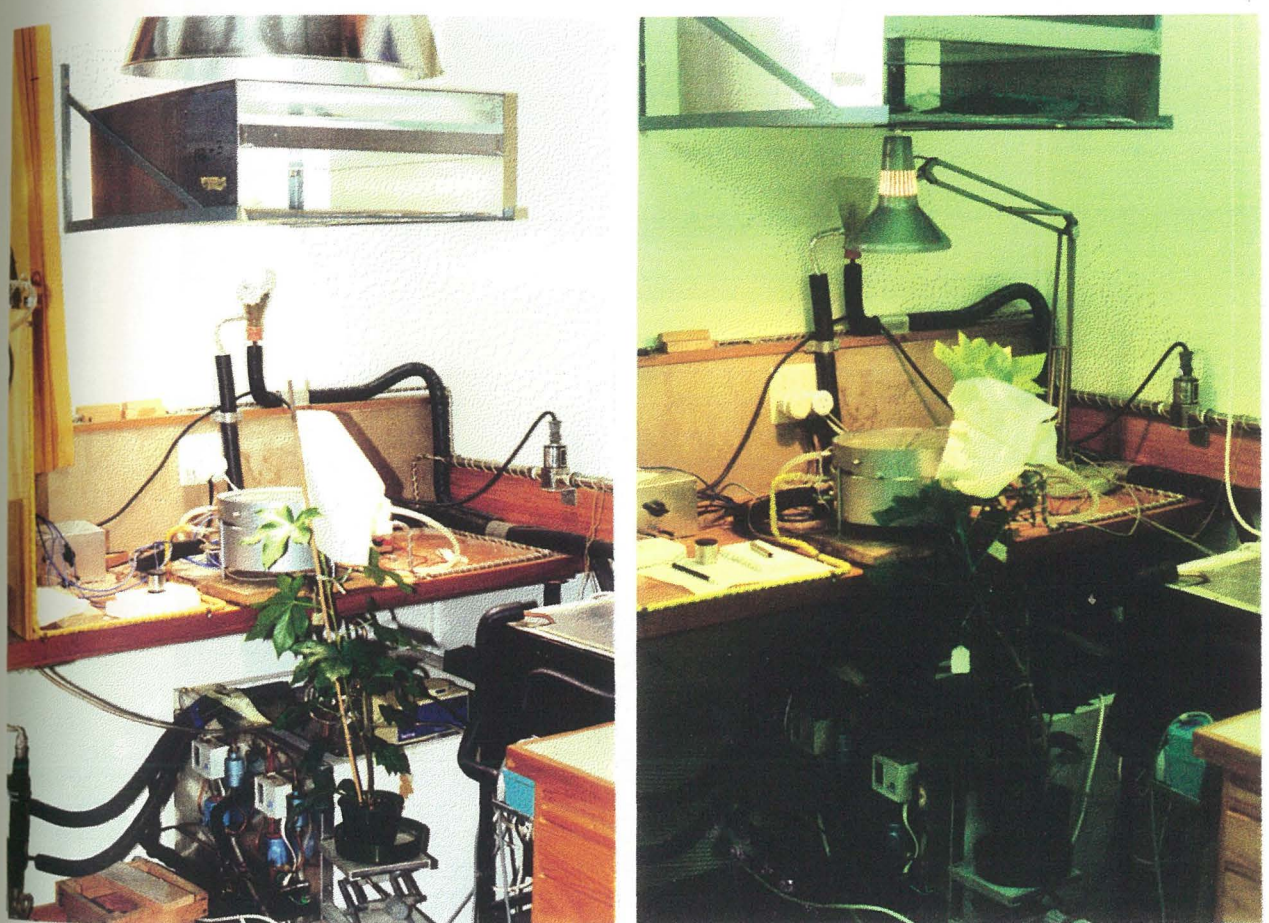


Plate 5-1. Lighting-rig used to expose leaves enclosed in the temperature-controlled leaf chamber to high PFD during photoinhibition (left photo) and to low PFD during recovery from photoinhibition (right photo).

Plate 5-2a A Fatshedera leaf was enclosed in the temperature-controlled leaf chamber while the upper portion of the shoot was shielded during induction of photoinhibition at high PFD (upper photo). Chlorophyll fluorescence during photoinhibition and recovery was measured in dark-acclimated leaves in a light-proof-box at 77 K. The signals detected by a photomultiplier were transmitted to the chart recorder (lower photo).

occurred at a range of treatment temperatures, the protocol employed did not allow acclimation of leaves to the assessment temperature (Bennett *et al.*, 1982), but was consistent with the procedures used for photoinhibition by other workers (Björkman *et al.*, 1978; Greer *et al.*, 1989).

5.2.4 Recovery treatments

After a standard photoinhibitory treatment of a 300 min exposure at 20 C and a PFD of ≈1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, recovery in intact leaves at a PFD of ≈20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (from a 40 W incandescent lamp) and at a range of constant leaf temperatures of 10, 20 or 30 ± 0.5 C was followed.

5.2.5 Photoinhibition and recovery assays

Net CO_2 fixation was monitored continuously throughout the high light treatment employing functions described by von Caemmerer and Farquahar (1981) and (W. A. Laing (pers. comm. 1990). During each photoinhibition and recovery experiment, 2-3 leaf discs (10 mm diam.) were punched randomly from the leaf at fixed intervals (0, 30, 60, 90, 150, 200, 300 and 450 min) throughout the experiment. Samples were stored on moist filter paper (in petri dishes) in the dark at room temperature (≈25 C) for at least 20 min to ensure the photosynthetic reaction centres and Q_A, the primary electron acceptor, were all fully oxidised (Ögren and Öquist, 1984; Björkman, 1987) before chlorophyll fluorescence was assessed.

Chlorophyll fluorescence at 77 K (Powles and Björkman, 1982) was then measured in the apparatus described by Greer *et al.* (1986, 1988). Leaf samples were transferred in low light to a pedestal in an insulated cup and kept in complete darkness for at least 4 min before freezing in liquid nitrogen. After a 1 min delay to allow cooling to 77 K, chlorophyll fluorescence was excited with

weak (0.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ blue actinic light (480 nm) transmitted to the sample by a fibre-optic cable and an optically-polished quartz glass rod. Kinetics of fluorescence emission at 692 nm were measured using a potentiometric chart recorder (Linseis Co., Princeton, NJ, USA) to observe the instantaneous fluorescence (Fo) and the maximum fluorescence (Fm) measured at least 2 min after exposure to saturating light on the chart recorder trace (Fig. 5-12). The variable fluorescence (Fv = Fm - Fo) and the fluorescence ratio (Fv/Fm) were calculated from corrected values of Fo and Fm. All data were normalised to Fm = 100 prior to photoinhibition as described by Björkman (1987) to eliminate optical differences between individual leaves.

At intervals of 0, 150 and 450 min, a 10 cm^2 leaf disc was punched from the leaf to measure the photon yield of O_2 evolution on an incident light basis (Delieu and Walker, 1981; 1983). Light-limited photosynthetic oxygen evolution was quantified in a leaf disc-type oxygen electrode unit (LD2; Hansatech, Kings Lynn, UK.) maintained at 25 C, ≈4% CO_2, 20-23% O_2 and at several constant PFDs between 0 and 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The photon yield was determined from the initial slope of the light-limited rate of photosynthetic oxygen evolution as a function of PFD.

During growth at 20 or 30 C, prior to photoinhibition treatments photosynthetic characteristics were quantified on leaves from intact plants at 20 C. Net rate of photosynthesis (Ps) was measured after approximately 1 h at a PFD of 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ using the leaf chamber described above. The PFD was altered by interposing neutral density metal screens between the light source and the leaf chamber. Ps was monitored continuously and the PFD held constant until the rate was stable over at least a 15 min period. Dark CO_2 efflux was measured after induction of photosynthesis. Each experiment was repeated three times for Fatshedera and twice for Epipremnum.

At the conclusion of the experiments the following data were collected: shoot growth, leaf number, leaf area, leaf thickness and specific leaf area .

5.2.6 Data analysis

The net photosynthesis versus PFD plots and the light saturated photosynthetic rate were calculated from a least squares fit of the data to the hyperbolic tan function (Jassby and Platt, 1976; Laing *et al.*, 1989):

$$Ps = Psm \times \tanh (\phi_{app} \times PFD/Psm) - R_d \qquad [5.8]$$

where Ps = photosynthetic rate at any given PFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$), Psm = light saturated photosynthesis ($\mu mol \cdot m^{-2} \cdot s^{-1}$), ϕ_{app} = apparent photon yield of oxygen evolution ($mol \cdot mol^{-1}$), PFD = photon flux density ($\mu mol \cdot m^{-2} \cdot s^{-1}$) and R_d = dark respiration ($\mu mol[CO_2] \cdot m^{-2} \cdot s^{-1}$) at 20 C.

Photoinhibition and recovery were measured by changes in Fo, Fv, Fv/Fm and ϕ_i. In Epipremnum and Fatshedera leaves the relationship between the photon yield of oxygen evolution (ϕ_i) and fluorescence ratio (Fv/Fm) or variable fluorescence (Fv) were essentially linear (Fig. 5-5). This resulted in modest correlations between photon yield and Fv or Fv/Fm (r^2 = 0.65 or 0.55, respectively). Data from both species were combined as the regression lines for each species were coincident (P = 0.001).

The slopes of linear regression lines fitted to data for ϕ_i and Fv/Fm or Fv were not significantly different between each other, or between each species. In spite of the marginally better fit for the Fv data, the linearity of the relationship between ϕ_i and Fv/Fm data indicated this was a valid method of quantifying changes in chlorophyll fluorescence in both Epipremnum and Fatshedera leaves. The bipartite model of the photochemical apparatus was assumed (Butler, 1978) and used to interpret the influence of environmental factors on the low temperature (77 K) fluorescence parameters.

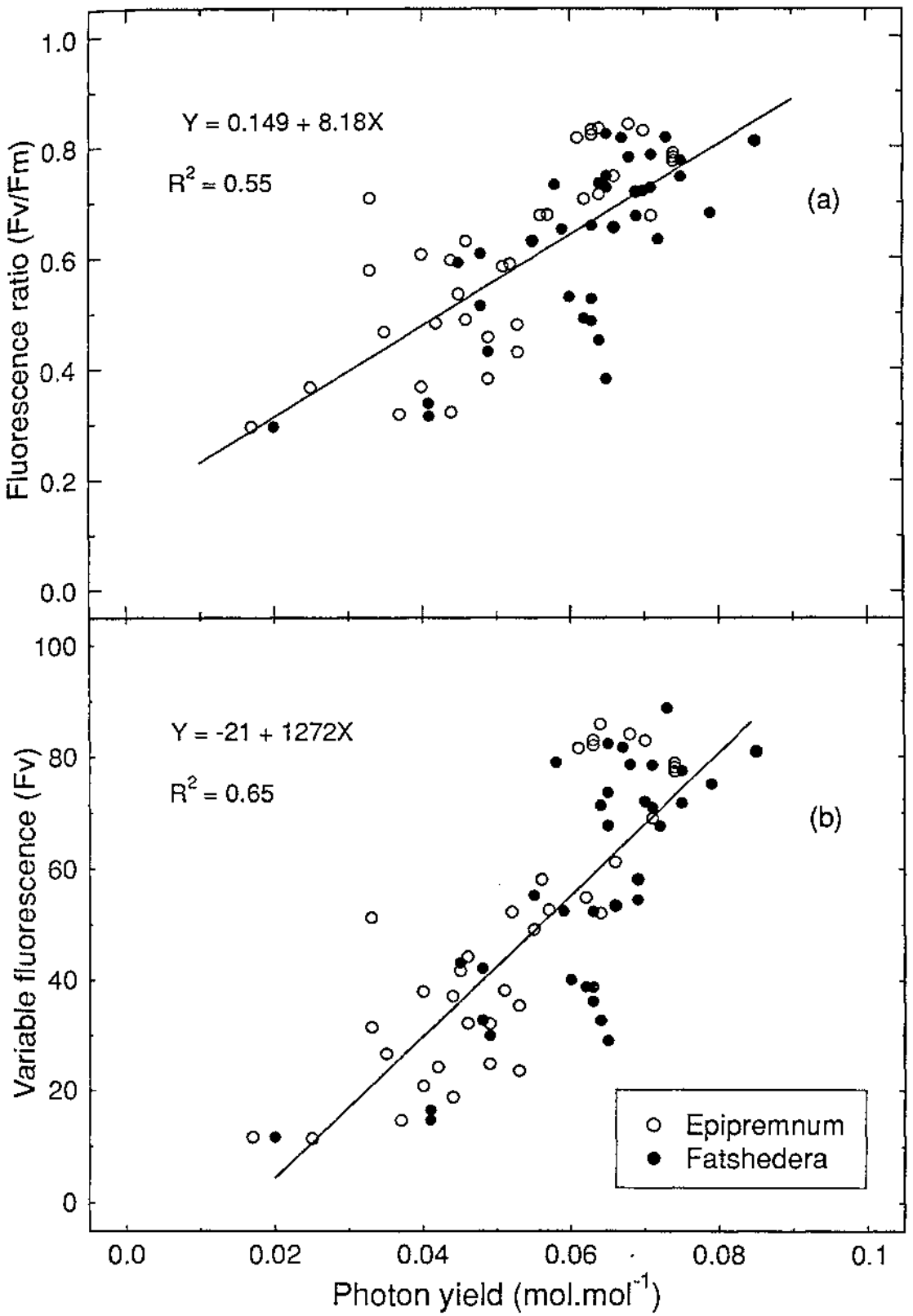


Fig. 5-5. The relationship between the photon yield of oxygen evolution (mol[O_2].mol[photons]$^{-1}$) and (a) the fluorescence ratio (Fv/Fm) or (b) the variable fluorescence (Fv) during exposure of Epipremnum and Fatshedera leaves to photoinhibition at a PFD of 1200 μmol.m^{-2}.s^{-1} and leaf temperatures between 15 and 30 C. Solid lines were fitted using least squares regression.

The data for Fv/Fm and Fo were fitted with an exponential equation using a least significant squares non-linear regression analysis and asymptotic standard errors calculated for a first order kinetic model (Bard, 1974, Greer and Laing, 1988); viz.,

$$F_t = F_\infty - (F_\infty - F_i)e^{-kt} \qquad [5.9]$$

The extent of photoinhibition and recovery were calculated from the following relationships:

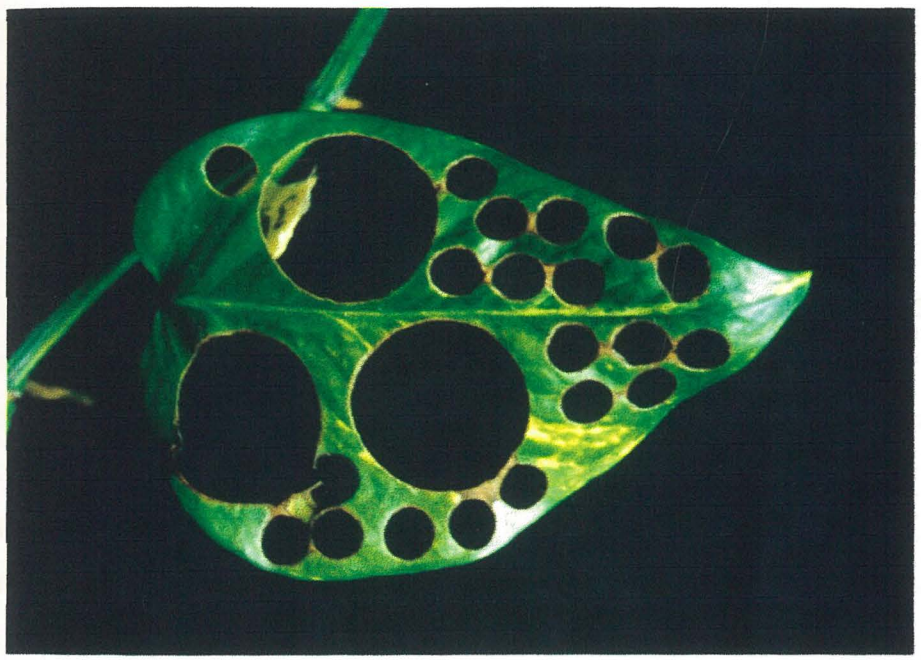
$$\% \text{ photoinhibition} = 1-(F_\infty/F_i) \qquad [5.10]$$

$$\% \text{ recovery} = (F_\infty - F_i)/(F_c - F_i) \qquad [5.11]$$

Where: F_t is the chlorophyll fluorescence at any time (t) during photoinhibition or recovery. $F_i = F_t$ at $t = 0$; $F_\infty = F$ or ϕ_i at $t = \infty$; $F_c = F$ prior to photoinhibition (= control value) and k = the first order rate constant.

5.2.7 Chlorophyll analysis

Leaf discs used for photon yield of oxygen evolution measurements were later frozen at -70 C to arrest chlorophyll degradation in storage. Chlorophylls were extracted using the method described by Moran (1982) and Porra *et al.* (1989). Frozen leaf discs (1.0 cm^2) were extracted in 20 ml of N,N'-dimethylformamide at 0 C for four days in complete darkness. Re-extraction of leaves in the solvent did not elute any further chlorophylls. Absorbance spectra were measured with a Hitachi L2000 scanning spectrophotometer calibrated with a user baseline using a 0.2 nm bandwidth measuring beam. Absorbance peaks were measured at 663.8 and 646.8 nm, then corrected for turbidity by subtracting the absorbance at 750 nm. Chlorophyll a + b and chlorophyll a:b ratio were determined using extinction coefficients developed by Porra *et al.* (1989).



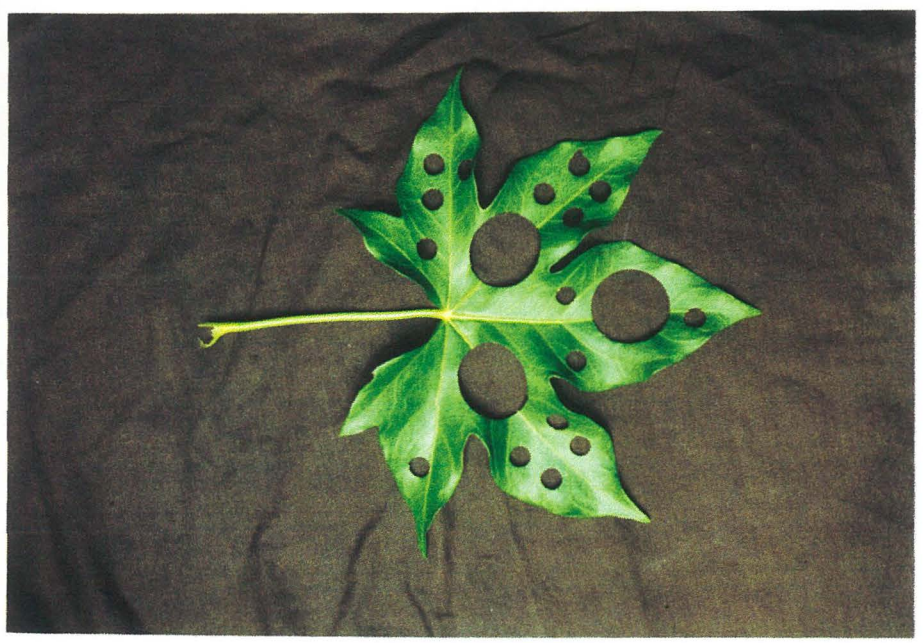


Plate 5-2b. Typical Epipremnum (upper photo) and Fatshedera (lower photo) leaves after sampling for chlorophyll fluorescence and chlorophyll concentration.

5.2.8 Electron and light microscope section preparation

Leaf discs were cut transversely into 0.5-1 mm sections in primary fixative (3% glutaraldehyde and 2% formaldehyde in 0.1M phosphate buffered to Ph 7.2). The methodology employed was similar to Spiers and Hopcroft (1992). Specimens were vacuum infiltrated for 5 min. The fixative was replaced and specimens kept at room temperature for up to 12 h. Secondary fixation in buffered 1% OsO_4 was preceded by a brief phosphate buffer wash. Specimens were dehydrated in an acetone series and infiltrated in two steps with Polarbed '812' acrylic resin, then cured at 60 C for 48 h. Light microscope sections (1 μm) were cut with an ultramicrotome and stained with phosphate-buffered toluidine blue. Thin sections (90-100 nm) were also cut with an ultramicrotome, and attached to copper specimen grids prior to double staining in saturated uranyl acetate followed by lead citrate. Thin sections of each specimen were examined with a Philips 11201C transmission electron microscope.

5.3 Results

5.3.1 Growth data after 14 weeks

There were significant differences in the vegetative growth of each species at each growth temperature over the 14 week growth period (Table 5.1). Epipremnum plants produced shoot growth of 848 mm and 1864 mm at 20 and 30 C, respectively. Leaf production was significantly higher at 30 C (26.2) compared with 20 C (8.6). There was no significant difference in the thickness of leaves developed (0.42 mm) at either growth temperature. Similarly there was no difference in the average leaf area for the 10 most recently expanded leaves (100 cm^2), or the stem diameter (9.8 mm) produced at either growth temperature. The specific leaf area increased significantly from 168 to 259 $cm^2 \cdot g^{-1}$ with increasing growth temperature.

Leaves developed at 30 C contained significantly less chlorophyll than leaves from the lower growth temperature (Table 5.2), this is reflected in the development of fewer functional chloroplasts (Plate 5-3) and markedly more chlorophyll-deficient tissue in leaves (Plate 5-4).

In contrast to Epipremnum, Fatshedera shoots grew most rapidly at 20 C, producing 847 mm extension growth compared with 628 mm at 30 C. The average leaf area of the expanded leaves in Fatshedera plants was significantly larger at 157 $cm^2 \cdot leaf^{-1}$ at 20 C than 122 $cm^2 \cdot leaf^{-1}$ at 30 C. Leaf production at 20 and 30 C was 26 and 20, respectively during the 14 week growth period. Leaves produced at 30 C were 0.44 mm thick, approximately 1.6 times thicker than the 0.28 mm when grown at 20 C. Transverse sections of the thicker leaves from the higher growth temperature showed that they usually had three palisade layers instead of two (Plate 5-5). The higher total chlorophyll concentration in Fatshedera grown at 30 C relative to 20 C (Table 5.2) is reflected in the darker

Table 5.1 Plant growth characteristics: shoot length, mean leaf area, number of leaves per plant, laminar thickness, specific leaf area ratio and stem diameter of Epipremnum and Fatshedera after 14 weeks at 20 or 30 C. (Mean ± s.e.; n=12)

Species	Growth temperature (C)	Shoot length (mm)	Mean leaf area per leaf (cm^2)	Number of leaves per plant	Laminar thickness (mm)	Specific leaf area ($cm^2.g^{-1}$)	Stem diameter (mm)
Epipremnum	20	847 ± 21	100.2 ± 3.6	8.6 ± 0.2	0.42 ± 0.01	167.5 ± 5.7	10.1 ± 0.2
		(+220)	(+1)	(+305)	(0)	(+35)	(-6)
	30	1864 ± 106	101.4 ± 3.3	26.2 ± 0.3	0.42 ± 0.01	258.9 ± 4.7	9.5 ± 0.4
Fatshedera	20	848 ± 21	156.7 ± 11.6	26.3 ± 0.5	0.28 ± 0.01	147.8 ± 5.6	9.8 ± 0.6
		(-26)	(-22)	(-24)	(+157)	(-36)	(-8)
	30	628 ± 18	121.6 ± 8.4	20.0 ± 0.4	0.44 ± 0.01	94.1 ± 3.5	9.0 ± 0.2

Numbers in parentheses represent % change in each characteristic at a growth temperature of 30 C compared to 20 C.

Table 5.2 Effect of growth temperature on chlorophyll a, chlorophyll b, total chlorophyll, the a/b chlorophyll ratio and chlorophyll per unit leaf dry weight in Epipremnum and Fatshedera leaves.

Species	Growth Temperature (C)	Chlorophyll a concn. ($nmol \cdot m^{-2}$)	Chlorophyll b concn. ($nmol \cdot m^{-2}$)	Total Chlorophyll ($nmol \cdot m^{-2}$)	Chlorophyll ratio a/b	Chlorophyll /leaf dw[z] ($nmol \cdot g^{-1}$)
Epipremnum[y]	20[w]	35.7a	15.9a	51.7a	2.31b	8.65
	30[v]	22.4b	6.5c	28.9c	3.43a	7.47
Fatshedera[x]	20[v]	27.2b	9.2bc	36.4bc	2.99a	5.38
	30[v]	29.9b	12.5ab	42.4ab	2.44b	4.00

Means in columns separated by different letters are significantly different ($P \leq 0.01$)

[z] based on mean leaf dry weight
[y] Leaves developed at PFD 135 $\mu mol \cdot m^{-2} \cdot s^{-1}$
[x] Leaves developed at PFD 370 $\mu mol \cdot m^{-2} \cdot s^{-1}$
[w] n=4, [v]n=3 replicates

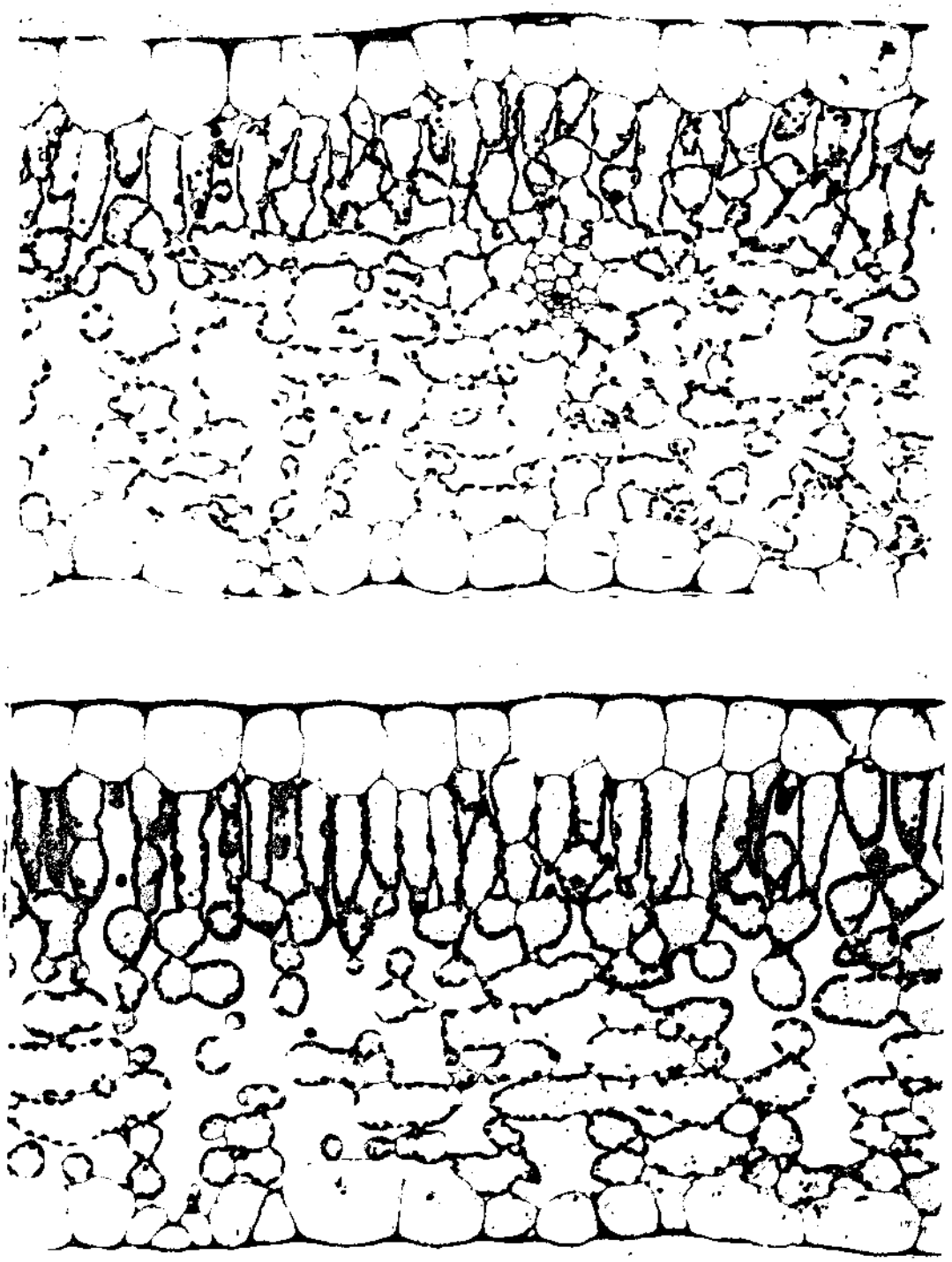


Plate 5-3. Transverse sections of Epipremnum leaves developed at 20 C (upper photo) and 30 C (lower photo). Sections were about 1 µm thick and stained with toluidine blue. (Magnification ca. 200 x).

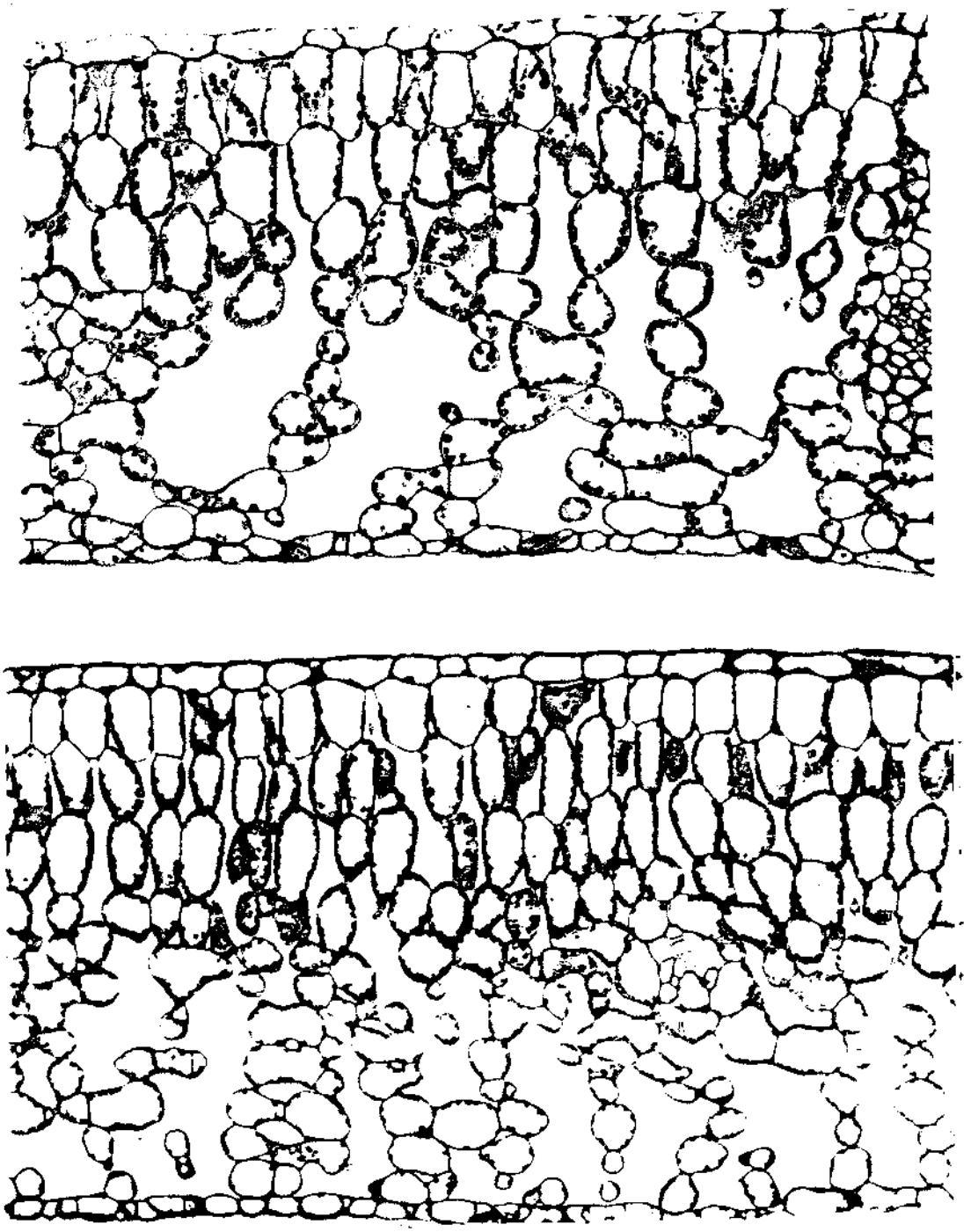


Plate 5-4. Transverse sections of Fatshedera leaves developed at 20 C (upper photo) and 30 C (lower photo). Sections were about 1 µm thick and stained with toluidine blue. (Magnification of upper and lower photos, ca. 300 and 200 x, respectively).

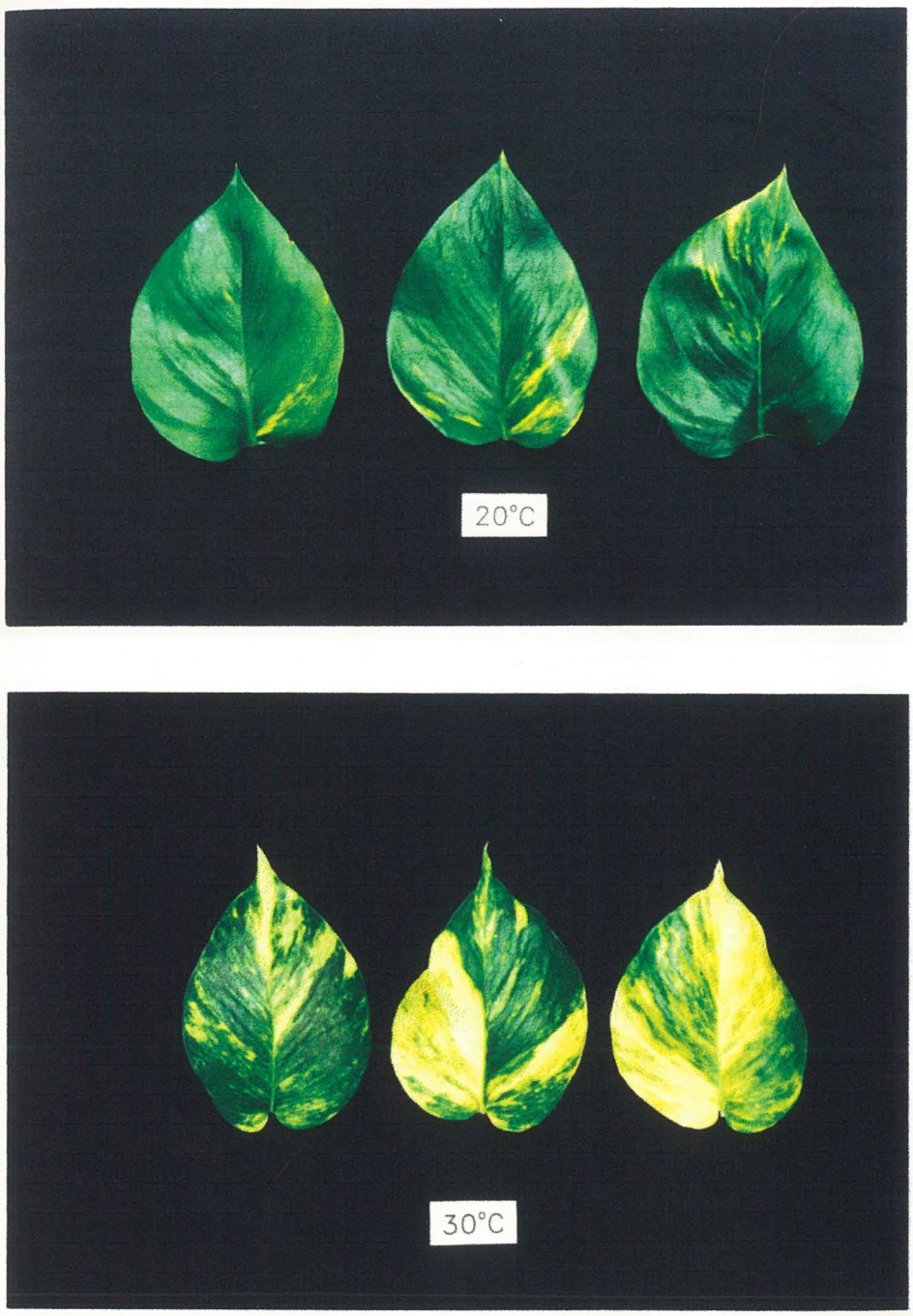


Plate 5-5. Epipremnum leaves developed at 20 C (upper photo) and 30 C (lower photo). (Number height = 1 cm)

Plate 5-6. Fatshedera leaves developed at 20 C (upper photo) and 30 C (lower photo) (Number height = 1 cm)

green appearance of these leaves (Plate 5-6). In comparison to Epipremnum, the specific leaf area of Fatshedera leaves decreased significantly from 148 to 94 $cm^2 \cdot g^{-1}$ with increasing growth temperature. Stem diameter of Fatshedera plants was significantly larger at 9.8 mm when developed at 30 C compared with 9.0 mm at 20 C.

5.3.2 Photosynthetic characteristics measured at 20 C.

5.3.2.1 Response of photosynthesis to PFD.

In Epipremnum and Fatshedera leaves developed at 20 C, markedly higher rates of net photosynthesis occurred compared with leaves developed at 30 C. However, in both temperature regimes (20 and 30 C, respectively) maximum photosynthetic rates in the Epipremnum leaves were 11.5 and 6.8 $\mu mol[CO_2] \cdot m^{-2} \cdot s^{-1}$ (Fig. 5-6). In Fatshedera net photosynthetic rates were higher, at 16.9 and 12.5 $\mu mol[CO_2] \cdot m^{-2} \cdot s^{-1}$, than in Epipremnum (Fig. 5-7).

The apparent photon yield of oxygen evolution (ϕ_{app}) represents the photochemical efficiency of leaves (i.e., the slope of the light response curve in the light-limited portion of the response curve in ambient CO_2). In Epipremnum leaves ϕ_{app} was markedly different at 20 C (0.037) compared with 30 C (0.030 $mol[CO_2] \cdot mol[photons]^{-1}$). In contrast, in Fatshedera leaves ϕ_{app} was between 0.045 and 0.047 $mol[CO_2] \cdot mol[photons]^{-1}$ (Table 5.3).

The light saturation points of both species at 20 C occurred at a PFD between 800 and 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Epipremnum and Fatshedera, respectively). In contrast at 30 C the light saturation point occurred at PFDs of 650 and 750 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively (Table 5.3).

Light compensation points (derived from the fitted function based on Eqn.[5.8]) in Epipremnum leaves developed at 20 and 30 C were 27 and 33 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. In contrast, in Fatshedera leaves there was no effect of growth

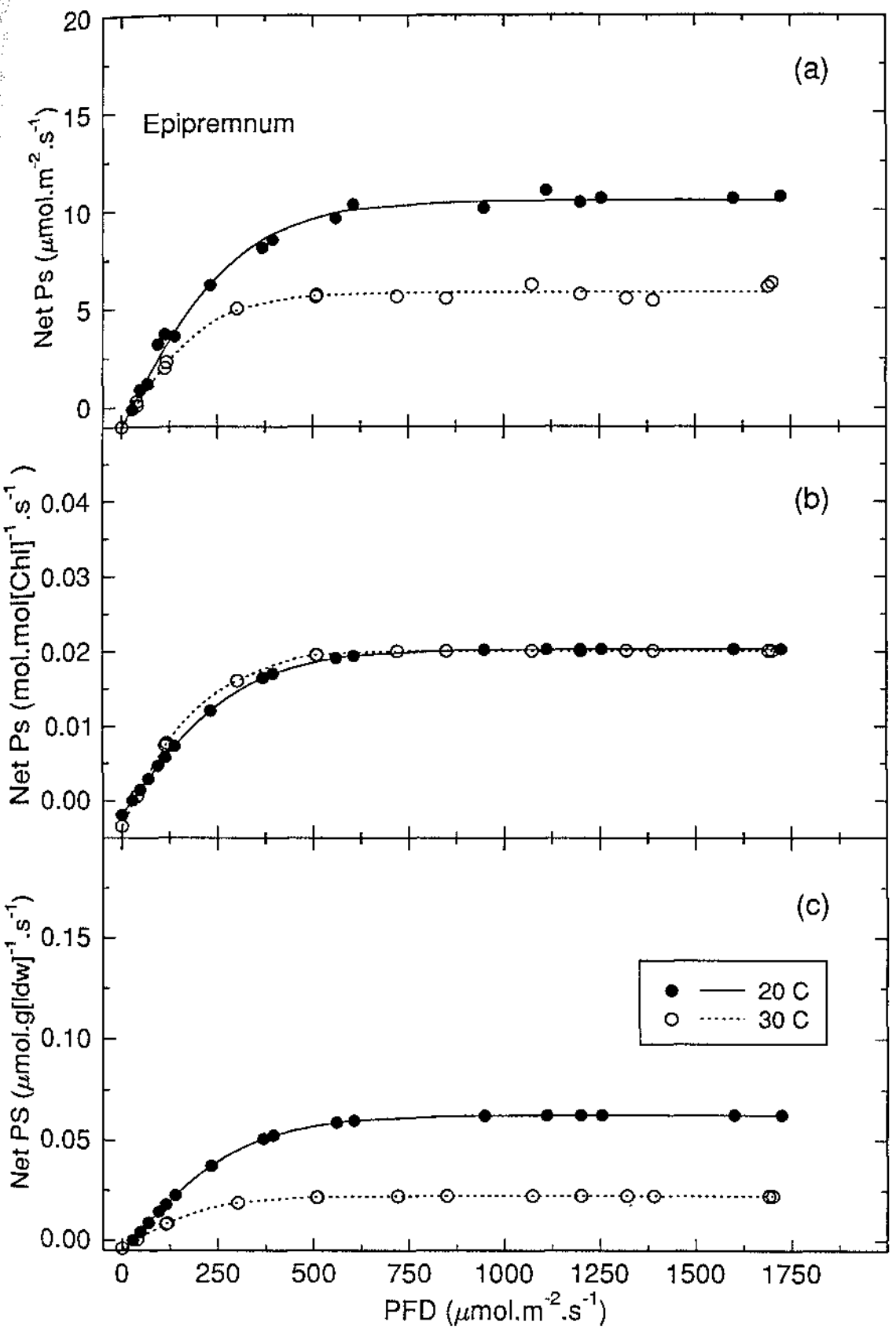


Fig. 5-6. Photosynthetic light response curves measured at 20 C for Epipremnum leaves developed at 20 C and 30 C expressed on the basis of net CO_2 fixed (a) per unit leaf area, (b) per unit of chlorophyll and (c) per unit leaf dry weight. Solid and dotted lines were the best fit to the mean of 2 or 3 leaves using the hyperbolic tan function Eqn.[5.8].

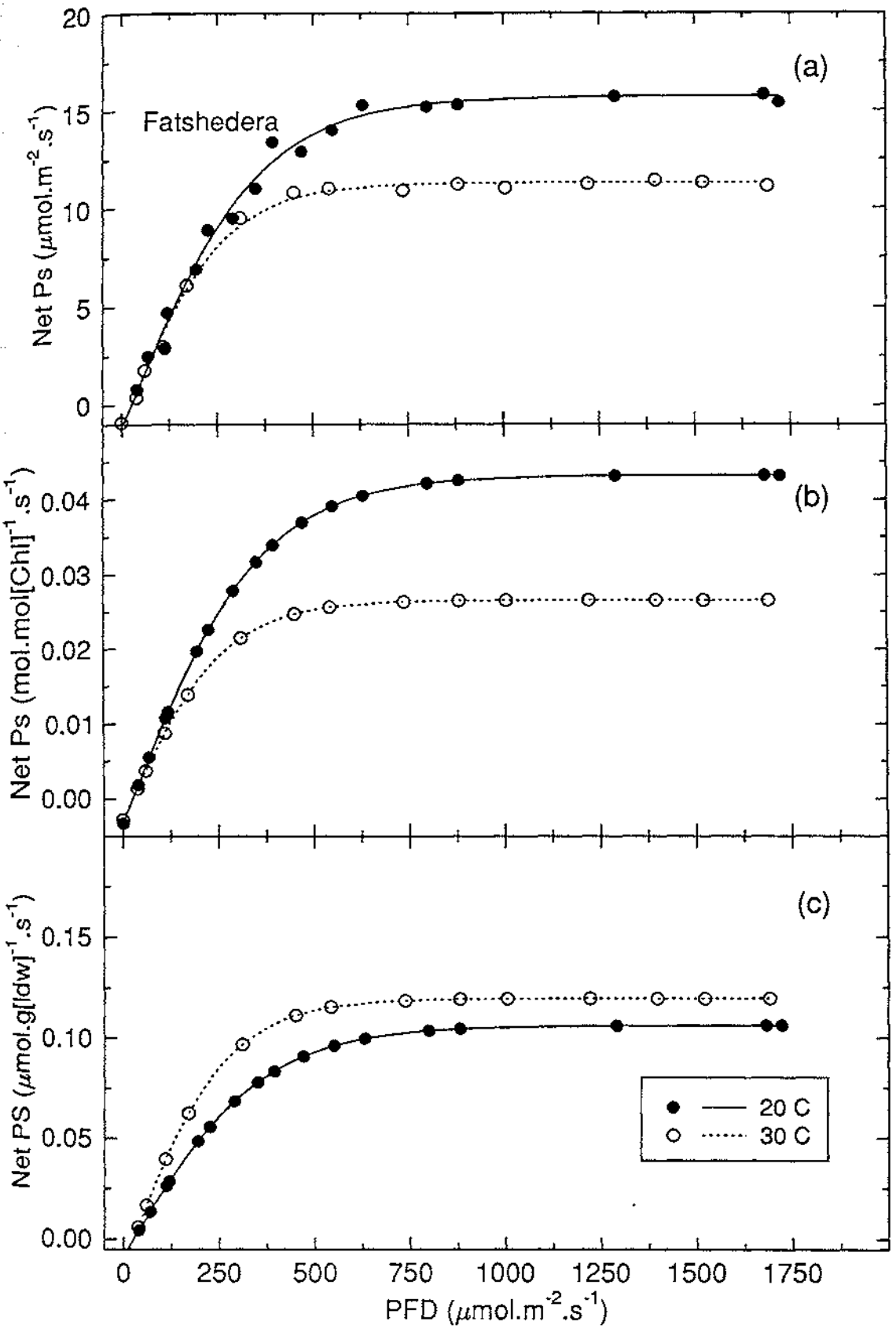


Fig. 5-7. Photosynthetic light response curves measured at 20 C for Fatshedera leaves developed at 20 C and 30 C expressed on the basis of net CO_2 fixed (a) per unit leaf area, (b) per unit of chlorophyll and (c) per unit leaf dry weight. Solid and dotted lines were the best fit to the mean of 2 or 3 leaves using the hyperbolic tan function Eqn.[5.8].

Table 5.3 Effect of growth temperature on maximum rate of photosynthesis, apparent photon yield, PFD saturation point and PFD compensation point of Epipremnum and Fatshedera leaves measured at 20 C. (means ± s.e.; n=3)

Species	Growth Temperature (C)	Photosynthetic criteria			
		Ps(max)[z]	Apparent photon yield (ϕ_{app})[y]	PFD 95% saturation point[z]	PFD compensation point[z]
Epipremnum[x]	20	11.5 ± 0.2	0.037 ± .001	800	27
	30	6.8 ± 0.1	0.030 ± .002	650	33
Fatshedera[w]	20	16.9 ± 0.6	0.047 ± .003	1000	25
	30	12.5 ± 0.1	0.045 ± .002	750	25

[z] $\mu mol[CO_2] \cdot m^{-2} \cdot s^{-1}$ up to PFD 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$
[y] $mol[CO_2] \cdot mol[photons]^{-1}$
[x] Leaves developed at PFD 135 $\mu mol \cdot m^{-2} \cdot s^{-1}$
[w] Leaves developed at PFD 370 $\mu mol \cdot m^{-2} \cdot s^{-1}$

temperature; the light compensation point occurred at a PFD of 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Table 5.3).

Chlorophyll (a, b and total) concentrations in Epipremnum leaves were significantly higher ($P \leq 0.05$) at 20 C than those in Fatshedera (Table 5.2). However, at 30 C the reverse occurred. The chlorophyll a/b ratio in Epipremnum developed at 20 C was lower than that in Fatshedera, but higher than Fatshedera at 30 C. Chlorophyll concentration per unit of leaf dry weight was 73% higher in Epipremnum than in Fatshedera leaves at both growth temperatures. In both species the chlorophyll concentration was 16 and 35% lower, respectively, at 30 C than 20 C (Table 5.2).

Photosynthetic light responses of Epipremnum leaves expressed on the basis of CO_2 fixation per unit of leaf chlorophyll converged to a common maximum rate of 0.02 $mol[CO_2] \cdot mol[chl]^{-1} \cdot s^{-1}$ (Fig. 5-6b) irrespective of the growth temperature. In contrast, at 20 C in Fatshedera leaves the maximum rate of photosynthesis was 0.046 $mol[CO_2] \cdot mol[chl]^{-1} \cdot s^{-1}$ whereas at 30 C the maximum rate was 0.029 $mol[CO_2] \cdot mol[chl]^{-1} \cdot s^{-1}$ (Fig. 5-7b).

On a dry weight basis, the photosynthetic light responses of Epipremnum leaves were lower than those of Fatshedera in both temperature regimes (20 and 30 C). The rate of photosynthesis in Epipremnum at 20 C was higher (0.06 $\mu mol[CO_2] \cdot g[leaf\ dw]\text{-}1 \cdot s^{-1}$) than at 30 C (0.02 $\mu mol[CO_2] \cdot g[leaf\ dw]\text{-}1 \cdot s^{-1}$) (Fig. 5-6c). The opposite was observed in Fatshedera where maximum rates were 0.12 and 0.15 $\mu mol[CO_2] \cdot g[leaf\ dw]\text{-}1 \cdot s^{-1}$ in leaves grown at 20 and 30 C, respectively (Fig. 5-7c).

5.3.2.2 Response of photosynthesis during photoinhibition to leaf temperature.

Epipremnum had a generally flatter response of photosynthesis to temperature, irrespective of the growth conditions; compared with Fatshedera it had a

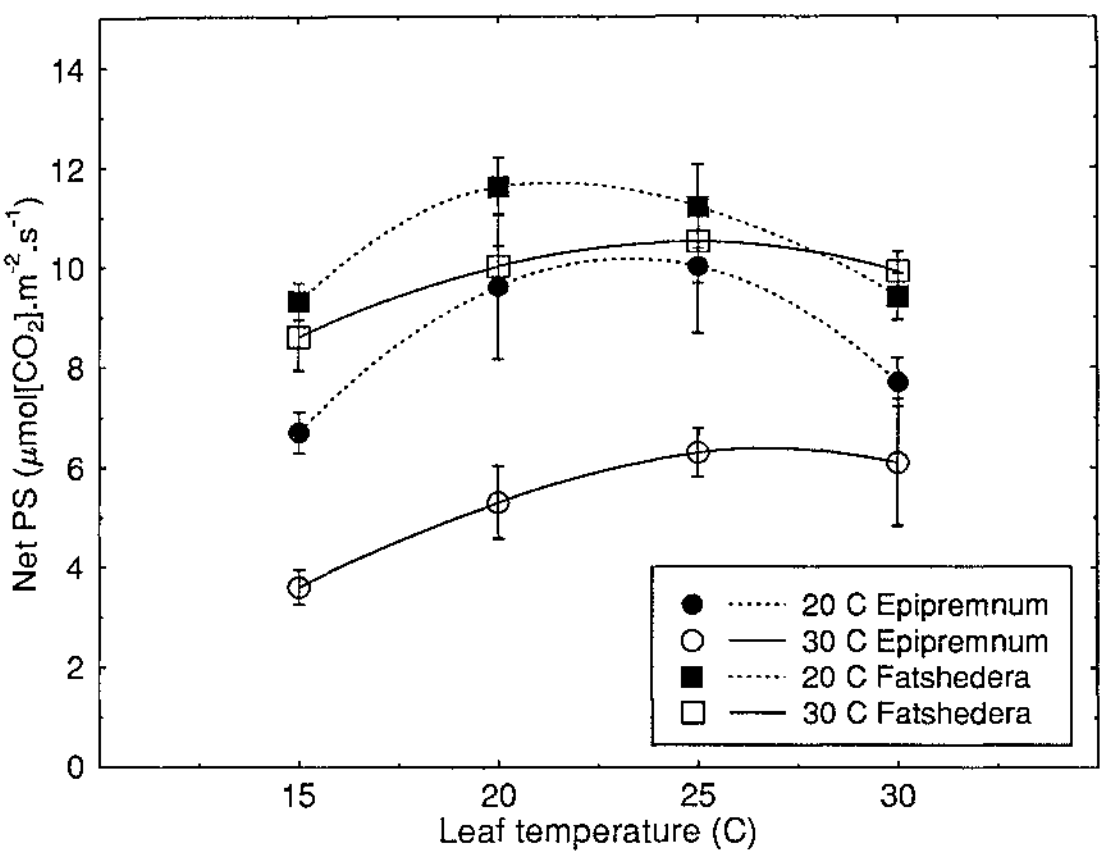


Fig. 5-8. Effect of leaf temperature on maximum rate of light saturated photosynthesis during photoinhibition treatments at PFD of 1200 μmol.m^{-2}.s^{-1} in attached Epipremnum and Fatshedera leaves as influenced by growth temperature. Vertical bars represent standard errors (n=3).

Table 5.4 The control values of 77 K chlorophyll fluorescence characteristics of photon yield for oxygen evolution on an incident photon basis (ϕ_i) and the derived constant for non-radiative dissipation (K_D) for the upper leaf surface of Epipremnum and Fatshedera leaves grown at 20 or 30 C. Data were collected at the end of 12 h dark period. (Fo, Fm, Fv and K_D are reported in relative units).

Species	Growth temperature (C)	Fo	Fm	Fv	Fv/Fm	ϕ_i (mol·mol^{-1})	K_D
Epipremnum	20	9.1±0.2	43.5±0.6	34.4±0.6	0.789 ± 0.005	0.069± 0.002	20.4
		(-15)	(+5)	(+10)	(+5)	(-4)	(+24)
	30	7.7±0.2	45.6±0.9	38.2±0.8	0.830 ± 0.003	0.066± 0.001	15.4
Fatshedera	20	10.6±0.2	44.4±0.9	33.7±0.9	0.767 ± 0.006	0.070± 0.001	22.3
		(-16)	(+5)	(+11)	(+5)	(<1)	(+20)
	30	8.9±0.3	46.7±0.6	37.9±0.6	0.809 ± 0.006	0.070± 0.003	17.9
LSD (P≤0.05)		0.54	2.20	2.12	0.015	0.013	

Numbers in parentheses represent % difference between parameters for leaves grown at 30 compared with those at 20 C. (Mean ± s.e.; n = 12)

pronounced optimum temperature for photosynthesis. The net photosynthetic rate in plants developed at 20 C were markedly higher than at 30 C (Fig. 5-8). Maximum rates of photosynthesis (during photoinhibition treatments) for Epipremnum grown at 20 C and 30 C were 10.0 and 6.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. The Ps maxima occurred at about 25 and 27 C in plants grown at the low and high growth temperature, respectively. In contrast, the maximum rate of photosynthesis for Fatshedera grown at 20 and 30 C were higher than in Epipremnum (12.1 and 10.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and occurred at about 22 and 24 C, respectively (Fig. 5-8).

5.3.3 Control values for chlorophyll fluorescence and photon yield characteristics of Epipremnum and Fatshedera leaves.

5.3.3.1 Epipremnum

The instantaneous chlorophyll fluorescence (Fo) measured at 77 K in dark-acclimated Epipremnum leaves depended on the growth temperature. In leaves developed at 20 C, Fo was 9.1 (relative units) while at 30 C Fo was 15% lower (7.7) (Table 5.4). In contrast, the maximum fluorescence (Fm) increased by 5% with increasing growth temperature from 43.5 at 20 C to 45.6 at 30 C. Similarly, the variable fluorescence (Fv), increased by 10% from 34.4 to 38.2. The fluorescence ratio (Fv/Fm) at 20 C was 0.789 and at 30 C was 0.830, the difference corresponding to a 5% increase with the increase in growth temperature. The mean photon yield of oxygen evolution (ϕ^{i}) was higher (0.069) at the lower growth temperature compared with 0.066 at 30 C. The constant for non-radiative dissipation (K_D) at 20 C was 20.4, while at 30 C it was 24% lower at 15.4.

5.3.3.2 Fatshedera

The control chlorophyll fluorescence parameters for Fatshedera leaves, like Epipremnum, were influenced by growth temperature. The initial chlorophyll fluorescence (Fo) in Fatshedera leaves developed at 20 C and 30 was 10.6 and 8.9, respectively (Table 5.4).

Maximum fluorescence (Fm) increased by 5% with increasing growth temperature from 44.4 at 20 C to 46.7 at 30 C. Similarly, Fv increased by 11% from 33.7 at 20 C and 37.9 at 30 C, respectively. The fluorescence ratio increased in a parallel manner to Fm, being 0.767 at 20 C and 0.809 at 30 C. Growth temperature did not influence the photon yield in Fatshedera (0.070) while in Epipremnum leaves it was marginally (4%) lower at the higher growth temperature.

The non-radiative dissipation (K_D) in Fatshedera leaves developed at 20 C was 22.3 and at 30 C was lower at 17.9.

No significant differences in dark respiration rates within each species were found for leaves from either growth temperature. In contrast, higher dark respiration rates occurred in Fatshedera (1.88 ± 0.17) compared with 1.33 ± 0.17 $\mu mol[CO_2]\cdot m^{-2}\cdot s^{-1}$ in Epipremnum. The control values for chlorophyll fluorescence reported here indicate that Epipremnum and Fatshedera exhibit a similar underlying response to growth temperature.

5.3.3.3 Effect of leaf age on chlorophyll fluorescence.

The influence of leaf age on chlorophyll fluorescence characteristics of leaves was investigated to determine its significance on the management of subsequent experiments. In Epipremnum leaves from nodes 2-7 (numbered basipetally from the first expanding leaf visible in the apex) Fo fell by 5% for each successively

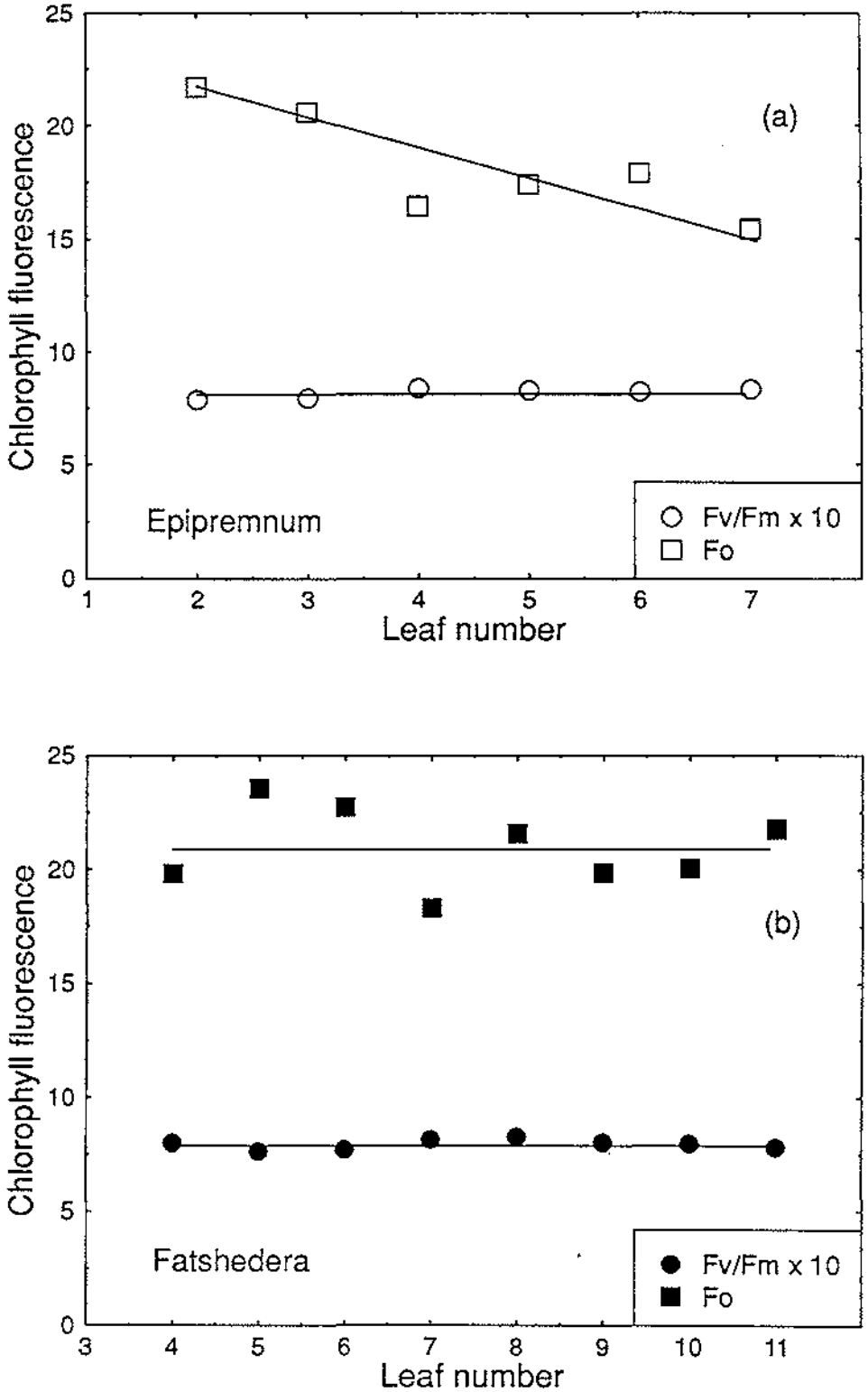


Fig. 5-9. Influence of leaf position from the apex on the instantaneous chlorophyll fluorescence (Fo) and chlorophyll fluorescence ratio (Fv/Fm) in (a) Epipremnum and (b) Fatshedera. Fitted lines were the best fit of 2 or 3 leaves for each data point.

older leaf sampled, whereas Fv/Fm was constant over the range of leaf ages investigated (Fig. 5-9a). In contrast, in Fatshedera leaves no systematic changes in Fo or Fv/Fm occurred with increasing leaf age over nodes 4-11 (numbered as for Epipremnum) (Fig. 5-9b).

These findings suggest that the instantaneous fluorescence, Fo in Epipremnum leaves was influenced by leaf age more than Fatshedera whereas in both species Fv/Fm remained stable during ontogenetic development. The most recently fully-expanded leaves available in each species were used for all further experimentation.

5.3.4 Effect of PFD on net photosynthesis.

After induction of photosynthesis following a dark period, net photosynthesis declined steadily during the standard exposure treatment of intact leaves to a PFD of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Figs. 5-10, 5-11). The decrease in photosynthetic rate at 20 C over time was slightly curvilinear and this coincided with the reduction in photon yield in both species. Mean reductions in photosynthesis at 20 C were 54% and 71% for intact Epipremnum leaves developed at 20 and 30 C, respectively (Fig. 5-10). In similar experiments with intact Fatshedera leaves, the photosynthetic rate decreased by 42% and 49% for leaves developed at 20 and 30 C, respectively (Fig. 5-11).

The inhibition of photosynthesis was more severe in leaves developed at 30 C compared with 20 C. The inhibition of photosynthesis was also more severe in Epipremnum leaves than in Fatshedera leaves for each growth temperature and for all of the current leaf temperatures (15 to 30 C) investigated. These results suggest Epipremnum leaves may be more sensitive to photoinhibition of photosynthesis than Fatshedera leaves.

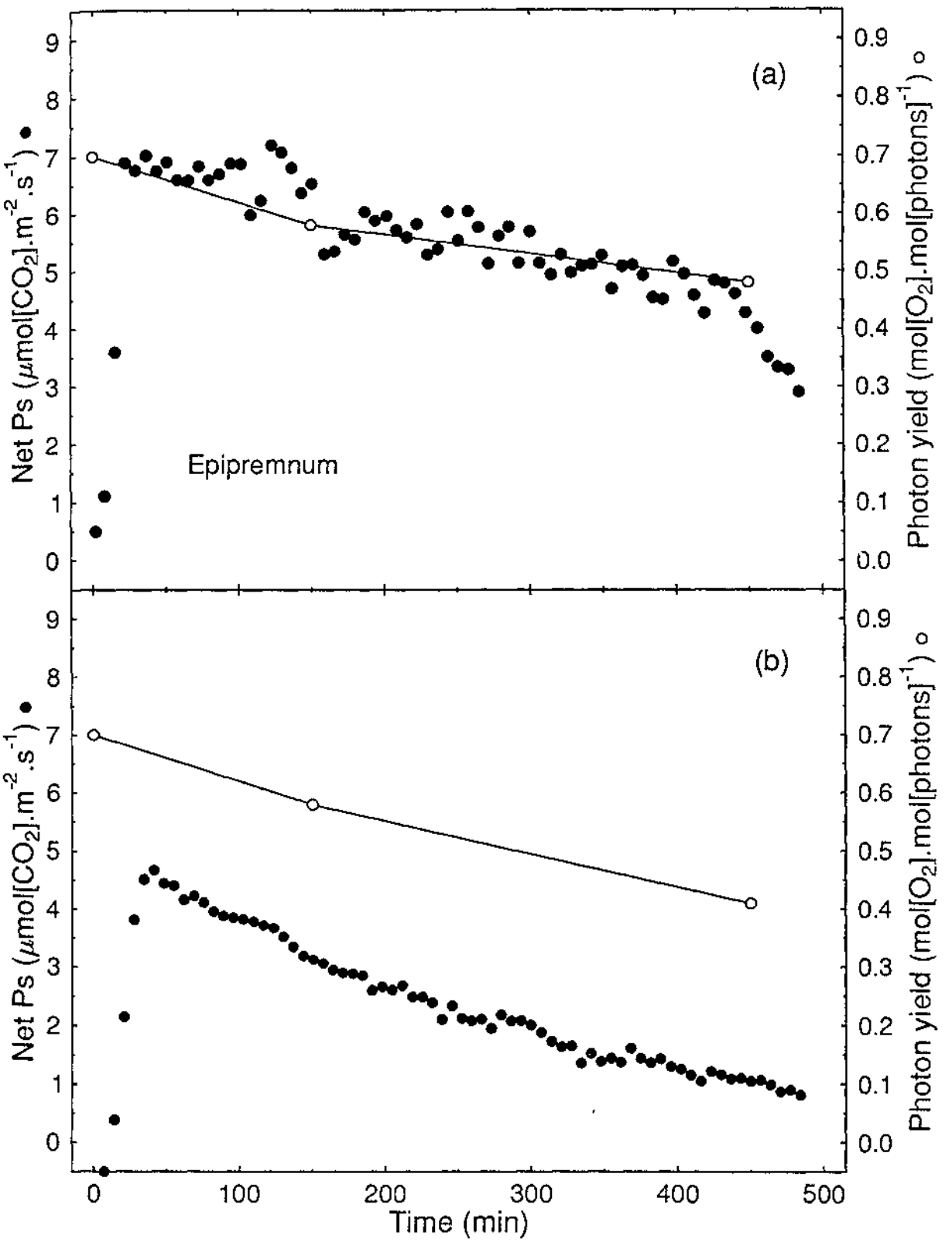


Fig. 5-10. Time course of reduction in net photosynthesis and photon yield in Epipremnum leaves measured at 20 C and exposed to PFD of 1200 μmol.m^{-2}.s^{-1} as influenced by growth temperature (a) 20 C and (b) 30 C.

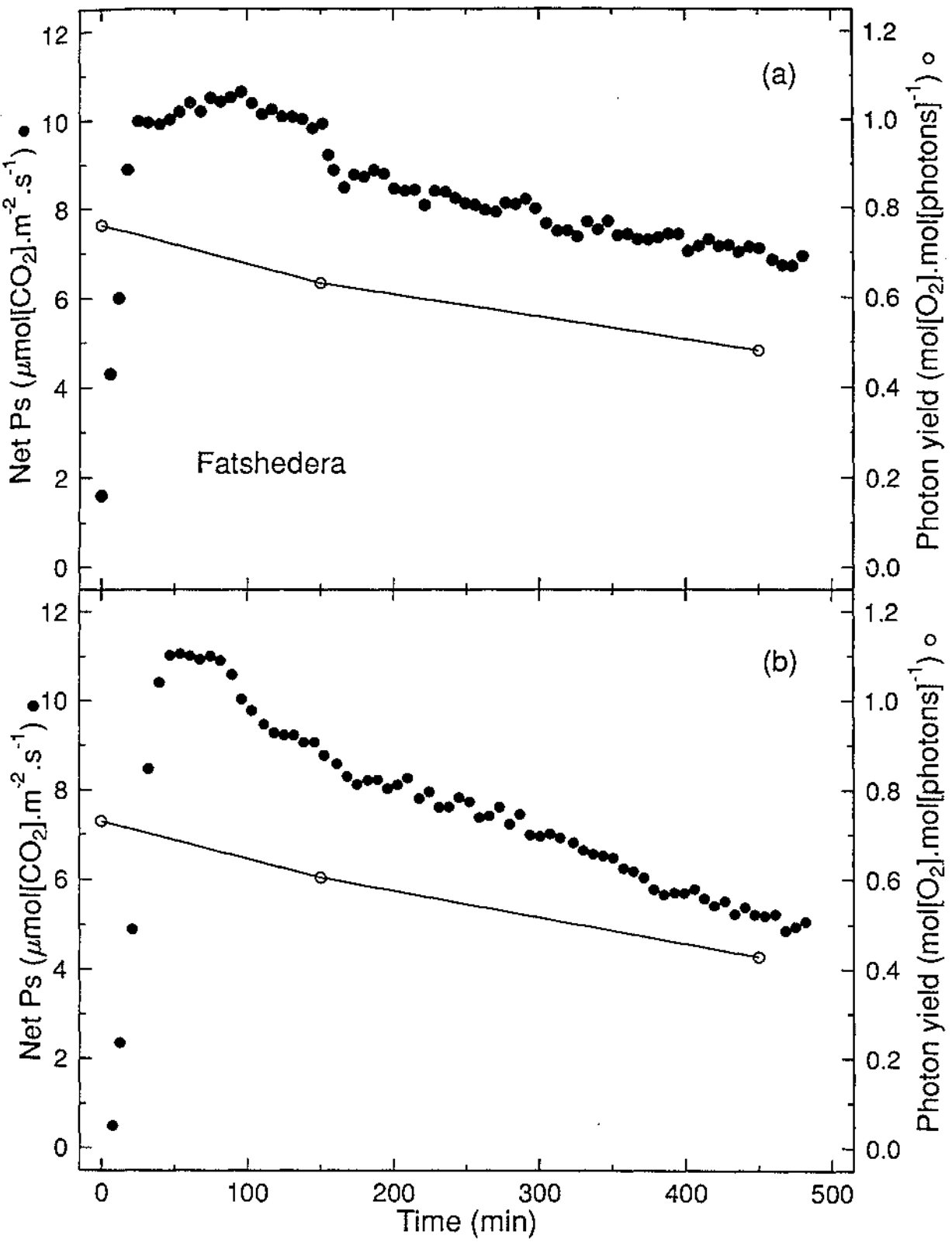


Fig. 5-11. Time course of reduction in net photosynthesis and photon yield in Fatshedera leaves measured at 20 C and exposed to PFD of 1200 μmol.m^{-2}.s^{-1} as influenced by growth temperature (a) 20 C and (b) 30 C.

The change in the rate of photosynthesis during the standard photoinhibition treatments was related in a linear manner to the current leaf temperature. No significant differences ($P \leq 0.001$) between the slopes of the regression lines were observed for Epipremnum and Fatshedera leaves developed at 20 C or 30 C (Fig. 5-15a). The intercepts for these regression lines were significantly different between species and between growth temperatures indicating that the growth temperature had an important effect on determining the sensitivity of Epipremnum and Fatshedera leaves to photoinhibition. At each growth temperature the reduction in photosynthesis was about 3% per 1 C rise in leaf temperature. The reduction in photosynthesis during photoinhibition was about 10% higher in each species when grown at 30 C instead of at 20 C. Overall, this data shows that Fatshedera leaves were less prone to reduction in photosynthesis than Epipremnum and for both species development at higher temperatures increased the susceptibility to photoinhibition of photosynthesis during exposure to bright light.

5.3.4.1 Effect of PFD on photon yield of oxygen evolution

During photoinhibition of photosynthesis, exposure of leaves to treatments with increasing PFD's decreased the photon yield of oxygen evolution in a CO_2 saturated atmosphere (ϕ_i). In Epipremnum and Fatshedera leaves ϕ_i decreased by 17 and 14%, respectively at a PFD of 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$ while at a PFD of 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ the corresponding decreases in ϕ were 68 and 46% (Table 5.5).

5.3.4.2 Effect of high PFD on chlorophyll fluorescence

Kinetics of typical PSII fluorescence induction (at 692 nm) of Epipremnum and Fatshedera leaves before and after exposure to a PFD of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 200 min are presented in Fig. 5-12. Following excitation of the upper leaf surface by actinic light, chlorophyll fluorescence 'instantly' reaches the Fo level. At 77 K the leaf continues to absorb photons, but reoxidation of the primary electron

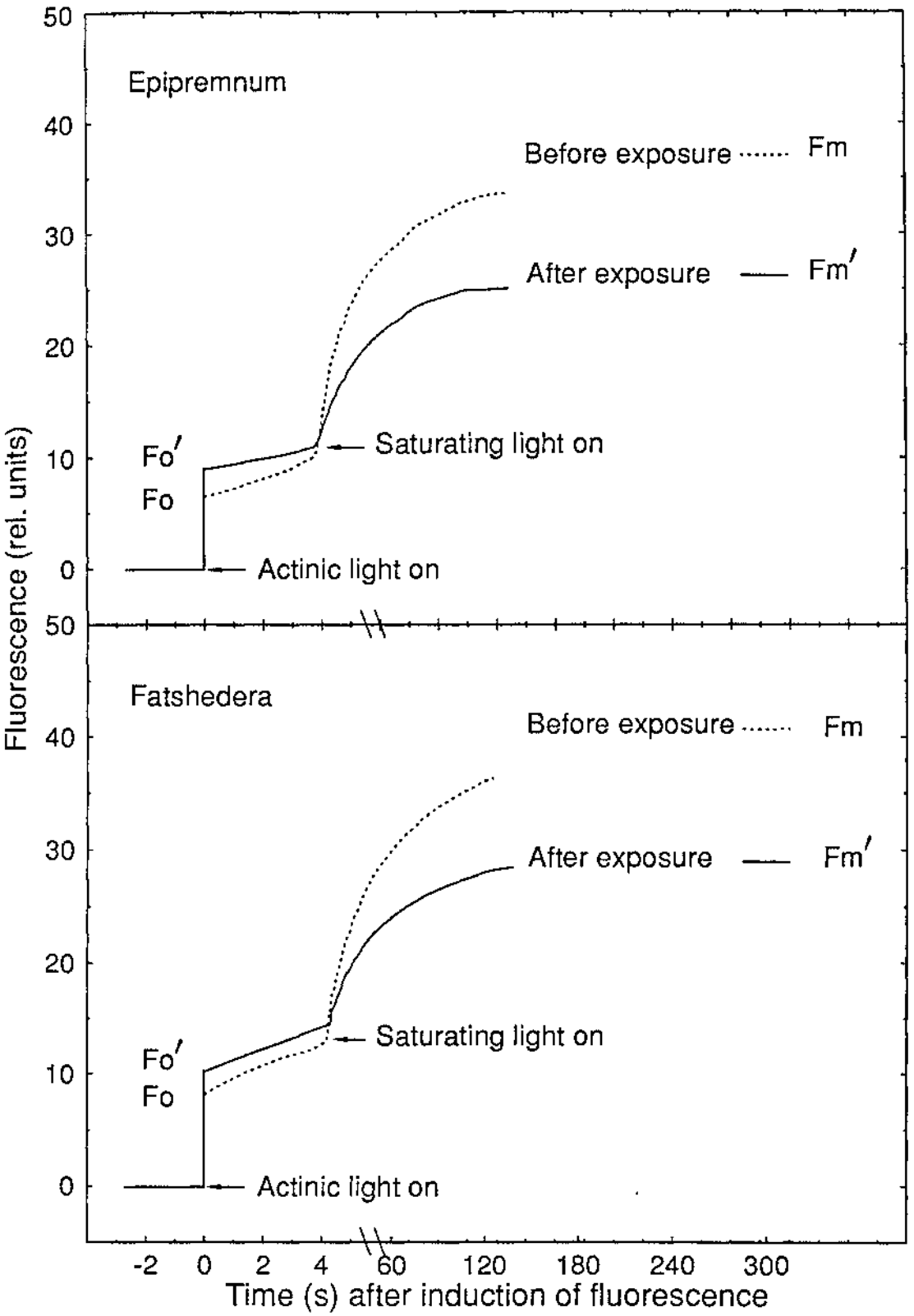


Fig. 5-12. Typical digitised plots of chlorophyll fluorescence induction kinetics at 77 K in dark-adapted Epipremnum and Fatshedera leaves before and after exposure to bright light (PFD 1200 μmol.m^{-2}.s^{-1} for $\simeq$200 min). Fo, Fo′, Fm and Fm′ were measured using actinic and saturating light of PFD 0.4 and 4.0 μmol.m^{-2}.s^{-1}, respectively.

acceptor Q_A is suspended. As Q_A is reduced, chlorophyll fluorescence increases slowly in the actinic light and more rapidly in the saturating light up to the maximum value (Fm). Figure 5-12 shows that photoinhibition of photosynthesis is characterised by a simultaneous increase in Fo and a decrease in Fm. Within each species, leaves subjected to identical photoinhibitory treatments showed little variation in chlorophyll fluorescence (<10%) between samples from the same leaf or other plants exposed to identical treatments.

Fv/Fm decreased exponentially in leaves exposed to high light at 20 C over the next 450 min. Non-linear regression curves for data pooled from replicated experiments with duplicate or triplicate samples were fitted to the data using Eqn. [5.9].

5.3.4.3 Effect of PFD on time course of photoinhibition

Following exposure of both Epipremnum and Fatshedera to a PFD of 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$, photoinhibition was evident within 30 min as reduced chlorophyll fluorescence (Fig. 5-13). After 450 min exposure, Fo had increased by 26% and 9%, respectively (Table 5.5). In Epipremnum leaves, Fv/Fm decreased rapidly for the first 100 min, and thereafter change proceeded almost linearly towards a steady state condition where leaves were 17% photoinhibited (Fig. 5-13a). At higher PFDs of 850 and 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ the initial rate of photoinhibition was higher and this is reflected in the exponential decrease in chlorophyll fluorescence. The steady state condition was not obtained until after 450 min exposure to bright light. Fo increased by more than 30% and the final extent of photoinhibition in Epipremnum increased from 47% to 78% as PFD increased from 850 to 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Table 5.5).

The kinetics of Fv/Fm during photoinhibition followed a similar pattern in Epipremnum and Fatshedera, and in both species were described by Eqn. [5.9]. In Fatshedera leaves, like Epipremnum, the extent of photoinhibition at steady state conditions was also related to the incident PFD (Table 5.5).

Table 5.5. Effect of PFD on initial rate of photoinhibition, half time to reach steady state conditions, extent of photoinhibition of Fv/Fm, percentage change in instantaneous fluorescence (Fo) and CO_2-saturated photon yield characteristics of Epipremnum and Fatshedera leaves after 450 min exposure to the PFD treatment of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Plants were grown in a greenhouse at 25 ± 5 C with PFD max. 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ prior to placement in the treatments.

Species	PFD $\mu mol \cdot m^{-2} \cdot s^{-1}$	Characteristic				
		Initial rate of PI[z]	Half time for PI[y]	Extent Fv/Fm (%)[x]	Fo (%) change[w]	% change $\delta\phi_i$[v]
Epipremnum	550	-0.450 ± .086	1658	17.1	25.8	17
	850	-1.446 ± .144	365	47.1	30.6	32
	1500	-2.009 ± .167	162	78.6	27.6	68
Fatshedera	550	-0.315 ± .075	6133	5.7	9.0	14
	850	-1.333 ± .100	436	51.0	23.5	26
	1500	-1.937 ± .133	193	77.7	21.2	46

[z] Initial slope (change in fluorescence.min^{-1})
[y] Time to 50% of the steady state photoinhibited condition (Fv/Fm)
[x] Final extent of photoinhibition (Fv/Fm) = (1-Finf/Fin) where Fin and Finf are chlorophyll fluorescence at t=0 and t=∞
[w] % change in instantaneous fluorescence from the control values
[v] $\delta\phi_i$ % change in photon yield of oxygen evolution

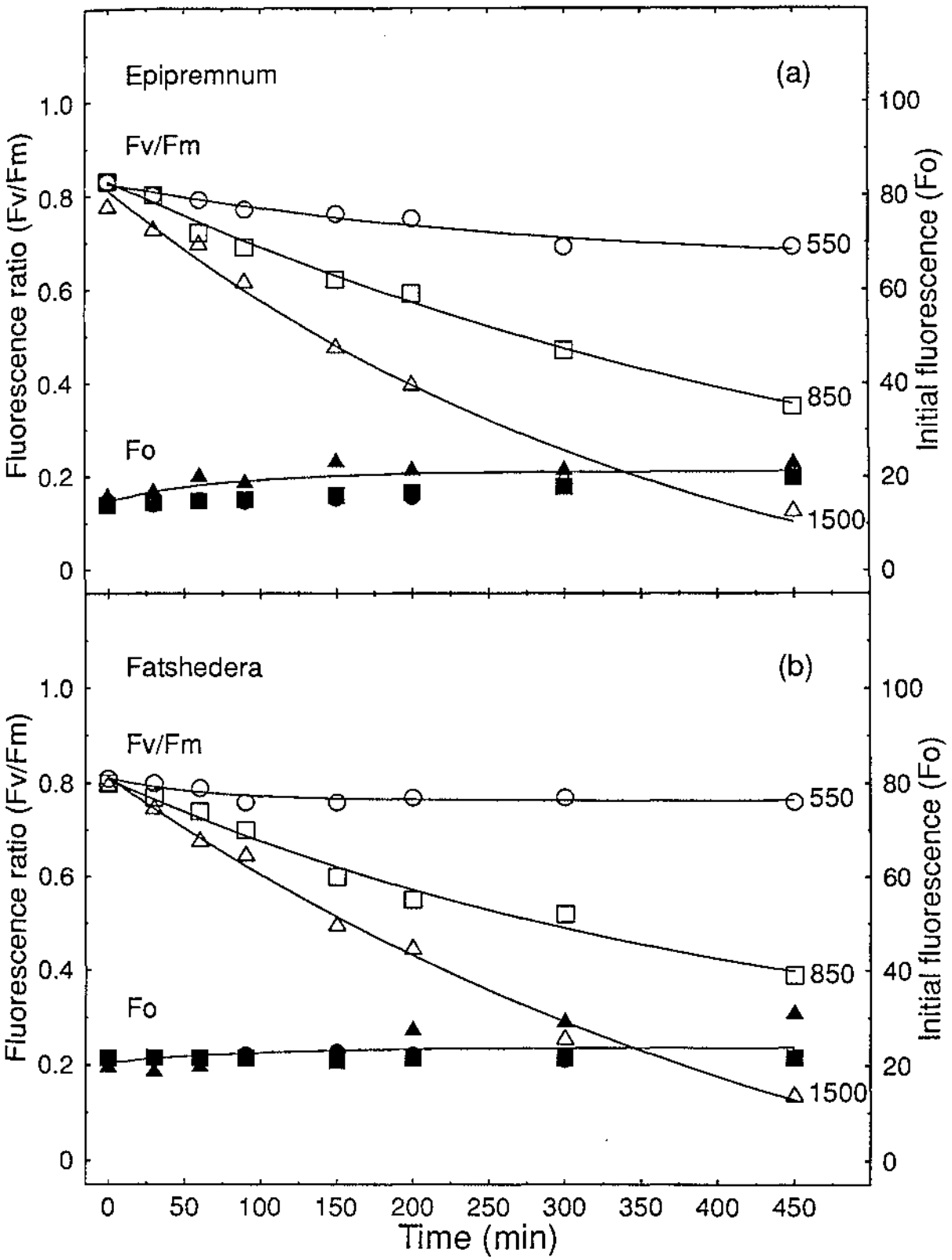


Fig. 5-13. Time course of change in the fluorescence ratio (Fv/Fm) and instantaneous fluorescence (Fo) in (a) Epipremnum and (b) Fatshedera leaves exposed to PFD of 550, 850 or 1500 μmol.m^{-2}.s^{-1}. Leaves were developed at 25 C and evaluated at 20 C. Solid lines are the best least squares fit of Eqn.[5.9] to data from 1-2 leaves.

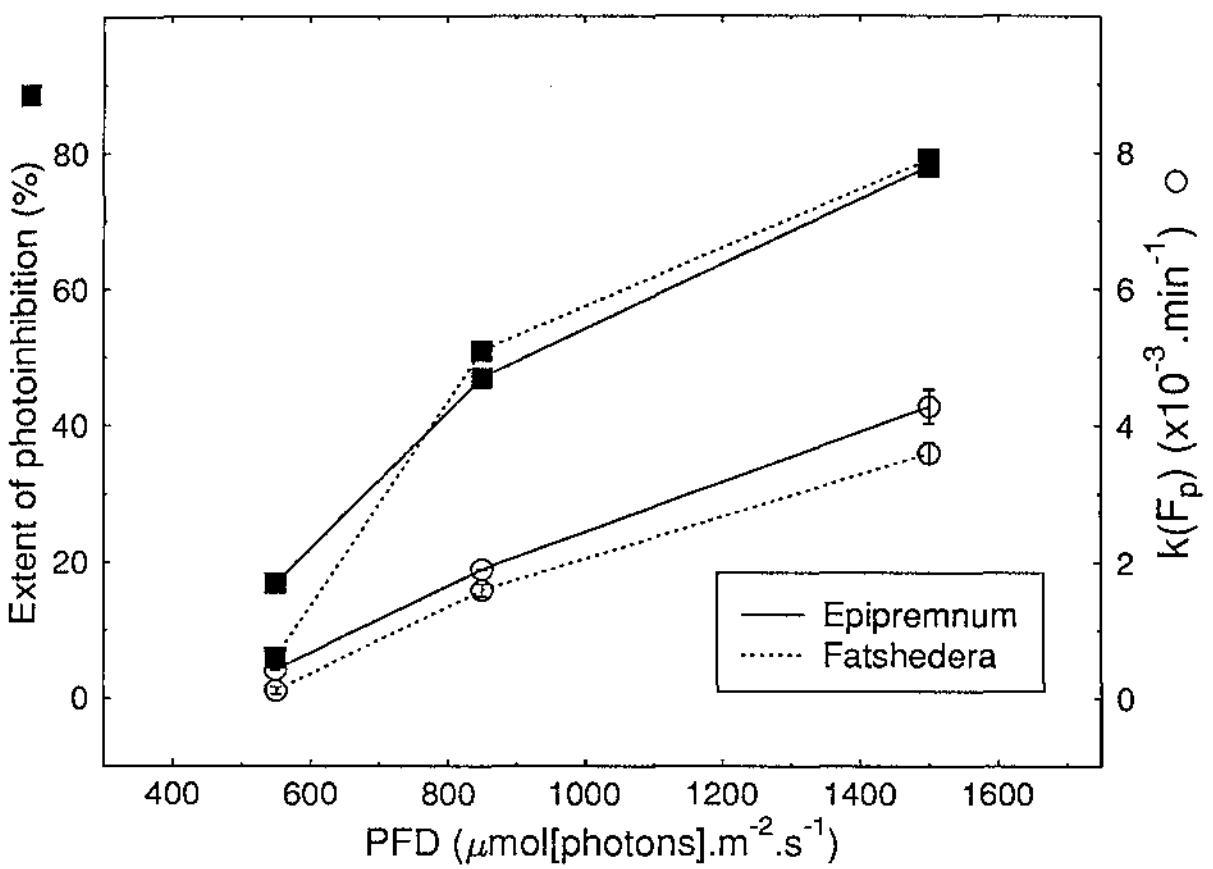


Fig. 5-14. Effect of PFD on the extent of photoinhibition (■) and the rate constant for photoinhibition, $k(F_p)$ (○) ,in Epipremnum and Fatshedera leaves after exposure to bright light for 450 min. (Vertical bars inside symbols represent standard errors)

A difference between the two species occurred in the lowest PFD treatment where Epipremnum was typically more photoinhibited than Fatshedera (Fig. 5-13)(Table 5.5).

To compare the response of each species at each PFD linear regressions were fitted to the first 150 min of each time course. The slope of each regression line in this region was indicative of the initial sensitivity of leaves to photoinhibition at each PFD. The initial slope for each PFD treatment was significantly different ($P \leq 0.001$) within each species, but was not significant between each species. Although there was a consistent trend for the rate of change in photoinhibition to be higher in Epipremnum than in Fatshedera at each PFD (Table 5.5). The first-order rate constants for photoinhibition, $k(F_p)$ at each PFD were significantly different ($P \leq 0.001$) and increased in a nearly linear manner with increasing PFD (Fig. 5-14). No significant difference in $k(F_p)$ was found between Epipremnum and Fatshedera when treated as a linear function of PFD. This indicates a similar dependency of the rate of photoinhibition on the incident PFD in leaves of both species. This was also evident in that the time to half the final steady state condition which strongly reflected the effect of incident PFD; at 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$ this time was >1500 min for each species, whereas at a PFD of 850 $\mu mol \cdot m^{-2} \cdot s^{-1}$ the time was between 360 and 440 min for Epipremnum and Fatshedera, respectively. At the high PFD of 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ the time to 50% of the steady state condition during photoinhibition was between 160 and 200 min (Table 5.5).

Prolonged exposure (> 300 min) of Epipremnum leaves to PFDs up to 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ resulted in permanent photo-oxidative damage in the directly-irradiated regions of the leaf after exposure. Some of the leaf in the leaf chamber was protected from direct exposure to high PFD by a nylon grid and was not damaged. Chlorophyll bleaching in exposed leaves developed over several days and persisted while the leaf remained attached to the plant (Plate 5-7a). Some damage also developed in chlorophyll-deficient Epipremnum leaves developed at 30 C (Plate 5-7b). Electron micrographs of the acutely photoinhibited Epipremnum leaves showed chloroplast membrane damage and extensive

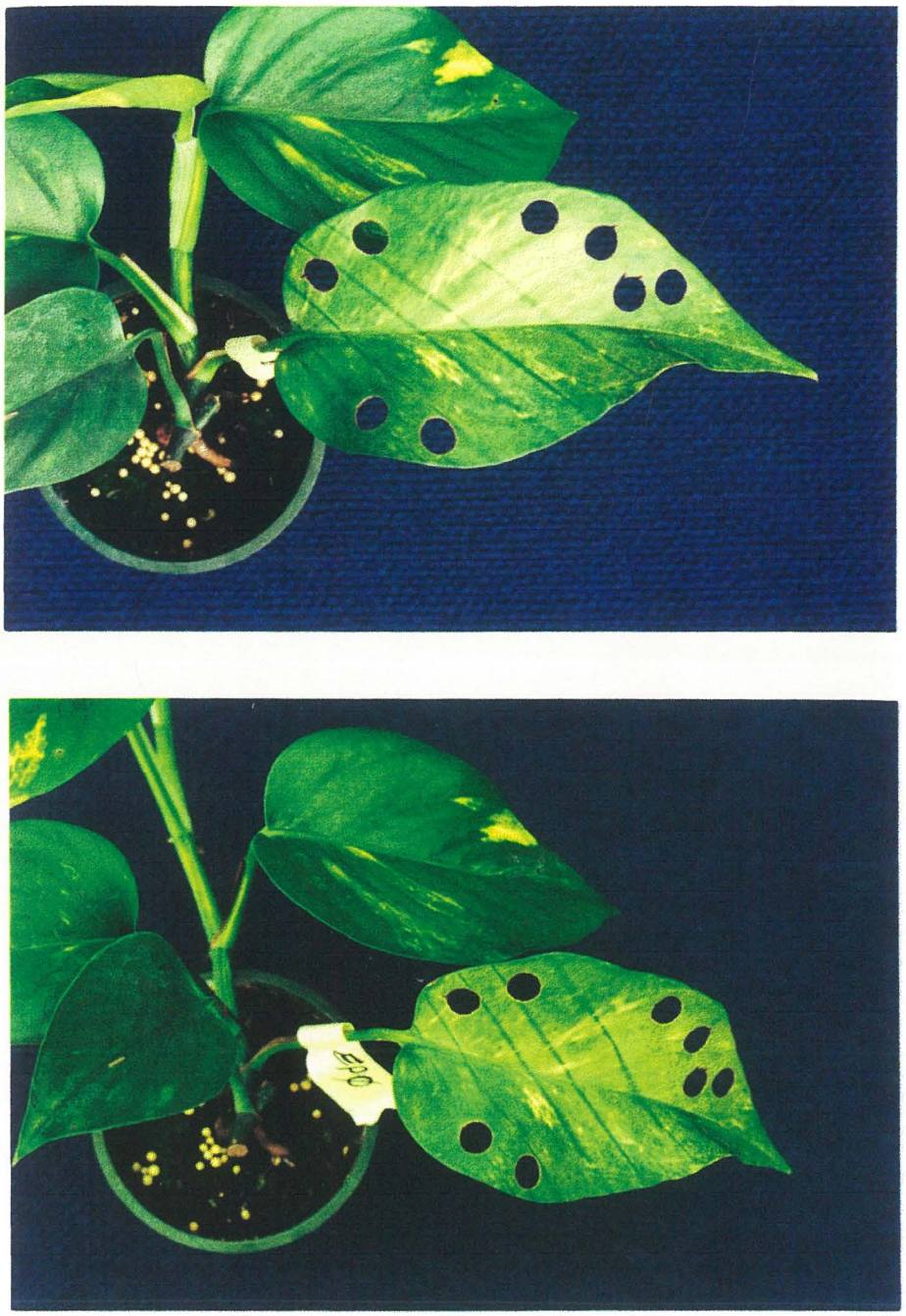


Plate 5-7a. Permanent damage induced by exposure of Epipremnum to high PFD at 20 C (upper photo). Lines of normal green leaf tissue occurred where the nylon supporting grid in the leaf chamber shaded the leaf from the high PFD. Leaf discs were removed from the leaf to monitor photoinhibition of photosynthesis. Photos were taken at 2 weeks (upper photo) and 6 weeks (lower photo) after treatment.

Plate 5-7b. Photo-oxidative damage in chlorophyll-deficient sectors of Epipremnum leaves grown at low PFD in the CE room at 30 C.

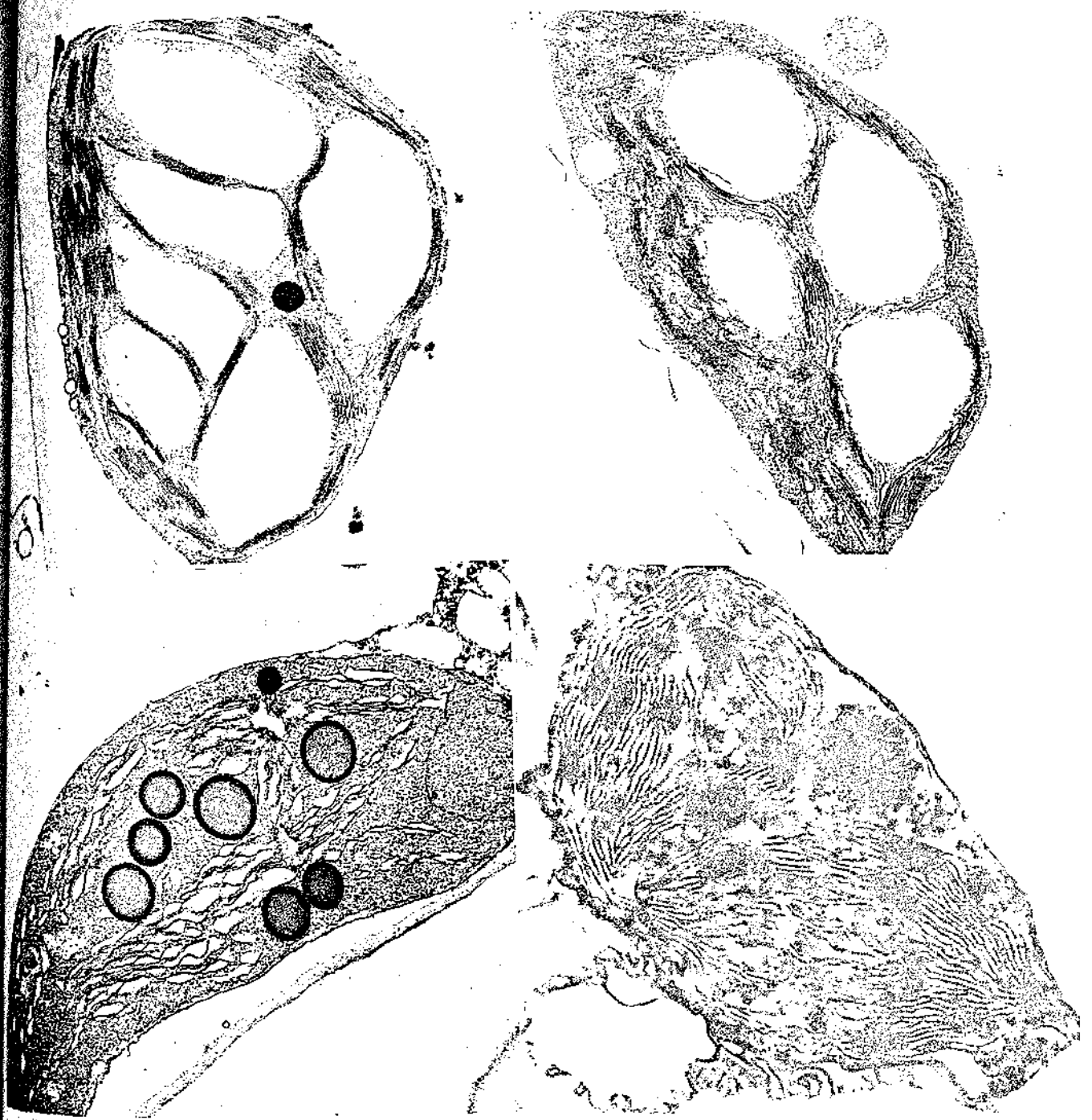


Plate 5-8. Electron micrographs of Epipremnum chloroplasts from the upper-most palisade layer in leaves developed at 30 C. Before exposure to high PFD (upper left). After exposure to high PFD for 450 min (upper right), seven days after exposure to high PFD (lower left) and from a leaf showing photo-oxidative damage after 30 days (lower right). (Magnification x 15300)

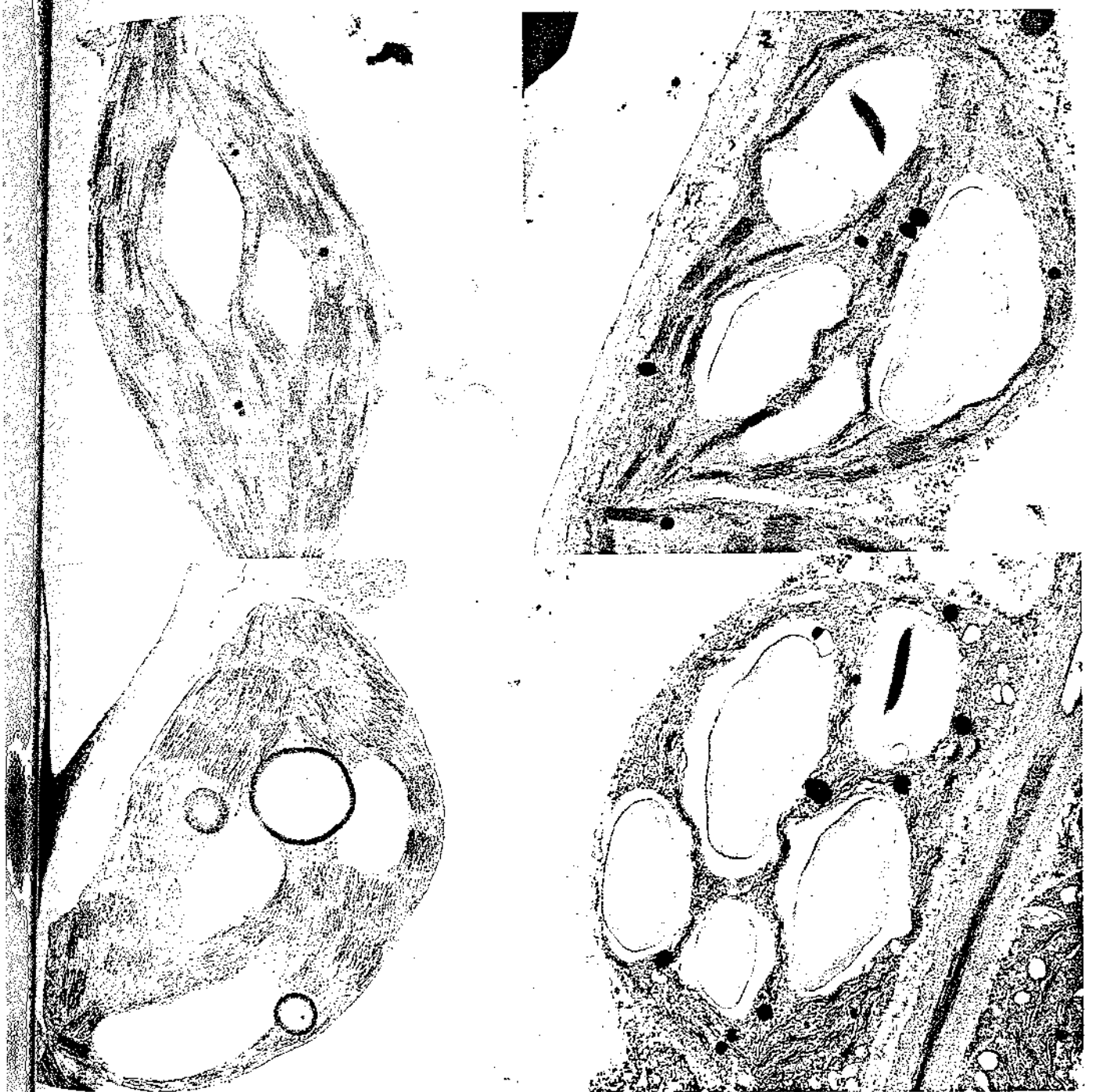


Plate 5-9. Electron micrographs of Fatshedera chloroplasts from the upper-most palisade layer. Before exposure to high PFD (GT=20 C) (upper left), after exposure to standard CE room PFD (GT=30 C) (upper right), after exposure to high PFD (GT=20 C) (lower left) and after exposure to high PFD (GT=30 C). (lower right). (GT = growth temperature) (Magnification x 15300)

thylakoid disruption, after leaves were exposed to high PFD for 450 min. Starch grains were less distinct and more diffuse on their periphery after exposure to high PFD (Plate 5-8).

Photo-oxidative damage of Fatshedera leaves was not evident on the intact leaves or electron micrographs at any stage following prolonged exposure to PFDs up to 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In some Fatshedera leaves disruption of the granal stacking arrangement was found when exposed to high PFD for 450 min. This was not correlated to permanent impairment of chloroplast function. Plate 5-9 show normal chloroplasts in both untreated leaves and leaves exposed to high PFD, respectively. In Fatahedera, like Epipremnum, starch grains were often less distinct and more diffuse on their periphery after exposure to high PFD.

5.3.5.1 Effect of leaf temperature on photoinhibition of photosynthesis

When leaves of Epipremnum and Fatshedera were exposed to bright light the net rate of photosynthesis declined in an almost linear relationship with increasing temperature (Fig. 5-15a). When treated as a linear function, there was no significant difference ($P \leq 0.01$) between the slopes of lines fitted to each species and growth temperature. This suggests photoinhibition of photosynthesis within each species has a similar underlying temperature dependency. Within each species the intercepts were significantly different ($P \leq 0.01$), indicating that with respect to growth temperature, exposure to bright light decreased net photosynthesis more when plants developed at a high growth temperature.

5.3.5.2 Effect of leaf temperature on photon yield of oxygen evolution

The change in photon yield during photoinhibition of photosynthesis was inversely related in a nearly linear manner to the current leaf temperature (Fig. 5-15b).

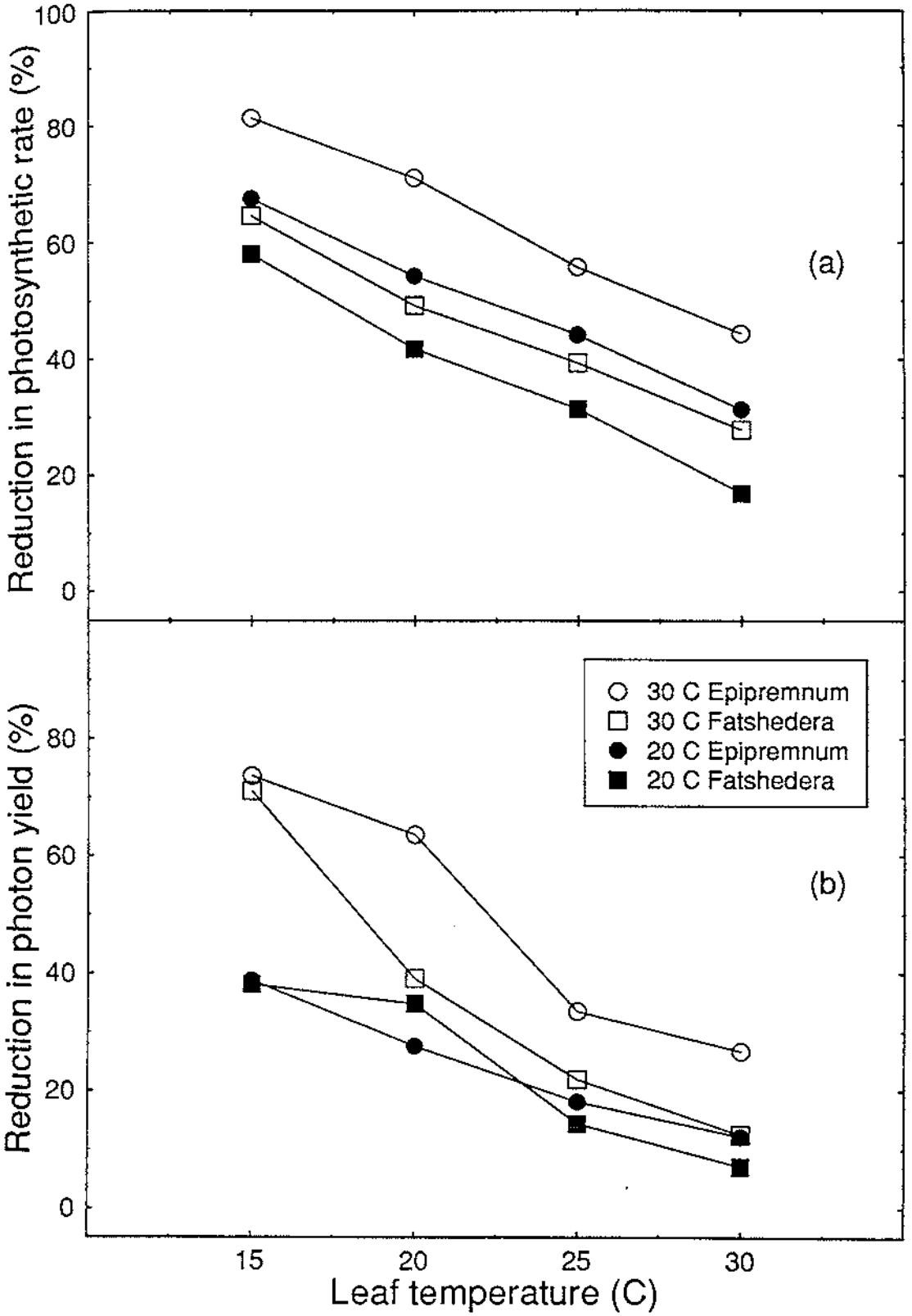


Fig. 5-15. Effect of leaf temperature on (a) reduction in photosynthetic rate and (b) reduction in photon yield during photoinhibition of Epipremnum and Fatshedera plants grown at 20 or 30 C.

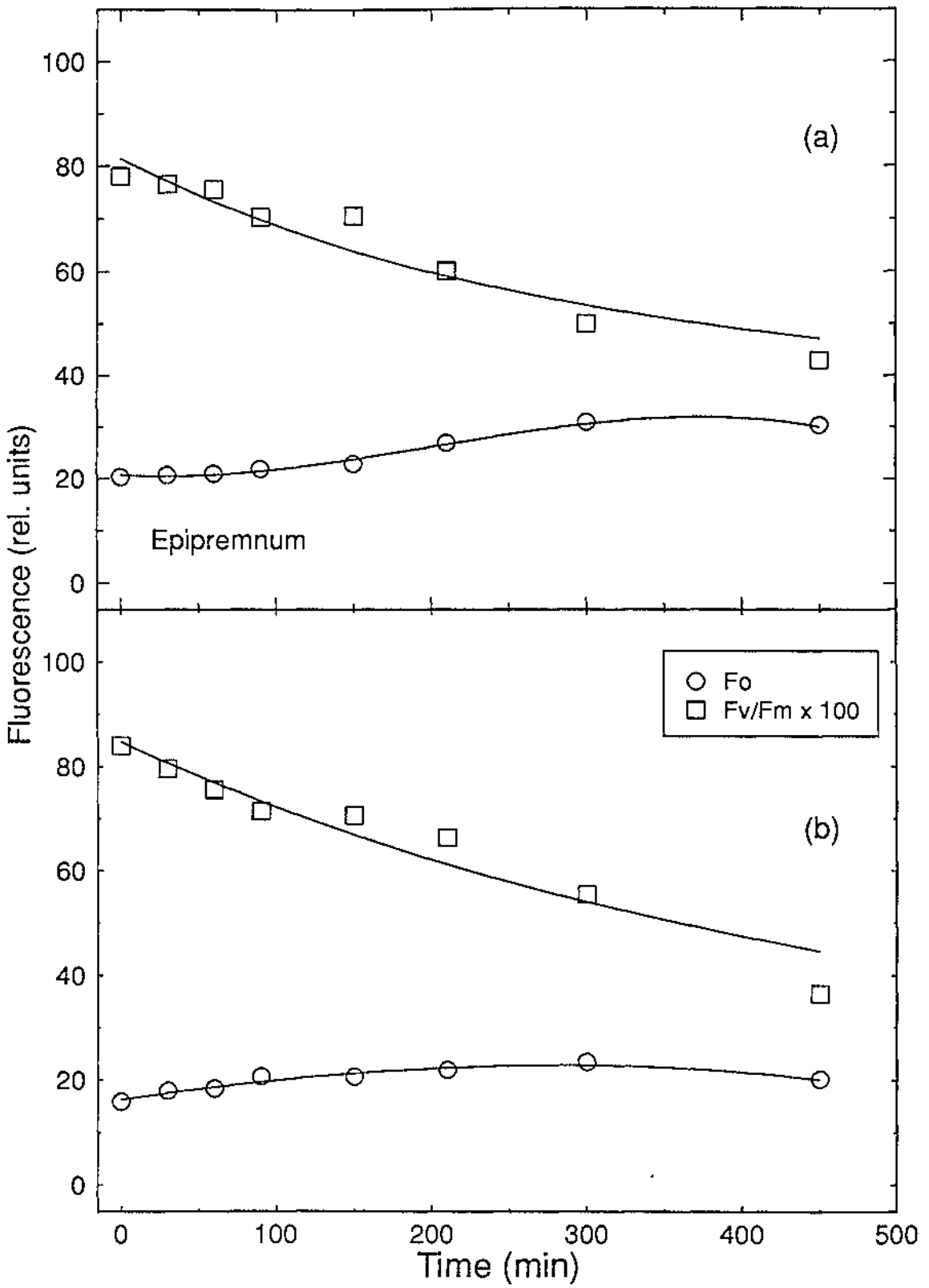


Fig. 5-16. Effect of growth temperature, (a) 20 C and (b) 30 C on the time course of chlorophyll fluorescence in Epipremnum leaves during photoinhibition at 20 C and PFD of 1200 μmol.m^{-2}.s^{-1}. Solid lines for Fv/Fm and Fo were the best fit to Eqn.[5.9] and a cubic polynomial, respectively. Data are the mean of 3 leaves.

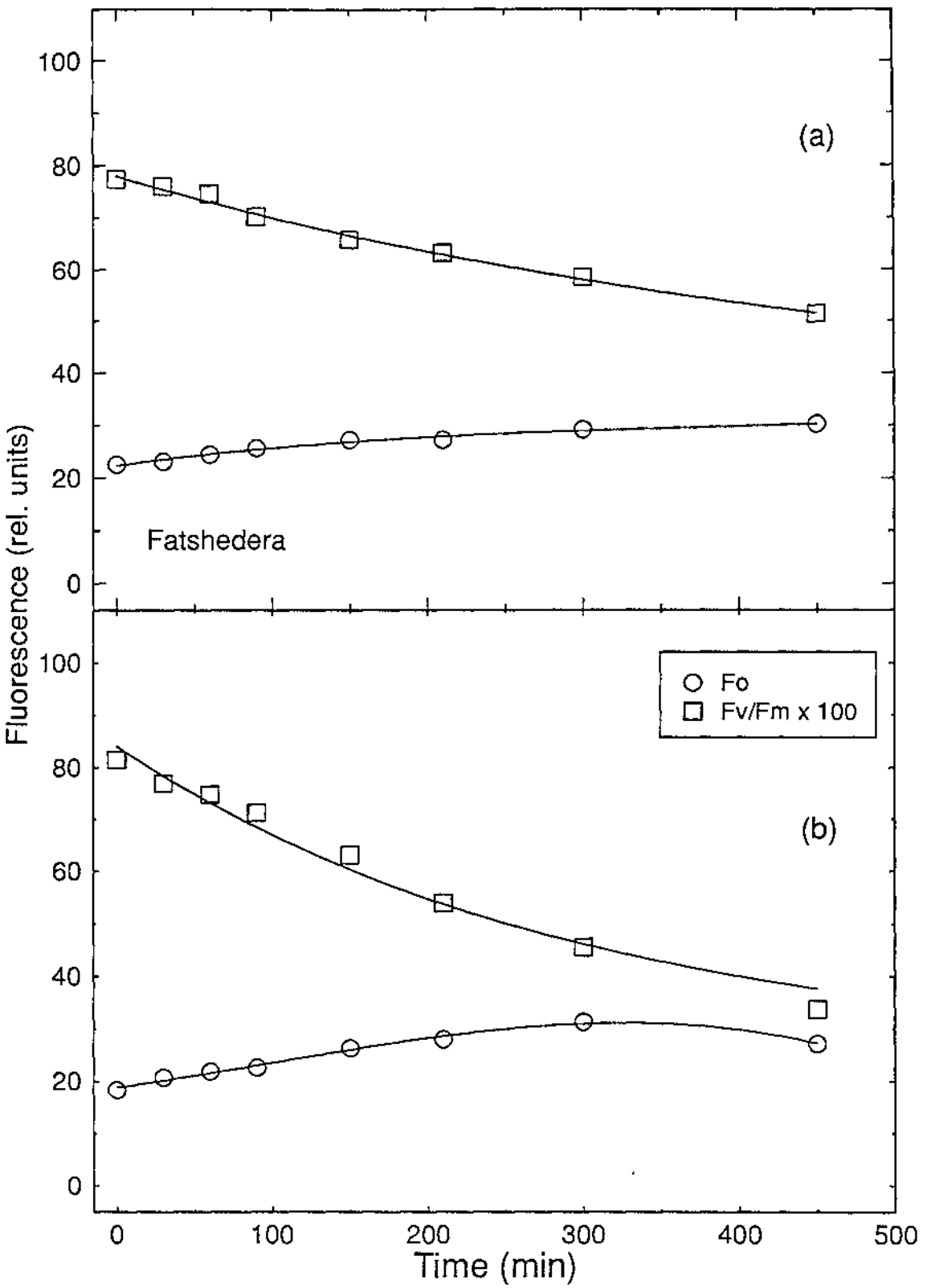


Fig. 5-17. Effect of growth temperature, (a) 20 C and (b) 30 C on the time course of chlorophyll fluorescence in Fatshedera leaves during photoinhibition at 20 C and PFD of 1200 μmol.m^{-2}.s^{-1}. Each line for Fv/Fm and Fo is the best fit to Eqn.[5.9] and a cubic polynomial, respectively. Data are the mean of 3 leaves.

When treated as a linear function, there was no significant difference ($P \leq 0.05$) between the slopes of lines fitted each species within each growth temperature, whereas there were significant differences in slopes and intercepts between the growth temperatures. Both Epipremnum and Fatshedera when grown at 30 C were twice as sensitive to photon yield reduction during photoinhibition than if grown at 20 C. Epipremnum was more prone than Fatshedera to a reduction in photon yield when grown at 30 C. However, leaves developed at 20 C in both species were equally resistant to change in photon yield.

5.3.6 Effect of leaf temperature on photoinhibition.

When leaves from plants grown at 20 or 30 C were exposed to a PFD about 4 times higher than the growth PFD, the changes in chlorophyll fluorescence measured at 77 K and 692 nm were dependent on the current leaf temperature and the growth temperature.

The time course of change in Fv/Fm in Epipremnum leaves developed at 20 or 30 C and photoinhibited at 20 C showed an exponential decrease between 51 and 53% of the initial value after 450 min exposure to a PFD of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 5-16). During the same time course, in leaves developed at 20 C, Fo increased curvilinearly by 52% up until 300 min and then decreased marginally by about 5%. At the higher growth temperature (30 C) Fo increased by 49% up until 300 min, thereafter decreasing from the maximum by about 5 %.

When Fatshedera leaves developed at 20 or 30 C were photoinhibited at 20 C, then Fv/Fm decreased exponentially over the time course of 450 min, finally reaching a steady state value between 60% and 70% of the original value (Fig. 5-17). Fo increased curvilinearly by 34% during the time course of the photoinhibition treatment in leaves from the lower growth temperature. There was no evidence of a decrease in Fo after the steady increase, whereas at the higher

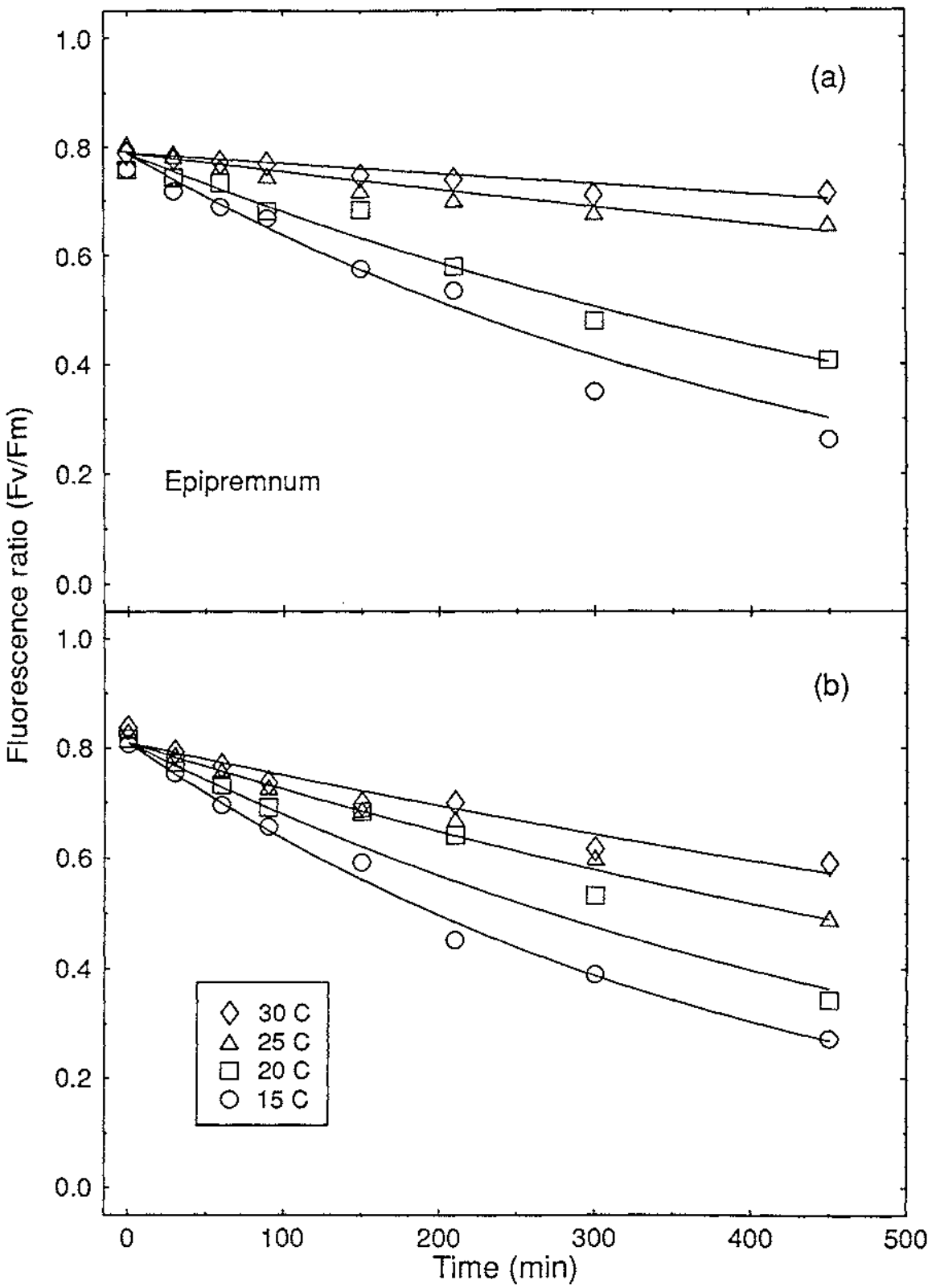


Fig. 5-18. Effect of current leaf temperature on the time course of Fv/Fm in Epipremnum leaves during photoinhibition at PFD of 1200 μmol.m^{-2}.s^{-1} as influenced by the growth temperature (a) 20 C and (b) 30 C. Fitted lines are best fit of Eqn.[5.9] to the mean of three leaves.

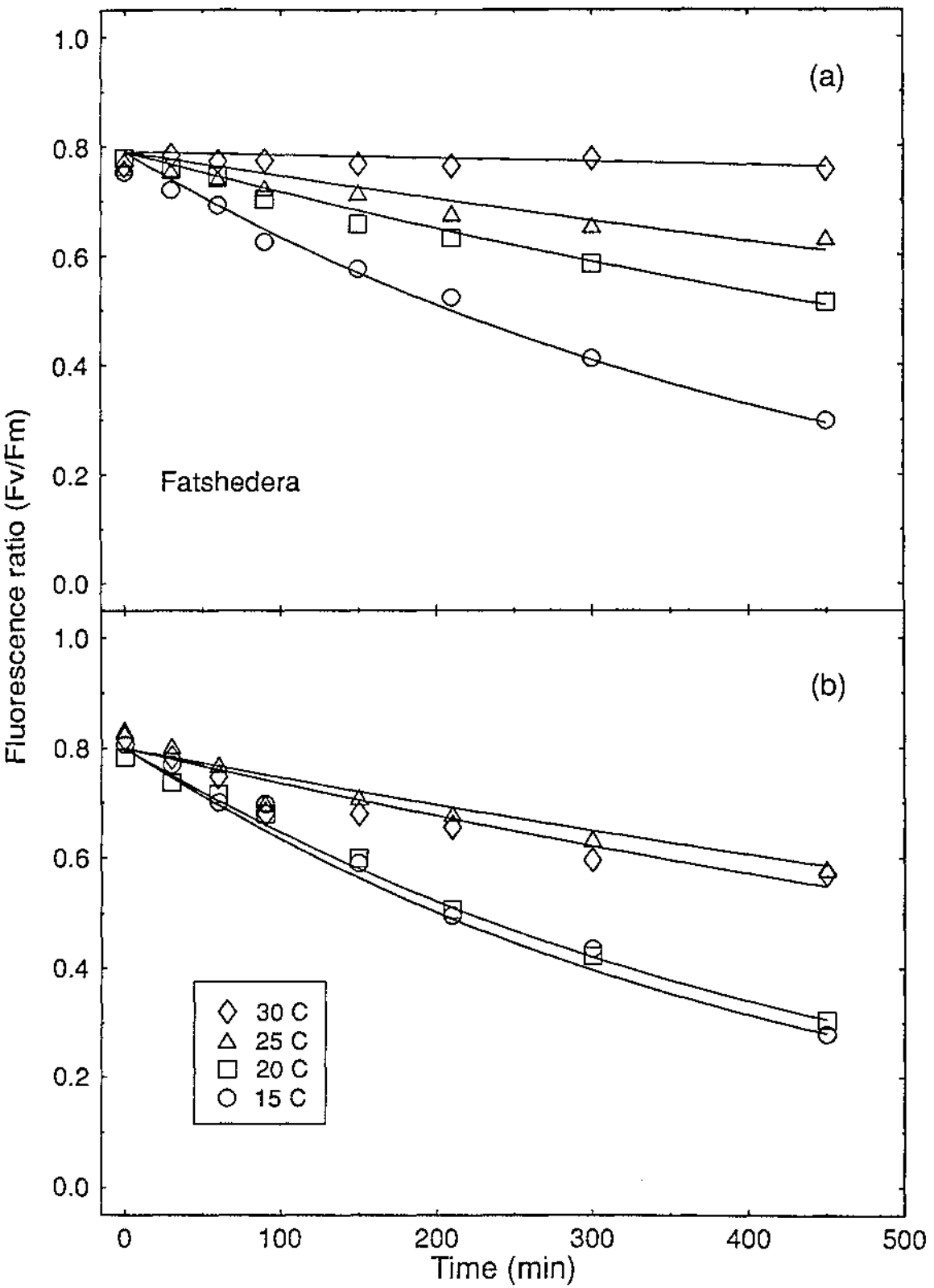


Fig. 5-19. Effect of current leaf temperature on the time course of Fv/Fm in Fatshedera leaves during photoinhibition at PFD of 1200 μmol.m^{-2}.s^{-1} as influenced by the growth temperature (a) 20 C and (b) 30 C. Fitted lines are the best fit of Eqn.[5.9] to the mean of three leaves.

growth temperature, Fo increased by 72% up until 300 min from the beginning of the photoinhibition treatment and then decreased from the maximal value by about 23% over the following 150 min.

Time courses for photoinhibition of photosynthesis (quantified as change in Fv/Fm) at other temperatures were similar (not shown). During exposure to bright light Epipremnum and Fatshedera leaves were progressively more prone to reduction in Fv/Fm with decreasing leaf temperature. In both species the fluorescence ratio decreased more rapidly in leaves at 15 C than at temperatures of 20 C or higher. Leaves treated at 25 C and 30 C were less photoinhibited during exposure to equivalent PFD than at lower leaf temperatures (Figs. 5-18, 5-19).

The first-order rate constants for photoinhibition, $k(F_p)$ in Epipremnum leaves at each temperature were each significantly different ($P \leq 0.05$) and decreased in an approximately linear manner with increasing leaf temperature (Fig. 5-20). Fatshedera, like Epipremnum exhibited a similar response to leaf temperature. The rate constant for photoinhibition in leaves developed at both growth temperatures were similar in their overall response to leaf temperature. In leaves developed at 30 C and photoinhibited at 20 C, then the rate constant for photoinhibition was higher in both Epipremnum and Fatshedera than in leaves developed at 20 C. The high rates of photoinhibition were observed at leaf temperature of 15 C with lower rates occurring with increasing leaf temperature up to 30 C.

At any leaf temperature examined between 15 and 30 C, leaves of Epipremnum and Fatshedera developed at 20 C were more resistant to photoinhibition than if developed at 30 C. Overall Fatshedera tended to be less photoinhibited than Epipremnum (Table 5.6).

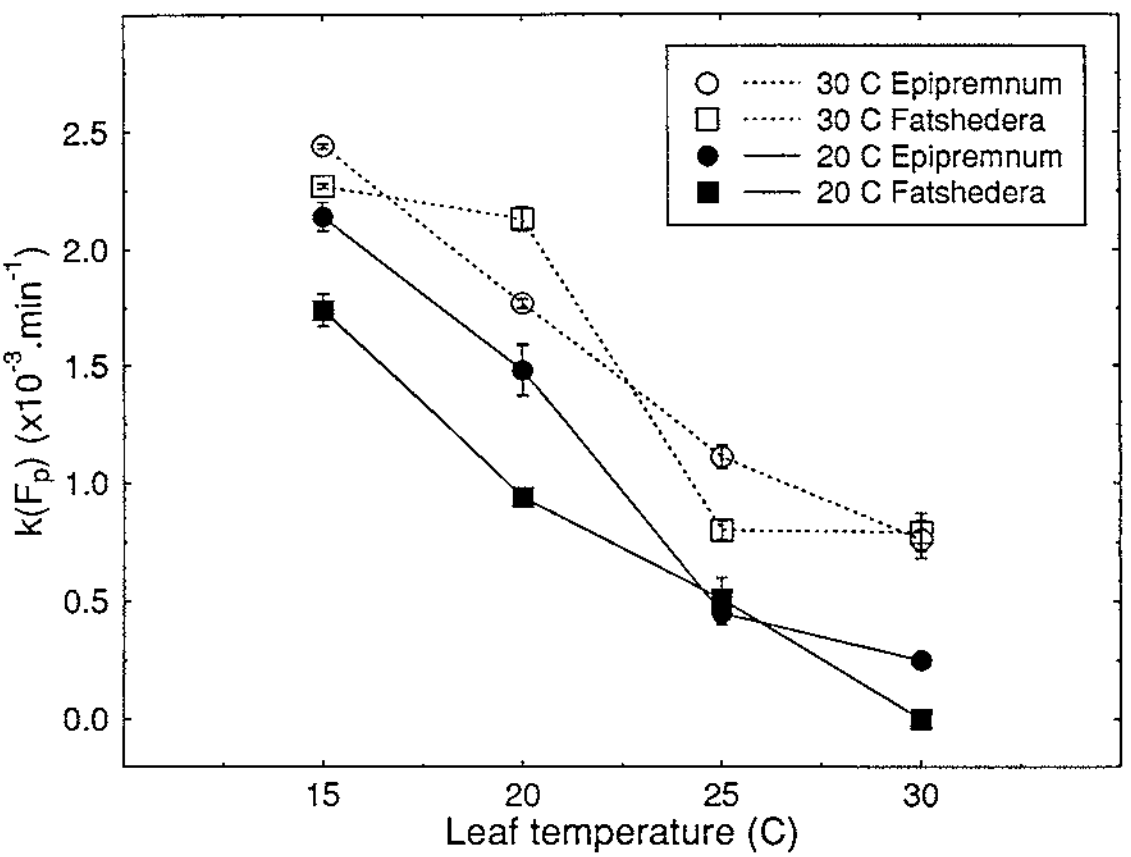


Fig. 5-20. Effect of growth temperature on the relationship between the rate constant for photoinhibition, $k(F_p)$ and leaf temperature in Epipremnum and Fatshedera leaves. (Vertical bars inside symbols represent standard errors for mean of three leaves)

Table 5.6 Initial slope of Fv/Fm during the first 150 min of photoinhibition and extent of photoinhibition when steady state conditions obtained after 450 min exposure to the PFD treatment of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. (means ± s.e.; n=3)

	Temperature (C)			
Species	Growth	Leaf	Initial slope[z]	Extent(%) of PI[y]
Epipremnum	20	15	-1.188±.090	73.0
		20	-0.560±.146	51.3
		25	-0.570±.039	21.7
		30	-0.269±.023	12.9
Epipremnum	30	15	-1.427±.119	91.2
		20	-0.907±.197	76.2
		25	-0.937±.083	58.5
		30	-0.907±.085	38.8
Fatshedera	20	15	-1.237±.133	67.4
		20	-0.842±.075	59.6
		25	-0.339±.047	27.3
		30	-0.051±.143	1.9
Fatshedera	30	15	-1.411±.144	98.1
		20	-1.185±.062	69.3
		25	-0.816±.033	44.7
		30	-0.934±.076	30.3

[z] Initial slope (change in fluorescence.min^{-1})
[y] Final extent of photoinhibition (Fv/Fm) = (1-Finf/Fin) where Fin and Finf are chlorophyll fluorescence at t=0 and t=∞

The effect of leaf temperature on photoinhibition of photosynthesis was quantified from the Fv/Fm data, collected from temperatures between 15 C and 30 C. Linear regressions were fitted to the first 150 min of each time course. The slope of the regression lines estimated the initial sensitivity of leaves to photoinhibition from each growth temperature which increased with decreasing leaf temperature. The slope of the regression line and the extent of photoinhibition at each treatment temperature were generally related (Table 5.6).

The relative change in Fv/Fm that occurred during photoinhibition with equivalent PFD was a linear function of the current leaf temperature (Fig. 5-21a). Increasing current leaf temperature reduced plant sensitivity to photoinhibition, the extent of photoinhibition decreasing by 4% for each degree C rise in leaf temperature. The slopes of lines regressing the change in Fv/Fm against the current leaf temperature for each species and growth temperature were not significantly different ($P \leq 0.05$) from one another, while the intercepts were significantly different between each growth temperature, but not between species. This indicates that leaves developed at 30 C were more sensitive to photoinhibition than leaves from the lower growth temperature. Furthermore, within each species sensitivity to photoinhibition had a similar dependency on current leaf temperature.

During photoinhibition treatments, in leaves developed at 30 C, Fo increased by more than 40%, but showed no direct relationship with current leaf temperature (Fig. 5-21b). In contrast, the change in the Fo from leaves developed at 20 C was inversely related to the current leaf temperature. There was about 4% increase in Fo for each degree C leaf temperature decreased in both species. No significant difference was found between each species at each growth temperature. However, within each species the change in Fo with development temperature was statistically significant ($P \leq .05$).

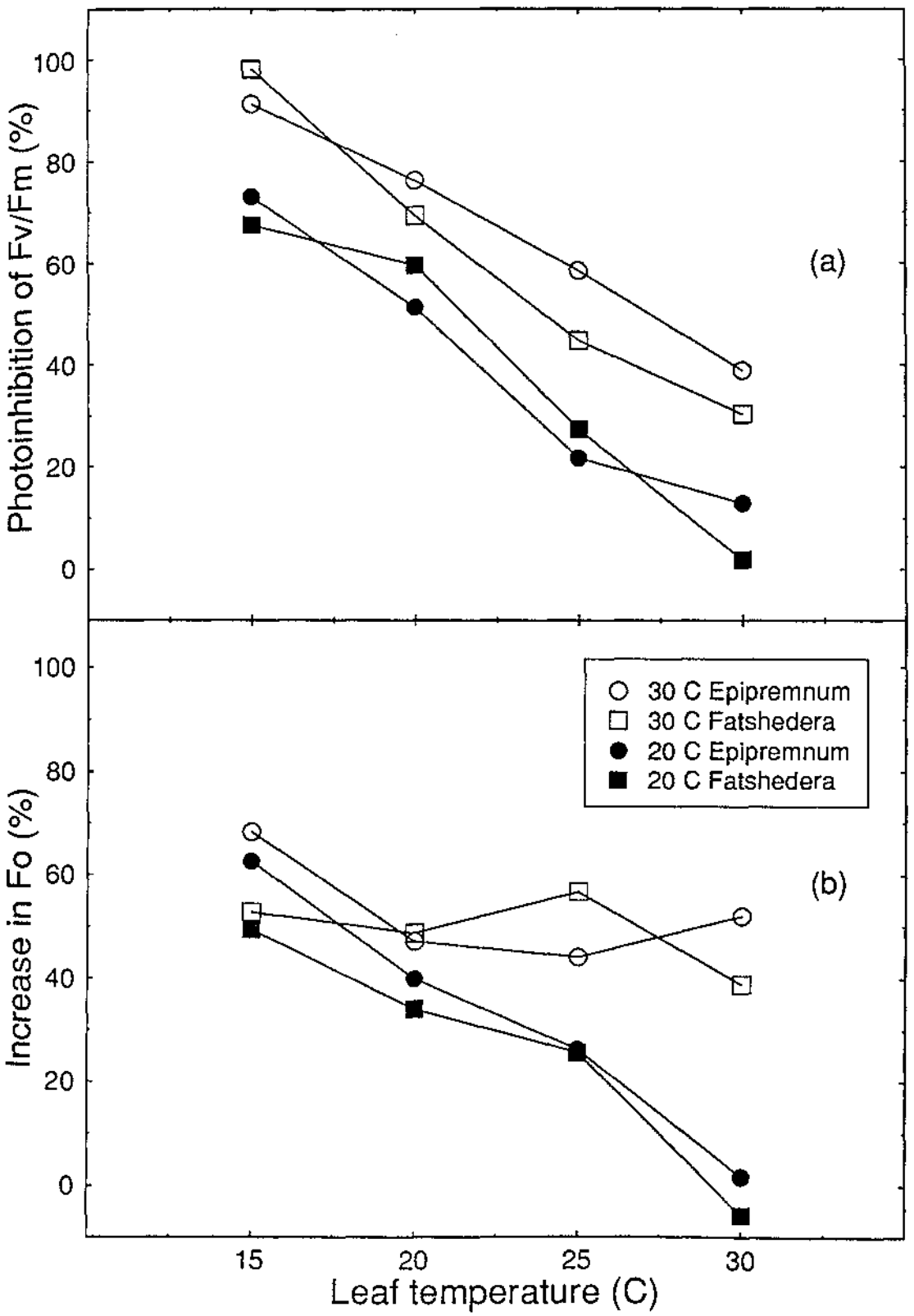


Fig. 5-21. Effect of leaf temperature on (a) change in Fv/Fm and (b) increase in Fo in Epipremnum and Fatshedera leaves during photoinhibition at PFD of 1200 μmol.m^{-2}.s^{-1} as influenced by growth temperature.

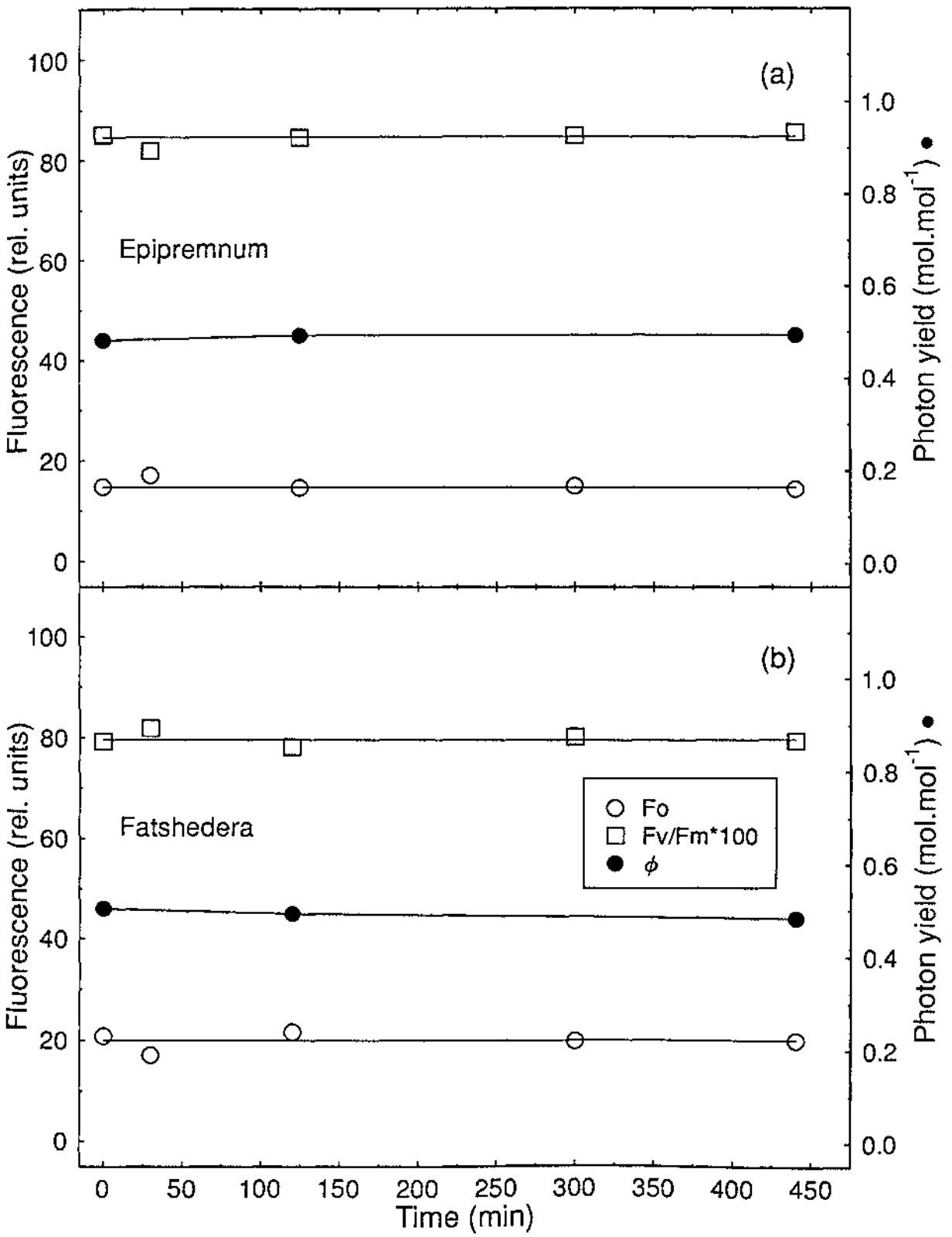


Fig. 5-22. Time course of change in chlorophyll fluorescence and photon yield (ϕ) on (a) Epipremnum and (b) Fatshedera leaves maintained in the dark at 10 C.

5.3.7 Effect of low temperature in the dark.

No significant changes in the fluorescence characteristics (Fo, or Fv/Fm) were observed when leaves of either Epipremnum or Fatshedera were exposed to 10 C in the dark for 450 min (Fig. 5-22). Similarly, photon yield did not change while the leaves were held at 10 C in the dark, indicating that low temperature alone did not cause damage to Epipremnum and Fatshedera. These particular results, when considered in conjunction with other results presented in this chapter indicate that light was an essential factor in the impairment of the photosynthetic apparatus at low temperature. The overall consistency of the data also suggested that the sampling procedures in the fluorescence assay *per se* were not responsible for any detectable change in chlorophyll fluorescence.

5.3.8 Recovery of leaves from photoinhibition of photosynthesis.

5.3.8.1 Effect of growth temperature on recovery of leaves from photoinhibition of photosynthesis

Following the standard photoinhibitory treatment, changes in chlorophyll fluorescence and photon yield were monitored during recovery over 450 min at low PFD. The initial fluorescence (Fo) in Epipremnum leaves developed at 20 C remained largely unchanged during recovery, while Fv/Fm increased exponentially by 49% (Fig. 5-23a). Over the same time course, photon yield of oxygen evolution (measured at 25 C) increased by 15%.

In Epipremnum grown at 30 C, Fo values in photoinhibited leaves showed a linear decrease of about 8% during recovery whereas Fv/Fm increased exponentially by 50% (Fig. 5-23b). Photon yield increased by 40% during the same time course.

Recovery of photoinhibited Fatshedera leaves grown at either 20 or 30 C showed similar kinetics when evaluated at 20 C. Fo decreased rapidly during the time

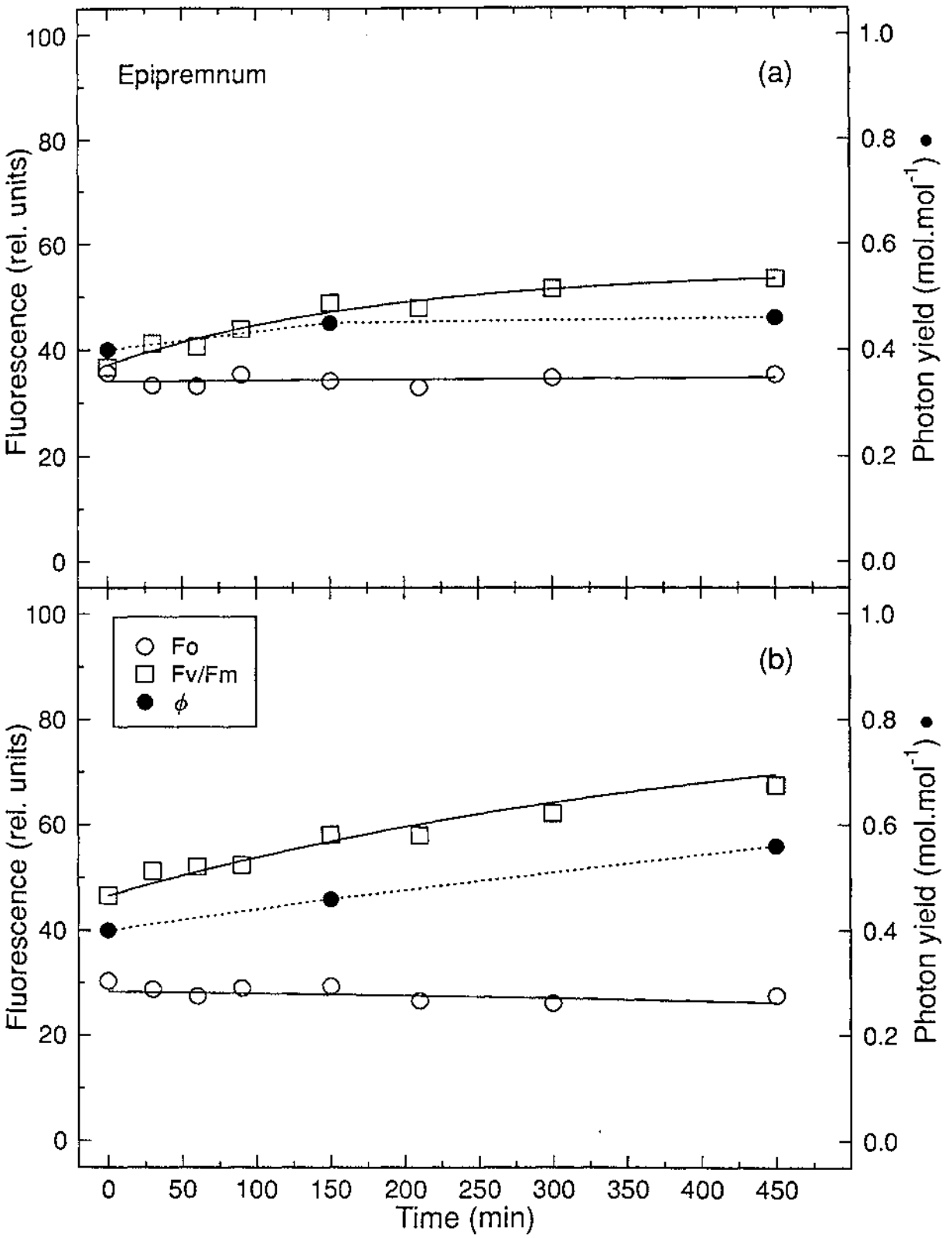


Fig. 5-23. Time course of recovery of Epipremnum leaves at 20 C after photoinhibition at 20 C and a PFD of 1200 μmol.m^{-2}.s^{-1} for 300 min. Effect of growth temperature (a) 20 C and (b) 30 C on chlorophyll fluorescence and photon yield (ϕ). Solid lines are the best fit of 2 or 3 leaves to Eqn.[5.9]

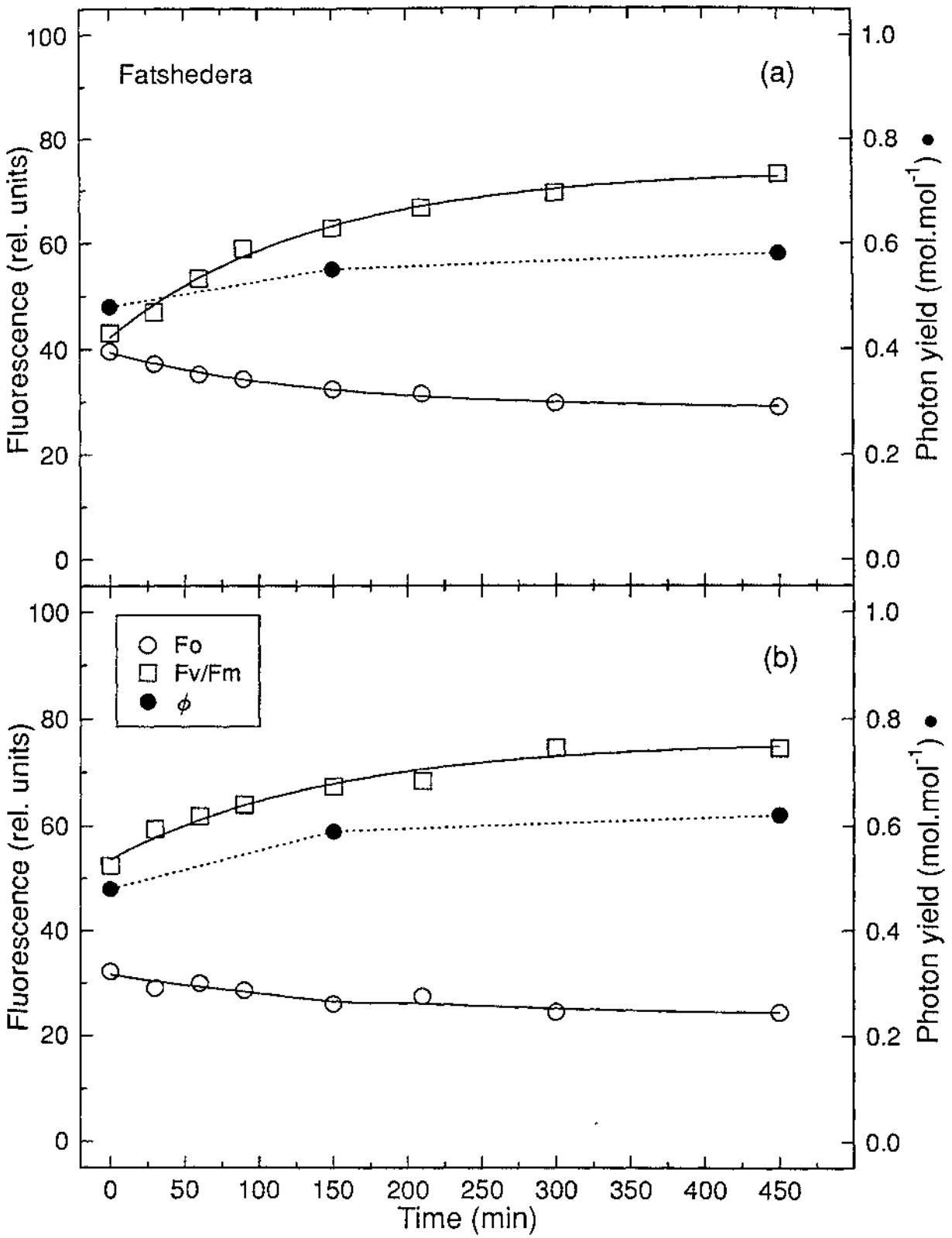


Fig. 5-24. Time course of recovery of Fatshedera leaves at 20 C after photoinhibition at 20 C and a PFD of 1200 μmol.m^{-2}.s^{-1} for 300 min. Effect of growth temperature (a) 20 C and (b) 30 C on chlorophyll fluorescence and photon yield (ϕ). Solid lines are the best fit of 2 or 3 leaves to Eqn.[5.9]

Table 5.7 Effect of growth temperature and current leaf temperature on the initial rate of recovery from photoinhibition and the rate constant for recovery in Epipremnum and Fatshedera leaves measured as change in Fv/Fm.

			Fv/Fm	
	Temperature (C)		Initial recovery rate ($x10^3$ min^{-1})	Recovery rate constant ($x10^3$ min^{-1})
Species	Growth	Leaf		
Epipremnum	20	10	0.0000051	n.d.
		20	.752	5.40 ± 2.12
		30	1.55	8.35 ± 2.02
Epipremnum	30	10	0.0000050	n.d.[z]
		20	.678	2.21 ± 1.59
		30	1.14	6.52 ± 1.11
Fatshedera	20	10	.0001	n.d.
		20	1.42	7.31 ± 2.26
		30	1.72	10.4 ± 1.70
Fatshedera	30	10	0.0000008	n.d.
		20	0.921	6.87 ± 1.75
		30	1.09	5.90 ± 0.96

[z]Not determined as time course was approximately linear (i.e. recovery was almost zero)

course to an asymptotic value between 24% and 26% lower than the initial photoinhibited value for each growth temperature (Fig. 5-24). Photoinhibited leaves from each growth temperature showed an exponential increase in Fv/Fm during recovery. At low growth temperature the final in Fv/Fm during recovery was to about 72% of the initial photoinhibited value, whereas at the higher growth temperature Fv/Fm increased by about 40%. Change in photon yield during recovery followed a similar pattern with an increase of about 21% (at 30 C) and 29% for the lower growth temperature.

In both species, the initial rate of recovery in Fv/Fm from photoinhibition proceeded more rapidly in leaves developed at the low growth temperature of 20 C compared with 30 C (Table 5-7).

5.3.8.2 Effect of leaf temperature on recovery of leaves from photoinhibition of photosynthesis

In addition to examining the recovery of Fv/Fm at 20 C, time courses of recovery from photoinhibition were also investigated at 10 and 30 C (Fig. 5-25, 5-26). The initial rate of recovery of Fv/Fm from photoinhibition was generally higher in Fatshedera than Epipremnum irrespective of the growth temperature or the recovery temperature (Table 5-7).

The initial rate of recovery of Fv/Fm from photoinhibition during the first 150 min at 10 C in Epipremnum leaves was negligible irrespective of the growth temperature, but was advanced by increasing leaf temperature above 10 C (Table 5-7). At 10 C the rate of recovery of Fv/Fm was also very slow irrespective of the growth temperature. Recovery of Fv/Fm in Fatshedera leaves proceeded more rapidly with increasing leaf temperature.

The final extent of recovery was calculated from the asymptotic values of exponential functions fitted to the Fv/Fm data. These results indicate recovery from photoinhibition was influenced more strongly by the current leaf temperature

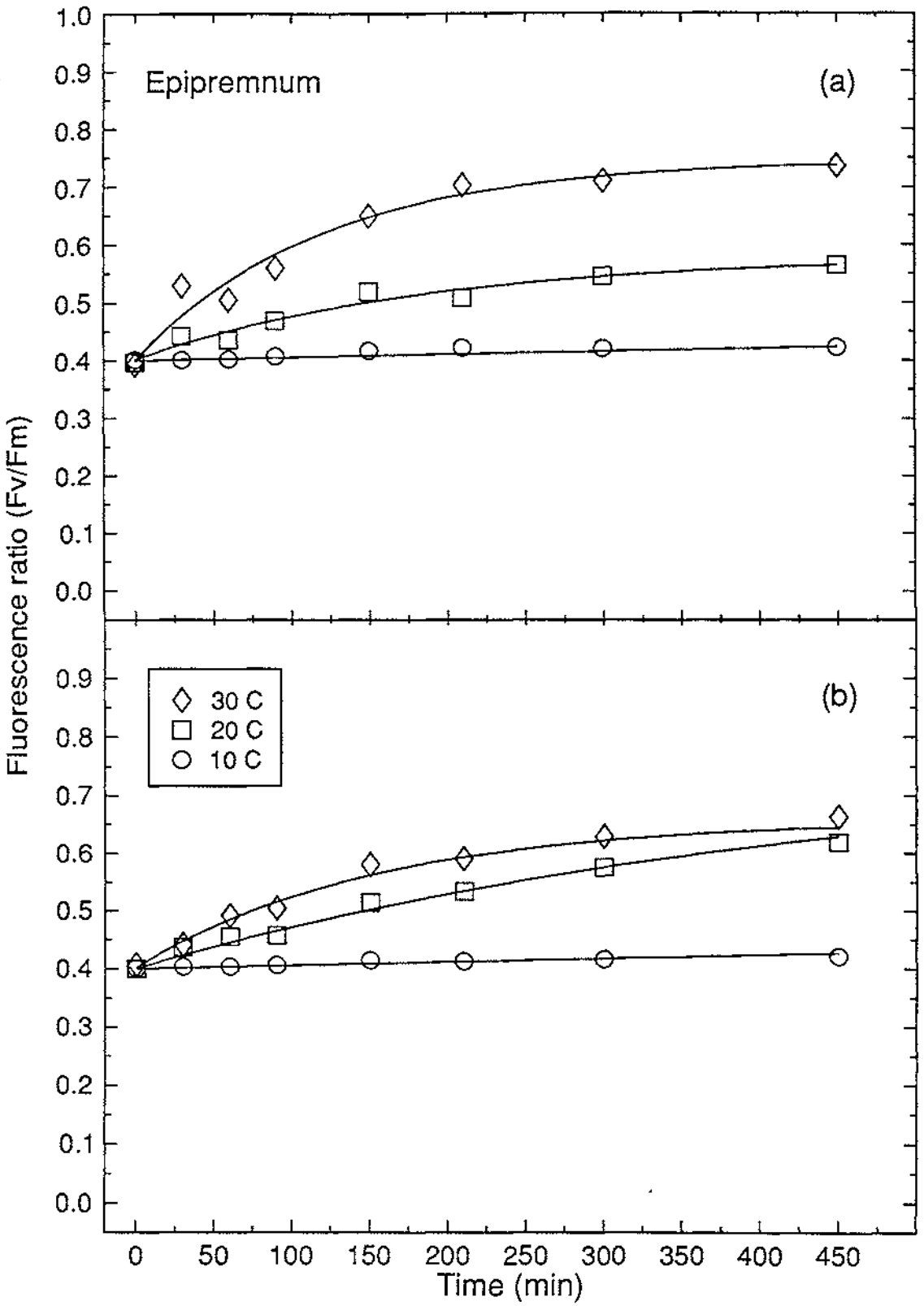


Fig. 5-25. Effect of growth temperature (a) 20C and (b) 30C and current leaf temperature (10, 20 and 30 C) on the time course of recovery of Fv/Fm in Epipremnum leaves following photoinhibition at 20 C with PFD of 1200 μmol.m^{-2}.s^{-1} for 300 min. Each line is the best fit to Eqn.[5.9] and the data are the means of 2 or 3 leaves. (Normalised to Fv/Fm = 0.4 at t = 0)

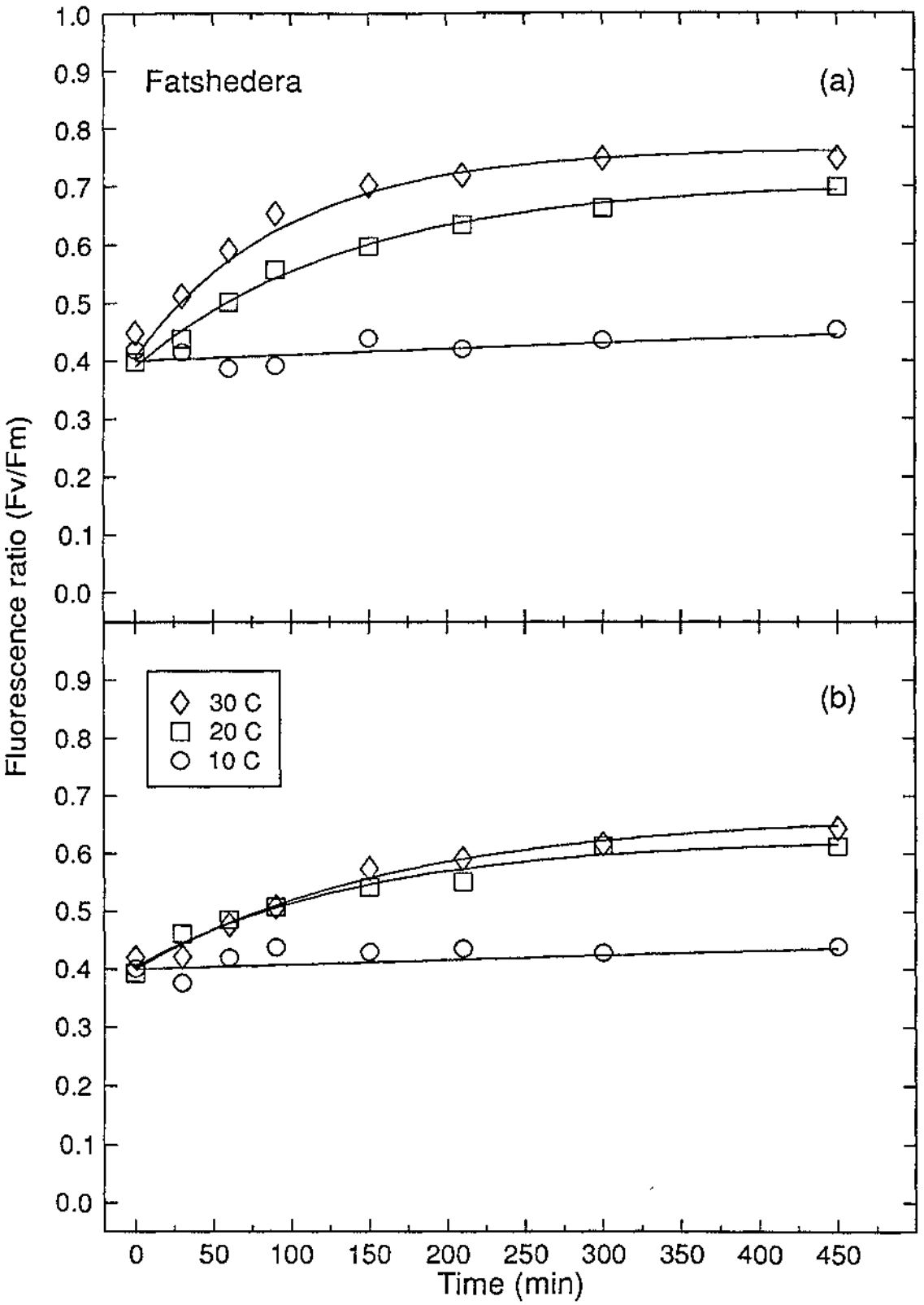


Fig. 5-26. Effect of growth temperature (a) 20C and (b) 30C and current leaf temperature (10, 20 and 30 C) on the time course of recovery of Fv/Fm in Fatshedera leaves following photoinhibition at 20 C with PFD of 1200 μmol.m^{-2}.s^{-1} for 300 min. Each fitted line is the best fit of Eqn.[5.9] and the data are the mean of 2 or 3 leaves. (Normalised to Fv/Fm = 0.4 at t = 0)

during recovery than the growth temperature. Recovery of both species at 10 C was limited to less than 10% of the control value, whereas at 20 or 30 C recovery was completed in less than 450 min (Figs. 5-25, 5-26). The initial slopes of regression lines fitted to data for each time course at leaf temperatures of 20 and 30 C were not significantly different from each other within each species and growth temperature. There was a consistent trend for the rate of recovery of Fv/Fm to proceed more rapidly in Fatshedera than Epipremnum at each leaf temperature examined between 10 and 30 C. This was most evident in leaves developed at 20 C and rather less apparent at 30 C. The temperature dependence of the recovery process indicated that approximately 50% more recovery occurred during the first 150 min for each 10 C increase in leaf temperature.

Figure 5-27 shows that the final extent of recovery of Fv/Fm from photoinhibition was influenced strongly by the current leaf temperature used for recovery. As noted previously recovery at 10 C was extremely slow in Epipremnum, whereas at 20 C recovery of Fv/Fm back to 60% of the controls was observed and at 30 C complete recovery occurred in less than 450 min. In Fatshedera leaves the extent of recovery at 10 C was less than 20% while at 20 and 30 C recovery was between 80 and 100%, respectively, at each leaf temperature.

These results show that the extent of recovery of Fv/Fm from photoinhibition of photosynthesis in Epipremnum and Fatshedera is dependent on the growth temperature and the current leaf temperature (Fig. 5-27).

5.3.8.3 Effect of temperature on recovery of Fo

During recovery from photoinhibition, reduction in Fo from the photoinhibited condition was directly related to the current leaf temperature (Fig. 5-28a). Relatively little change in Fo occurred at 10 C while the largest decrease in Fo occurred at 30 C. Each 10 C increase in leaf temperature used during recovery resulted in approximately 15% reduction in Fo.

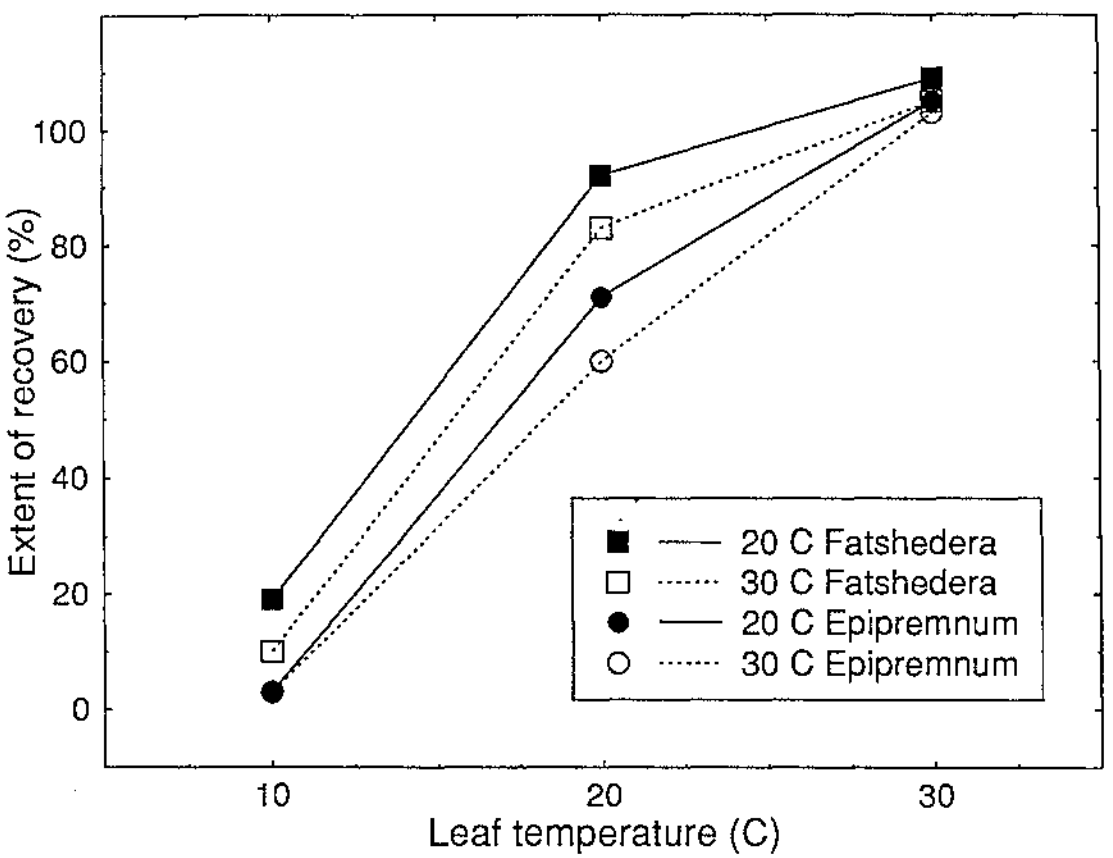


Fig. 5-27. The relationship between the leaf temperature and the extent of recovery of Fv/Fm (relative to controls) in Epipremnum and Fatshedera grown at either 20 or 30 C after photoinhibition at PFD of 1200 μmol.m^{-2}.s^{-1} for 300 min. Data are the mean of 2 or 3 leaves.

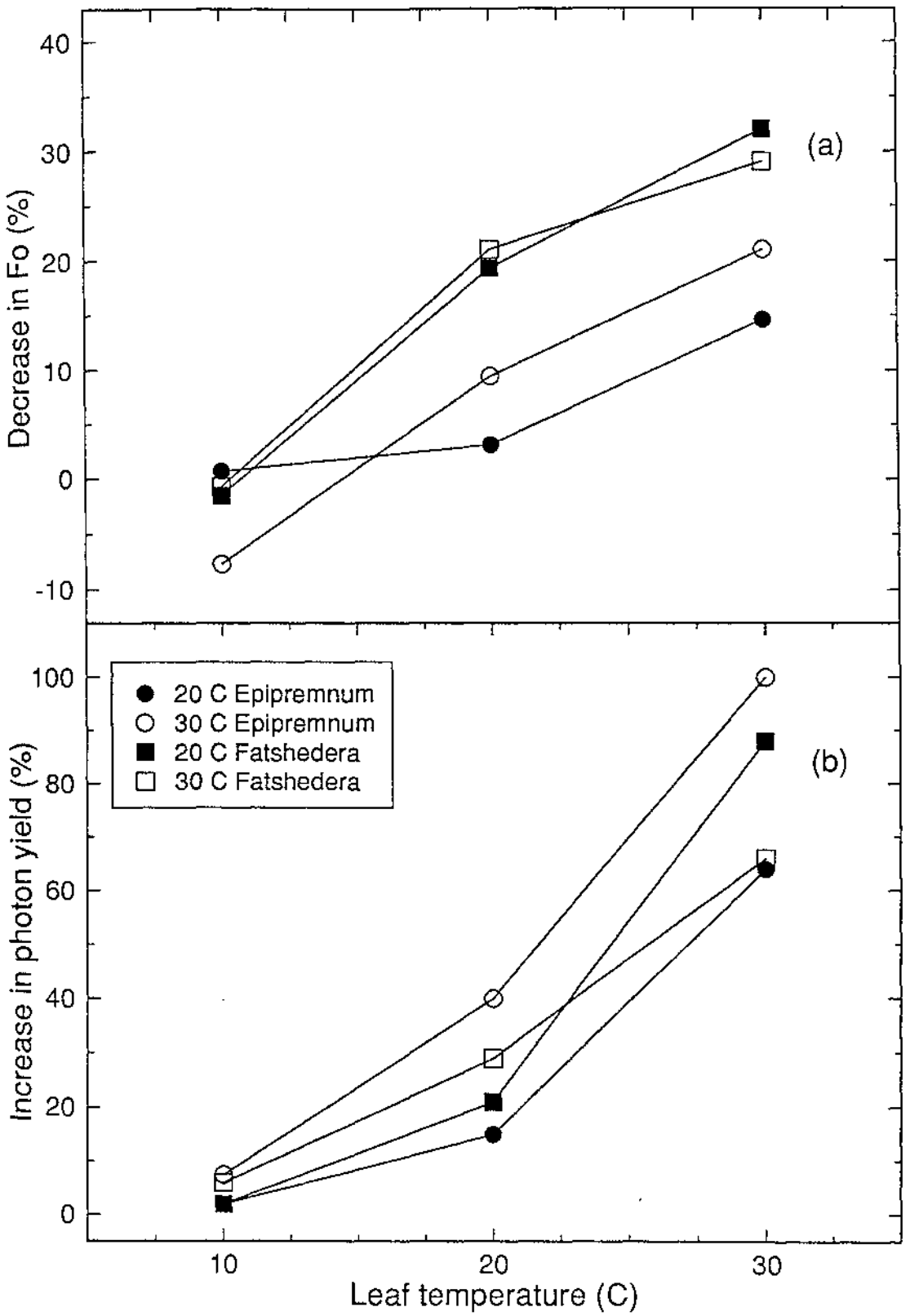


Fig. 5-28. Effect of leaf temperature on the extent of recovery in (a) Fo or (b) photon yield from photoinhibition at 20 C and PFD 1200 μmol.m^{-2}.s^{-1} for 300 min. Data are the mean of 2 or 3 leaves.

5.3.8.4 Effect of temperature on recovery of photon yield

The extent of change in photon yield during recovery was also temperature dependent. At 10 C about 8% increase in photon yield occurred in leaves of both Epipremnum and Fatshedera (Fig. 5-28b), as leaf temperature increased there was progressively more recovery of photon yield towards the original dark control values. The change in photon yield was markedly temperature-dependent in Epipremnum leaves where a curvilinear increasing occurred with increasing leaf temperature during recovery. In Epipremnum leaves grown at 30 C photon yield doubled during recovery at 30 C, this corresponded with complete recovery of Fv/Fm back to the control values. Epipremnum leaves developed at 20 C had higher photon yields after photoinhibition (than at 30 C), and recovered completely with regard to the change in Fv/Fm while photon yield increased by 65%.

In Fatshedera leaves at 20 C the change in photon yields during recovery were similar to Epipremnum irrespective of the growth temperature, but at 30 C Fatshedera leaves were less responsive than Epipremnum to increasing leaf temperature.

In Fatshedera leaves, like Epipremnum, photon yield increased in a curvilinear manner with increasing leaf temperature over the range from 10 to 30 C.
During recovery from photoinhibition each species was able to recover back to the control values for photon yield and Fv/Fm to a similar extent. The major difference between Epipremnum and Fatshedera was in the rate and not in the extent of recovery from photoinhibition.

5.4 Discussion

5.4.1. Growth response of Epipremnum and Fatshedera

Epipremnum produced more total leaf area and stem length at the higher growth temperature, whereas the opposite was true for Fatshedera (Table 5.1). Epipremnum was therefore better adapted to growth at 30 C as evident by the high shoot extension growth and increased leaf production at high temperature while, in contrast, more growth in Fatshedera occurred at the 20 C. The SLA was highest in both species at the temperature that was closest to their optimum for leaf development as found in Chapter three. Leaf development in Fatshedera was higher at 20 than at 30 C indicating the lower growth temperature was closer to the optimum for development whereas the opposite was found in Epipremnum. The growth response of each species in the constant 20 and 30 C CE treatments is consistent with results presented in Chapter three.

5.4.2 Effect of chilling temperatures in the dark

Experiments in Chapters three and four indicated that Epipremnum was more sensitive to chilling injury at low temperatures and in bright light than Fatshedera.

When Epipremnum and Fatshedera leaves were exposed to chilling temperature of 10 C for 450 min, the primary photochemistry and chlorophyll fluorescence characteristics were not adversely affected as long as leaves remained in the dark or under very low PFD conditions. This is consistent with reports of minimal effects of short periods of chilling on photon yield, and on either variable fluorescence (Fv) or the fluorescence ratio (Fv/Fm) with pea and cucumber (Peeler and Naylor,1988); spinach (Somersalo and Krause, 1988); kiwifruit (Greer, 1990) exposed in the dark or to maize under low PFD conditions (Ortiz-Lopez *et al.*, 1990).

Photosynthetic activity may be reduced after chilling of leaves (Martin *et al.*, 1981) or roots (Day *et al.*, 1991). Vallejos and Björkman (1983) reported that a single 12 h exposure to 5 C reduced net photosynthesis in tomato. Whereas Maenpää *et al.* (1988) demonstrated prolonged chilling for up to 4 days at 5 C in chilling-sensitive pumpkin caused a reversible reduction in photosynthesis that was largely restored when plants were returned to the original growth conditions (25 C). In contrast, Morgan *et al.* (1985) reported that growth at 10 C produced grossly impaired functioning of kiwifruit leaves that became evident as photo-oxidation and chlorophyll degradation. Similar effects were seen in earlier growth studies of Epipremnum and Fatshedera at 10 C (Chapter three).

Differences in the response of each species to growth temperatures may be related to the temperature dependence of photosynthesis and direct effects on the Calvin cycle (Berry and Raison, 1981; Leegood *et al.*, 1985; Brüggemann *et al.*, 1991). However, the differences may also have arisen from slow induction of photosynthesis (Sicher *et al.*, 1988) or reduced stomatal conductance at low temperature (Vallejos and Björkman, 1983; Peeler and Naylor,1988).

The thylakoid membrane in the chloroplasts of chilled leaves is probably the main site of temperature stress-induced photo-damage in leaves. This injury may be caused by structural or functional changes in membrane activity in chilling sensitive species and may be related to peroxidative destruction (Levitt, 1980; Maenpää *et al.*, 1988) or to changes in membrane glycolipids (Dekok and Kuiper, 1977; Wise and Naylor, 1987). However, when the underlying mechanisms considered responsible for this damage were investigated, Hodgson and Raison (1991) concluded that sensitivity to chilling-dependent photoinhibition could not be differentiated on the basis of the membrane lipids damaged by superoxides or by the radical scavenging activity of superoxide dismutase, but must rely on some unknown mechanism.

Chilling damage of the primary photochemistry sites (PS II) depends on the leaf temperature and interaction with moderate to high PFD levels. These results

show that impairment of the primary photochemistry does not occur from extended periods in darkness coupled with low temperature. Similar results have been reported by others (Greer, 1990; Somersalo and Krause, 1988; Ortiz-Lopez *et al.*, 1990; Smillie *et al.*, 1989) who indicated that little change in photon yield of photosynthesis or extent of photoinhibition occurred in the dark. Smillie *et al.* (1989) sought to differentiate between the chilling injury that occurred in the dark and in the light. They demonstrated that chilling intolerant species showed greater sensitivity to photoinhibition of photosynthesis at low temperatures and suggested that this may be due to greater sensitivity to high PFD.

5.4.3 Effect of leaf age on chlorophyll fluorescence.

There is limited information on the susceptibility of leaves of different ages to photoinhibition of photosynthesis. In this study there were no differences in the fluorescence ratio of Epipremnum and Fatshedera between leaves of different ages. This is indicative of a constant photon yield of oxygen evolution in young expanded leaves. In some woody plants like grape (Kriedemann, 1968), sour cherry (Sams and Flore, 1983) and kiwifruit (Buwalda *et al.*, 1991) high photosynthetic capability in individual leaves develops slowly and is maintained over an extended period. The rapid development of maximum photochemical efficiency and prolonged maintenance of high photosynthetic capacity observed in Epipremnum and Fatshedera are of adaptive significance to plants growing at low PFD. The decrease in photochemical efficiency in old sun-adapted leaves of beans (Powles *et al.*, 1979), potato (Prange, 1986), peas (Somersalo and Aro, 1987) and cucumber (Croxdale and Omasa, 1990) may correspond with increasing photoinhibition compared with younger leaves.

5.4.4 Photosynthesis

The light response curves for Epipremnum and Fatshedera were typical of relatively light-tolerant shade-plants with moderately high light compensation points and relatively high saturation PFD. A shade-adapted response was more apparent in Epipremnum than in Fatshedera. The maximum rates of photosynthesis obtained for Epipremnum and Fatshedera at 20 C were higher (69 and 35%, respectively) than those obtained at 30 C (Table 5.3) showing that both these species have greater capacity for photosynthetic electron transport at low temperatures. When Epipremnum and Fatshedera are transferred one temperature regime to another they are capable of functioning in that new environment, even if there has not been sufficient time for acclimation to occur.

Mature leaves of Nerium were capable of full photosynthetic acclimation in less than 2 weeks following transfer to a new growth temperature (Osmond *et al.*, 1980), which could be an important adaptive feature as seasonal changes in temperature occur outdoors, but would be of less concern in a temperature regulated environment. Björkman and Berry (1980) considered the acclimation of plants to low temperature required an increase in the net photosynthetic competence on a leaf area basis. This is in accord with the findings of this study. On the contrary, Pollock *et al.* (1984) and Araus *et al.* (1989) reported relatively little seasonal change in the photosynthetic capacity of ryegrass and several shade plants suggesting acclimation of plants to low temperature may not always be in accord with Björkman and Berry (1980).

Senser and Beck (1984) noted in chilling-resistant spinach, that the number of chloroplasts per cell decreased in the transition from summer to winter. Over the same period spruce chloroplast and mitochondria numbers increased. This organelle increase may be intended to ameliorate any low temperature stress damage.

Higher photosynthetic rates have been reported in leaves acclimated to cool compared with warm temperatures (Wilson and Cooper, 1969; Osmond *et al.*, 1980 and Sicher *et al.*, 1988). This may have been due to an increase in active mesophyll cells per unit area (Chabot and Chabot, 1977) or to differences in enzyme concentration (Björkman *et al.*, 1978) and probably not due to starch accumulation (Warrington *et al.*, 1977; Azcon-Bieto, 1983).

The higher photosynthetic capacity obtained for Epipremnum and Fatshedera at low temperature may be associated with greater capacity of the photosynthetic machinery in the leaves at low temperature and could be due to higher levels of $RUDP_2$ carboxylase. Pearcy (1977) showed that the activity of this enzyme (measured at a constant temperature) was about twice as high in low-temperature-grown *Atriplex lentiformis* plants as in high-temperature-grown plants of the same species. The photosynthetic capacity at low rate-limiting temperature was also twice as high in the low-temperature-grown plants.

Interestingly, Ceulemans *et al.* (1985) reported that in Epipremnum at 15 C the maximum photosynthetic rate was 4 $\mu mol \cdot m^{-2} \cdot s^{-1}$. This was between 35% and 60% of the photosynthetic rates for Epipremnum plants developed at PFD of 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and at a temperature of 30 or 20 C, respectively. The disparity between the current results and that of Ceulemans *et al.* (1985) arose from the differences in growth PFD. This is consistent with the findings of Chow *et al.* (1988) who showed that using a deep shade plant (*Alocasia macrorrhiza)* the light saturation PFD was a directly related to the growth PFD. Similar findings have been reported in sun plants such as *Atriplex* spp. (Björkman *et al.*, 1975) and rose (Lieth and Pasian, 1990).

The maximum rates of photosynthesis in Epipremnum and Fatshedera in this study were similar to those published by Demmig-Adams *et al.* (1989) in related plants such as *Hedera helix* and *Monstera deliciosa*. In contrast, they were higher than those reported by Araus *et al.* (1986) for *Fatsia japonica* and *Philodendron scandens*.

The light saturation point and the net photosynthetic rate at all PFD levels were higher in Fatshedera than in Epipremnum indicating that there were marked interspecific differences in the amount of photosynthetic machinery per unit area. This was correlated with the higher efficiency of the apparent light limited photon yield of oxygen evolution in Fatshedera than Epipremnum. The reduction in apparent ϕ in Epipremnum grown at 30 C compared to that at 20 C is indicative of higher sensitivity to photoinhibition of photosynthesis.

The PFD compensation point for each species was similar, irrespective of the growth temperature. Values obtained for Epipremnum were similar to plants grown at a PFD of about 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fonteno and McWilliams, 1978), but higher than reported by Ceulemans *et al.* (1985). The relative difference could be due to acclimation of plants to the growth PFD or some related environmental factor causing a shift in the balance of photosynthetic to non-photosynthetic tissue (Givnish, 1988).

Maximum photosynthetic rate, apparent photon yield, and PFD saturation point performance of Fatshedera was higher than in Epipremnum at 20 or 30 C. Related plants, such as Hedera and Fatsia have also shown similar photosynthetic characteristics (Araus, 1989). Jeong *et al.* (1983) reported that the PFD saturation point for Fatshedera did not vary with growth PFD, although the light compensation point decreased with decreasing PFD. This was probably due to a reduction in the dark respiration rate after adaptation to lower PFD as reported in other foliage plants (Fonteno and McWilliams, 1978).

A striking result of the present study was that Epipremnum plants grown at 20 C had a higher chlorophyll content per unit leaf area than those grown at 30 C. In contrast, Fatshedera leaves contained less chlorophyll per unit leaf area at 20 C than at 30 C. Araus *et al.* (1989) suggested in *Fatsia japonica* that increased leaf chlorophyll may protect thylakoids from damage during high light stress at low temperature. This further reinforces evidence from Chapters three and four suggesting that Epipremnum is less chilling tolerant than Fatshedera and better

adapted to growth at high temperatures. Bennett *et al.* (1982) reported that leaf chlorophyll changed in response to both growth and acclimation temperature. They showed that plants grown at 16 C had the lowest concentration of chlorophyll while those grown at 35 C had the highest.

Reduced chlorophyll concentration in Epipremnum was associated with the expression of a mericlinal chimera. The chimera produced large sectors of leaf tissue with negligible chlorophyll adjacent to normal chlorophyll bearing tissue. The chlorophyll deficient tissue was damaged by exposure to high PFD. The physiological characteristics of the green and the non-green tissues have been reported by Araus *et al.* (1986) and they suggested the development of the non-green tissue complied with Knoth's model (1975) for plastid degeneration in PS I deficiency mutants. Joiner (1981) reported that Epipremnum leaves were more variegated at light levels ca 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ without reference to any effect of growth temperature on pigmentation. The results in this study clearly demonstrate that the development of chlorophyll in Epipremnum is temperature dependent. The susceptibility of these leaves to photodamage may be linked to the inability of any functional PS II to perform normal photochemical activity in the absence of PS I and associated protective carotenoids (Sandman, 1991; Nie and Baker, 1991). Recently, Markgraf and Oelmüller (1991) showed that lutein accumulation, (the major carotenoid in the antennae of PS II) may regulate the appearance and functioning of PS II. This suggests that photons absorbed by the chlorophyll deficient tissue would not be utilised in normal photochemical electron transport and would prevent regeneration of the photosystems by continual photo-oxidation.

The results in the present study show that chlorophyll concentration in Fatshedera leaves was lower at 30 C compared to 20 C. Chlorophyll production in Fatshedera leaves at 30 C was impaired relative to 20 C. This suggests that some critical metabolic processes (including chlorophyll biosynthesis) may be controlled by the thermal inactivation of enzymes and/or be regulated by the chloroplastic genome at high temperatures, so that the gene expression is modulated in response to the environmental conditions (Gregory, 1989).

Epipremnum grown at 20 C was able to function effectively at 25 C and exhibited considerable flexibility in its temperature requirements. However, Epipremnum was less capable of photosynthetic activity at 15 C or 30 C. The temperature response curves for Epipremnum grown at 30 C indicated that generally photosynthetic activity was not influenced directly by the current leaf temperature. During photoinhibition of Fatshedera, leaves developed at 20 C showed little ability to maintain the level of photosynthesis over the temperature range 15 to 30 C. In contrast, leaves grown at 30 C exhibited some capacity to maintain photosynthesis at lower temperatures. This could suggests that when Fatshedera is stressed by growth above its optimum temperature it may develop heat shock proteins that facilitate tolerance of other temperature conditions (Vierling, 1992).

The temperature dependent photosynthetic responses of Epipremnum and Fatshedera were similar for each growth temperature. These results are in accord with findings discussed by Berry and Björkman (1980) in their review of temperature responses of photosynthesis and typical of many C_3 plants from cool temperate regions that show only a small effect of current leaf temperature. As growth temperature is increased there is an upward shift in the optimum temperature for light saturated photosynthesis. In a comparative study of *Nerium oleander* grown at contrasting temperatures the upward shift in photosynthesis with increasing temperature has been correlated with the activity of chloroplast fructose-1,6-bisphosphate phosphatase (Björkman and Badger, 1979).

5.4.5 Control Data

The chlorophyll fluorescence characteristics of Epipremnum and Fatshedera at growth temperatures of 20 and 30 C were similar, but the fluorescence characteristics of both species were higher at 20 C than at 30 C. This could be interpreted as both species having higher photochemical efficiency at lower growth temperature. Similar trends have been reported in kiwifruit (Greer and Laing, 1989) and contrasts with studies examining maize plants that varied in

their tolerance to low temperatures (Greer and Hardacre, 1989). No significant change in ϕ_i occurred in Epipremnum and Fatshedera leaves with increasing growth temperature, this is in accord with findings by Greer and Hardacre (1989). The chlorophyll fluorescence values obtained in this study were lower than those reported by Björkman and Demmig (1987). This suggests that the environmental conditions used for plant growth were responsible for some physiological stress on the plants. This would result in some impairment of the primary photochemistry of photosystem II occurring prior to the photoinhibition treatments (Powles and Björkman, 1982). Interestingly, Björkman (1987) reported little effect of growth environment on the chlorophyll fluorescence characteristics of unstressed leaves, although Demmig-Adams *et al.* (1989) noted a marked effect of PFD on the reduction in photosynthetic capacity, photon yield, and Fv/Fm in *Gossypium hirsutum*, *Rhizophora mangle* and *Monstera deliciosa*.

The rate constants for non-radiative dissipation (K_D) in Epipremnum and Fatshedera were approximately 20 % lower in leaves developed at 30 C instead of 20 C. Similar findings were reported in kiwifruit (Greer and Laing, 1989) and in related species such as Monstera and Hedera (Demmig-Adams, 1989), however their reported K_D values were higher than obtained in this study. The disparity may arise from differences in each growth environment (light and temperature). Increases in K_D probably reflect a mechanism for dissipation of excess absorbed energy rather than allowing photoinhibitory damage of the reaction centre (Cleland *et al.*, 1986) by thylakoid protein denaturation (Kyle and Ohad, 1986). The K_D values may increase during growth at high PFD (Greer and Laing, 1988) and is reflected in concomitant quenching of Fm and Fo. This can occur where Fo initially rises and then falls during photoinhibition with a concurrent reduction in Fm. In contrast, an increase in the rate constant for photochemistry (K_P) is associated with quenching of Fm and an increase in Fo (Demmig and Björkman, 1987; Demmig *et al.*, 1987).

5.4.6 Photoinhibition of photosynthesis

When intact Epipremnum and Fatshedera leaves were exposed to high PFD, photoinhibition of photosynthesis was manifested as a marked quenching of chlorophyll fluorescence (Fv/Fm) at 77 K, coupled with concomitant reduction in light-saturated photosynthesis and photon yield of oxygen evolution. All leaves exposed to PFDs higher than that received during growth showed similar behaviour. Similar findings have been reported by Demmig and Björkman (1987) and Greer and Laing (1989).

The reduction in photon yield, although indicative of photoinhibition, did not share the same kinetics as the change in photosynthesis and Fv/Fm. A similar disparity has been reported previously by Greer *et al.* (1988) and Ortiz-Lopez (1990). Adams *et al.* (1990) suggested that these differences may arise when several environmental factors (such as moisture and temperature stress), including light, interact during photoinhibition.

The results of this study show that the extent of photoinhibition in leaves of Epipremnum and Fatshedera, and hence the reduction in photochemical efficiency, was directly related to three main factors, (1) the PFD during photoinhibition, (2) the leaf temperature during photoinhibition and (3) the growth temperature.

When Epipremnum and Fatshedera leaves were exposed to PFD levels greater than the growth PFD, reduction in chlorophyll fluorescence proceeded with quasi first order kinetics with an initially high rate that declined as a steady state was approached. Similar findings have been reported for a range of plants (saltbush: Björkman *et al.*, 1972; oleander: Powles and Björkman, 1982; duckweed: Ögren and Öquist, 1984; bean: Greer *et al.*, 1986; monstera: Demmig and Björkman, 1987; kiwifruit: Greer and Laing, 1988) from widely differing habitats.

The time courses of photoinhibition induced in Epipremnum and Fatshedera leaves at high PFD are typical of both herbaceous (Greer *et al.*, 1986; Greer and Hardacre, 1989) and woody species (Powles and Björkman, 1982; Greer and Laing, 1989).

These experiments have shown that the extent of photoinhibition in bright light depended on the intensity and duration of exposure to high PFD. Greer (1990) and Greer *et al.* (1991) reported similar findings with a range of other crop plants. At low PFD minimal photoinhibition was observed and increasing PFD produced more severe photoinhibition. The high PFD of 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ produced chronic irreversible photoinhibition causing permanent chlorophyll loss in Epipremnum, but not in Fatshedera leaves. In both species a marked decrease in Fv/Fm and a rise in Fo occurred at the high PFD. The exacerbation of photoinhibition with increasing PFD may be anticipated as the absorption of light energy would increasingly exceed the rate of energy dissipation through normal photochemistry and non-radiative dissipation (Björkman, 1987).

Photo-oxidative bleaching of chlorophyll, occurring after prolonged exposure to high irradiance, is considered to be a secondary response developing from photoinhibition (Powles,1984). Epipremnum leaves were susceptible to chronic photoinhibition and chloroplast dysfunction evident by disintegration of thylakoid membranes following 450 minutes exposure to 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and loss of bulk chlorophyll (Plate 5-7). While no direct relationship may exist between the extent of photoinhibition and chlorophyll destruction (Powles *et al.*, 1979), permanent loss of chlorophyll may occur following severe photoinhibition of photosynthesis. It is clear that when damage occurs during exposure to high PFD then complete destruction of the light harvesting system could occur when the plant has little capacity to recover.

These experiments showed that chronic photoinhibition developed in Epipremnum leaves grown at 30 C and after prolonged exposure to high PFD at 15 or 20 C, whereas photoinhibitory treatments using higher leaf temperatures or lower PFD

did not cause permanent damage and probably permitted the repair of damaged chloroplasts by ongoing protein synthesis (Ohad *et al.*, 1984; Cleland *et al.*, 1986; Greer *et al.*, 1986). A stable equilibrium is attained when the rate of protein turnover in PS II following photoinhibitory damage is balanced by the rate of synthesis and replacement of the reaction centre D1-protein (Ohad *et al.*, 1984). Extreme levels of photoinhibitory damage are evidently irreversible at low temperature and are exacerbated by plant development under warm conditions.

Results from this investigation support earlier findings (Chapter three) that the growth of Epipremnum and Fatshedera at low temperature and high PFD is exhibiting evidence of chronic photoinhibition of photosynthesis resulting in reduced vegetative growth and permanent changes in leaf pigmentation. Evidence of ultrastructural alterations and photobleaching following exposure to high PFD at low temperature has been reported in sorghum and paspalum (Taylor and Craig, 1971), cucumber (Van Hasselt and Van Berlo, 1980), bean and cotton (Wise *et al.*, 1983) and in kiwifruit (Morgan *et al.*, 1985).

Leaf temperature during photoinhibition markedly influenced the concomitant reduction in net photosynthesis and Fv/Fm in Epipremnum and Fatshedera leaves exposed to bright light. Data from these experiments clearly showed that the extent of Fv/Fm quenching exhibited a pronounced linear dependence on leaf temperature and photoinhibition, increased dramatically as the leaf temperature decreased from 30 to 15 C in both species. These results are in agreement with findings by Greer *et al.* (1988) and at variance with Adams *et al.* (1990) who reported that the shade plant *Monstera deliciosa* was relatively insensitive to temperature (over the range 10 to 30 C) during photoinhibition and attributed this to its relatively low capacity to dissipate energy via electron transport. The strong temperature dependence of Epipremnum and Fatshedera leaves to photoinhibition is consistent with the view that temperature may be directly influencing the ongoing repair of damaged PS II sites during photoinhibition (Ohad *et al.*, 1984; Greer *et al.*, 1986; Greer *et al.*, 1991) .

The susceptibility of leaves to photoinhibition is reported to increase at low temperatures (Ögren *et al.*, 1984; Greer *et al.*, 1986). This may arise from an excess excitation of chlorophyll not being transferred via photochemistry to PS I or being dissipated harmlessly as non-radiative dissipation. The ongoing repair of PS II units is inhibited and other mechanisms for dissipating excess energy being incapacitated at low temperature (Öquist, 1987).

During photoinhibition reductions in net photosynthesis, Fv/Fm and photon yield were invariably less in leaves developed at the low growth temperature. The reduction in net photosynthesis was always less in Fatshedera than in Epipremnum in leaves grown at 20 instead of 30 C. A similar trend was evident in Fv/Fm and photon yield data. There were marked differences in the response of Fo during photoinhibition in leaves of both species from each growth temperature. In leaves developed at 30 C Fo decreased by 50 - 65% with a concomitant reduction in Fv/Fm. This could be interpreted as evidence of direct PS II impairment either in the reaction centre or nearby (Cleland *et al.*, 1986).

In leaves developed at 20 C the change in Fo paralleled the change in Fv/Fm. At a leaf temperature of 15 C there was an equal increase in Fo in leaves from each growth temperature, but as the leaf temperature was increased there was progressively less increase in Fo during photoinhibition, until at 30 C there was a small net decrease in Fo. Similar results have been reported in kiwifruit leaves (Greer and Laing, 1989).

Quenching of fluorescence ratio and instantaneous fluorescence during exposure to high PFD is evidence of harmless redistribution of energy trapped by PS II indicating that quenching was caused by an increase in non-radiative energy dissipation in the pigment bed (Demmig and Björkman, 1987). There is now considerable evidence that a parallel increase in zeaxanthin is responsible for the increased capacity to dissipate excess energy through the violaxanthin cycle (Demmig *et al.*, 1987, 1988; Demmig-Adams *et al.*, 1989) which is present in almost all plants (Hager and Stranksy, 1970). Although not evaluated in these

species it is highly probable that zeaxanthin is involved in the protection of the photosynthetic apparatus and is considered to be a general phenomena occurring widely in plants (Adams and Demmig-Adams, 1992).

The relatively high sensitivity of Epipremnum and Fatshedera leaves to photoinhibition at high growth temperatures may also be related to their restricted capacity to dissipate light excitation energy by electron transport from PS II as reported in *Monstera deliciosa* (Adams *et al.*, 1990). This is supported by the higher rates of photosynthesis found in Epipremnum and Fatshedera at the lower growth temperature.

5.4.7 Recovery

Leaves of low PFD-grown Epipremnum and Fatshedera recovered from photoinhibition induced by high PFD when transferred to low PFD. The time taken for recovery depended on the severity of photoinhibition and temperature during recovery. When leaves were exposed to high PFD and low temperatures, acute photoinhibition occurred. Greer and Laing (1988) also showed that rate of recovery depended on the extent of photoinhibition and the recovery conditions.

Recovery of leaves from photoinhibition induced by high PFD was highly dependent on the leaf temperature during the recovery phase, with the maximum rate of recovery occurred at 30 C, and with very little recovery at 10 C. This is consistent with the results of temperature dependence of recovery in widely differing plants such as bean (Greer *et al.*, 1986), maize (Greer and Hardacre, 1988), kiwifruit (Greer and Laing, 1988a,b; Greer *et al.*, 1988) and barley (Greer *et al.*, 1991). It is important to note that in Fatshedera leaves recovery always proceed more rapidly back towards the control values than in Epipremnum. This indicates that while both species were similar in their overall sensitivity to photoinhibition the chilling-tolerant Fatshedera was able to recover more efficiently than the chilling-sensitive Epipremnum at low leaf temperatures irrespective of the growth temperature.

In this study and in similar investigations complete recovery from photoinhibition in spinach (Krause *et al.*, 1985), Kiwifruit (Greer *et al.*, 1986; Greer and Laing, 1988), Hedera and Monstera (Demmig and Björkman, 1987) occurred where leaf temperatures were high enough for leaves to be physiologically active.

The time course of recovery in Epipremnum and Fatshedera leaves showed that recovery from photoinhibition commenced immediately the high PFD stress was removed, indicating that the enzymes required for chloroplast-encoded protein synthesis were already present and functioning. This suggests that the repair process could have been occurring during photoinhibition or at least been repressed, but not inactivated by photoinhibition as this would require the synthesis of enzymes to rebuild damaged thylakoid membranes or PS II units. This hypothesis supports similar results in higher plants (Greer *et al.*, 1986) and algae (Samuelsson *et al.*, 1985) that the net photoinhibition induced in leaves exposed to high light is the balance between the concurrent rate of damage and the rate of repair.

The higher initial rate of recovery in Epipremnum and Fatshedera leaves developed at 20 C relative to growth at 30 C suggests that they possess a greater capacity to sustain and counter photoinhibitory damage. Leaves acclimated to cooler temperatures (20 C) also have more ability to transfer excitation energy through electron transport in photosynthesis than those acclimated to warmer temperatures (30 C). Fatshedera plants have a temperature optima between 20-25 C for maximum vegetative growth, with marked growth repression occurring at higher temperatures. In contrast, the growth optima for Epipremnum is near 30 C. This is reflected in the recovery of Fo, Fv/Fm and photon yield, with increasing leaf temperature. In Fatshedera these parameters changed rapidly at 20 C and at slower rates at 30 C, whereas recovery in Epipremnum leaves showed no sign of abatement with increasing temperature.

These results confirm the findings of Somersalo and Krause (1989) using spinach and Greer and Laing (1989) using kiwifruit where growth at low temperatures was

reported to increase the competence of plants to recover from photoinhibitory stress.

Although not examined in the course of this study a number of mechanisms have been proposed to account for the role of growth temperature on recovery. This may arise from increased capacity to dissipate excess excitation energy through the violaxanthin-zeaxanthin pathway (Demmig *et al.*, 1987, 1988); or enhancement of the cytochrome b-559 cycle (Thompson and Brudvig,1988), protection from triplet oxygen species is also increased in cold acclimated plants (Schöner and Krause, 1990), while catalase activity is decreased (Volk and Feierabend,1989). The ascorbate-glutathione cycle (Foyer *et al.*, 1989) may play a role in protection of thylakoid membranes in some species. Membrane lipid composition may be altered to confer increased protection to photoinhibitory damage (Senser and Beck, 1984) and finally high chloroplast numbers (Araus *et al.*, 1989) may distribute light interception and trapping among a larger number of active reaction centres, and this coupled with an increased rate of protein turnover (Falk *et al.*, 1990) would facilitate rapid restoration of the reaction centres.

In Fatshedera, Fo generally decreased with a concomitant increase in Fv/Fm occurring during recovery, whereas in Epipremnum leaves minimal change in Fo occurred. Even at 30 C the increase in Fo did not match the increase observed in Fatshedera leaves at 20 C. The increase in photon yield of oxygen evolution during recovery in Epipremnum paralleled the change in Fv/Fm, but in Fatshedera leaves photon yield increased much more slowly suggesting that the repair process may be different or be proceeding less efficiently. A similar pattern was evident in the reduction of photon yield during photoinhibition in Epipremnum and Fatshedera leaves, indicating a similar temperature dependence in both photoinhibition and recovery.

It was beyond the scope of these experiments to investigate the underlying mechanisms operating in these plants. However three hypotheses are presented

to explain the exacerbation of photoinhibition during exposure to high PFD at low temperature:

Firstly, low temperatures are considered to lower the enzymatic activity and diffusion-dependent reactions of photosynthesis. This decreases the quantity of photons absorbed by photosystem II that can be utilised effectively in photochemical reactions. Low temperatures act by limiting the dissipation of excitation energy in photochemistry, which exacerbates photoinhibition (Ögren *et al.*, 1984; Tyystjarvi *et al.*, 1989; Bilger and Björkman, 1991).

Secondly, low temperatures may have a direct effect on recovery from photoinhibition (Greer *et al.*, 1986, 1991; Greer and Laing, 1988; Peeler and Naylor, 1988; Greer and Hardacre, 1989; Burke, 1990). During normal functioning of PS II the D1 protein in the reaction centre is denatured during electron transfer. The damaged protein is removed from the reaction centre and replaced by a functional D1 protein (Guenther and Melis, 1990). Although this process occurs extremely rapidly, it is temperature dependent (Baker, 1991). At low temperatures the rate of repair and recovery may be insufficient to cope with the rate of damage incurred, while the interception of light continues unabated. Photoinhibition will increase in severity as the recovery process is inhibited by low temperatures and bright light.

Thirdly, low temperatures cause perturbation of membrane composition. Membrane lipids can undergo lateral phase separation in chilling-sensitive plants. Lipids gel near the point of chilling injury and contribute to the chilling injury response (Terzaghi *et al.*, 1989). Damage to thylakoid membranes may follow dissipation of the proton gradient through leaks formed when the integrity of the membranes is disrupted at low temperatures and high PFD

(Jurinsic, 1986). The absence of some thylakoid proteins at low temperature may also be due to an inability of plants to stabilise newly synthesised proteins or polypeptides in the membranes due to temperature induced changes in polypeptide processing or lipo-protein interactions (Nie and Baker, 1991).

Further experiments are required to critically evaluate these ideas and to develop a unifying hypothesis explaining the underlying mechanisms of fluorescence quenching and recovery that will be applicable to chilling-sensitive and chilling-resistant plants.

5.4.8 Summary

In summary, when Epipremnum and Fatshedera leaves were exposed to PFD levels greater than the growth PFD, reduction in chlorophyll fluorescence proceeded with quasi first order kinetics, with an initially high rate, that declined as it approached a steady state. Both species were similar in their sensitivity to photoinhibition manifested as a temperature-dependent quenching of chlorophyll fluorescence (Fv/Fm) at 77 K, coupled with concomitant parallel reduction in light-saturated photosynthesis and photon yield of oxygen evolution.

The chlorophyll fluorescence characteristics of Epipremnum and Fatshedera at growth temperatures of 20 and 30 C were similar, while the fluorescence characteristics of both species were higher at 20 C than at 30 C. This could be interpreted as both species having higher photochemical efficiency at the low growth temperature and reflects the high maximum rates of photosynthesis in Epipremnum and Fatshedera. This response is typical of light-tolerant-shade plants with relatively high saturation PFD.

Fatshedera leaves were more resistant to change in photosynthesis than Epipremnum during photoinhibition. Chronic photoinhibitory damage developed in Epipremnum leaves grown at 30 C after prolonged exposed to high PFD at

20 C or 15 C, whereas photoinhibitory treatments using higher leaf temperatures or lower PFD did not cause permanent damage. Bright light was a regulating factor determining impairment of the primary photochemistry and quenching of chlorophyll fluorescence in leaves.

Both species were similar in overall sensitivity to photoinhibition, however chilling-tolerant Fatshedera was able to recover more efficiently than the chilling-sensitive Epipremnum at low temperatures irrespective of the growth temperature. This was an important factor in explaining the differences in environmental response of each species.

CHAPTER SIX

Final Discussion

'The time has come', the Walrus said,
'To talk of many things:
Of shoes——and ships——and sealing wax——
Of cabbages——and kings——
And why the sea is boiling hot——
And whether pigs have wings.'

Through the looking-glass.
Lewis Carroll. 1896.

6.0 Introduction

Vegetative growth of many foliage plants is promoted by warm temperate conditions and by photon flux densities (PFDs) less than full sunlight. The ability to define the environmental requirements for development and vegetative growth of plants like Epipremnum and Fatshedera should provide the opportunity to schedule the greenhouse production of these crops more accurately. The information gained in this study may also have application to other plant species in the vegetative growth phase.

The relationship between growth and development of Epipremnum and Fatshedera with respect to temperature and light has not been examined systematically before, presumably because of the perceived relatively low importance of ornamental plant crops. Furthermore, few people have examined the relationships between growth and physiology of chilling and non-chilling sensitive plants with environmental factors. This study has depended heavily upon controlled environment (CE) facilities to establish the environmental conditions used. Non-invasive techniques were used in this study to monitor photosynthetic efficiency of intact leaves when exposed to different light and temperature conditions. The influence of growth and current leaf temperature on the inhibition of photosynthesis by bright light and its subsequent recovery were

followed using chlorophyll fluorescence techniques developed by Greer and Laing (1988).

Temperature-based models have been developed to assist in the production and scheduling of some flowering greenhouse crops like Easter Lily (Karlsson *et al.*, 1988) and chrysanthemum (Heins and Carlson, 1990; Larsen and Gertsson, 1992) but, no similar models appear to have been published for foliage plants. Although not of major economic concern in New Zealand, these plants have export potential. The environmental response information obtained could also be of increasing importance in resolving current ecological issues. Furthermore, understanding how these crops interact with environmental factors can help growers develop a more efficient and more effective competition to plants imported from countries where greenhouse heating may be of lesser importance.

The production time for Epipremnum or Fatshedera is dependent upon the time required for development of an acceptable plant height, and plant leafiness which will be a function of leaf number and leaf area at time of sale. Understanding how these factors are influenced by temperature and light would be a significant step towards providing greenhouse managers with essential environmental physiology information. This would enable production decisions to be made on a more informed basis as managers gain some appreciation of how temperature and light influence production of plants to particular market specifications.

Growth and development of both Epipremnum and Fatshedera can be manipulated by temperature and light during plant production. Each environmental factors must be present within a range close to optimum allowing for acceptable rates of physiological activity while minimising stress.

Temperature proved to be the most important environmental factor investigated. Plant growth and development was usually related to the mean daily temperature and was only influenced slightly by the PFD. Formation of photoassimilates and

dry matter accumulation was increased with higher PFD, but this was reflected in only minor differences in the appearance of the foliage plants studied.

Where plants are exposed to environmental conditions far removed from the optimal situation then the response of each species depends on the particular combination of temperature and light. Both species were of similar sensitivity to high light induced photoinhibition, but the more chilling resistant Fatshedera had greater capacity to recover from photoinhibition at low temperatures than Epipremnum.

This thesis has been concerned with the comparison of temperature and light on the growth and development of Epipremnum and Fatshedera. These relationships have been discussed in the preceding chapters.

While it was beyond the scope of this study to investigate all aspects relating to the interaction of temperature and light on the growth and development of Epipremnum and Fatshedera; a simple schematic model describing the qualitative relationships reported in this study and in other related published work is illustrated in Figures 6-1 and 6-2.

In this chapter the relationships between temperature and light and their interaction with each species will be discussed in relation to these models.

6.1 Simple Model

The growth of whole plants can be described by either growth analysis or biochemical techniques and this model attempts to integrate these two approaches. Plants can be considered as comprising 5 active compartments (Fig. 6-1). Photosynthesis can increase the pool of soluble low molecular weight carbohydrates when photosynthetic tissues (mainly leaves) are exposed to adequate PFDs and appropriate temperatures. Soluble carbohydrates from this labile pool may be channelled into structural components as the plant grows or

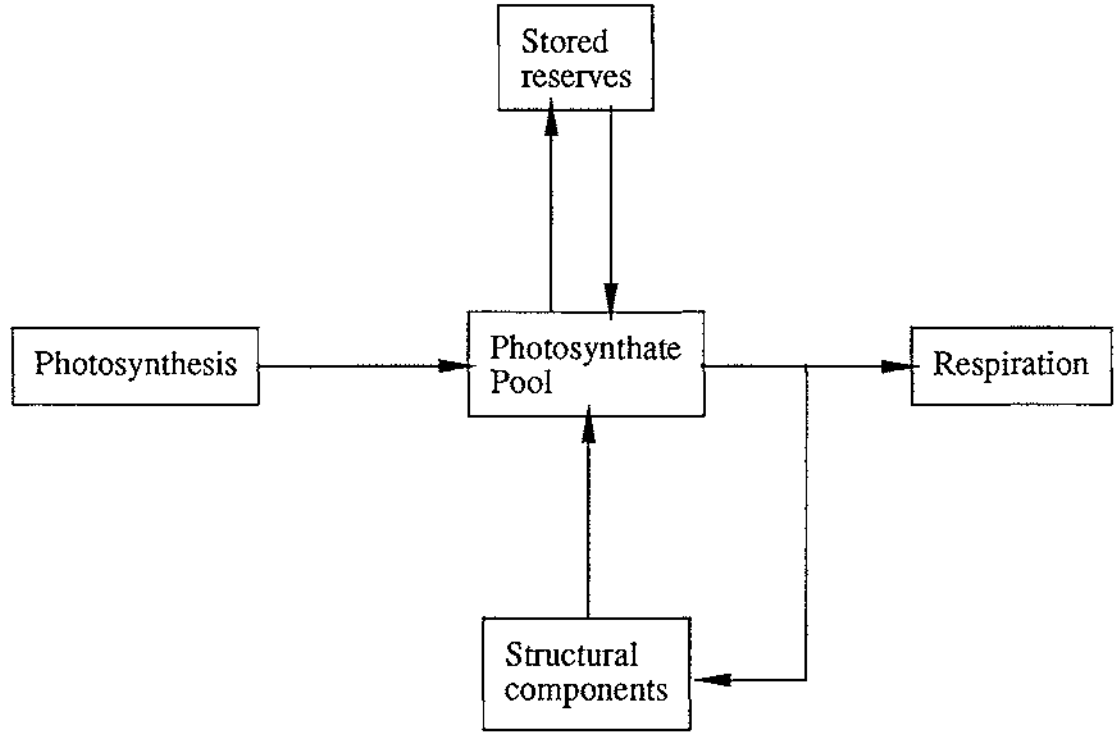


Fig. 6-1. A simple schematic model of a foliage plant.

into storage as either soluble sugars and complex polymers like starch. These polymers may be converted back into soluble forms to maintain the carbohydrate pool utilised for maintenance and growth. Anabolic processes related to growth depend on energy released through respiration of carbohydrates, while catabolic metabolism releases energy as biological materials are broken down and recycled. Models of this type allow partitioning of fixed carbon and other resources in a relatively complex manner (McCree and Amthor, 1982). However, this simple model attempts to allocate photoassimilates without cognisance of how environmental factors may influence the production of resources, and their distribution between competing sources and sinks within the plant. The response of Epipremnum and Fatshedera to the effects of temperature and light are both complex and species dependent.

6.2 Extended Model

The extended schematic model (Fig. 6-2) will attempt to address some of the limitations of the simple model and incorporate the findings arising within this thesis and other published work into a model that more closely represents the functioning of foliage plants.

6.2.1 Effect of Temperature

6.2.1.1 Growth Temperature

All plants have minimum, optimum and maximum temperatures for growth. The temperature response is governed by a complex interaction of genetic, developmental and cultural factors that moderate the environmental response of each species. Excessively high or low temperatures inactivate normal metabolism. Growth temperature has an important bearing on the development of metabolic components that determine physiological capacity and activity. The

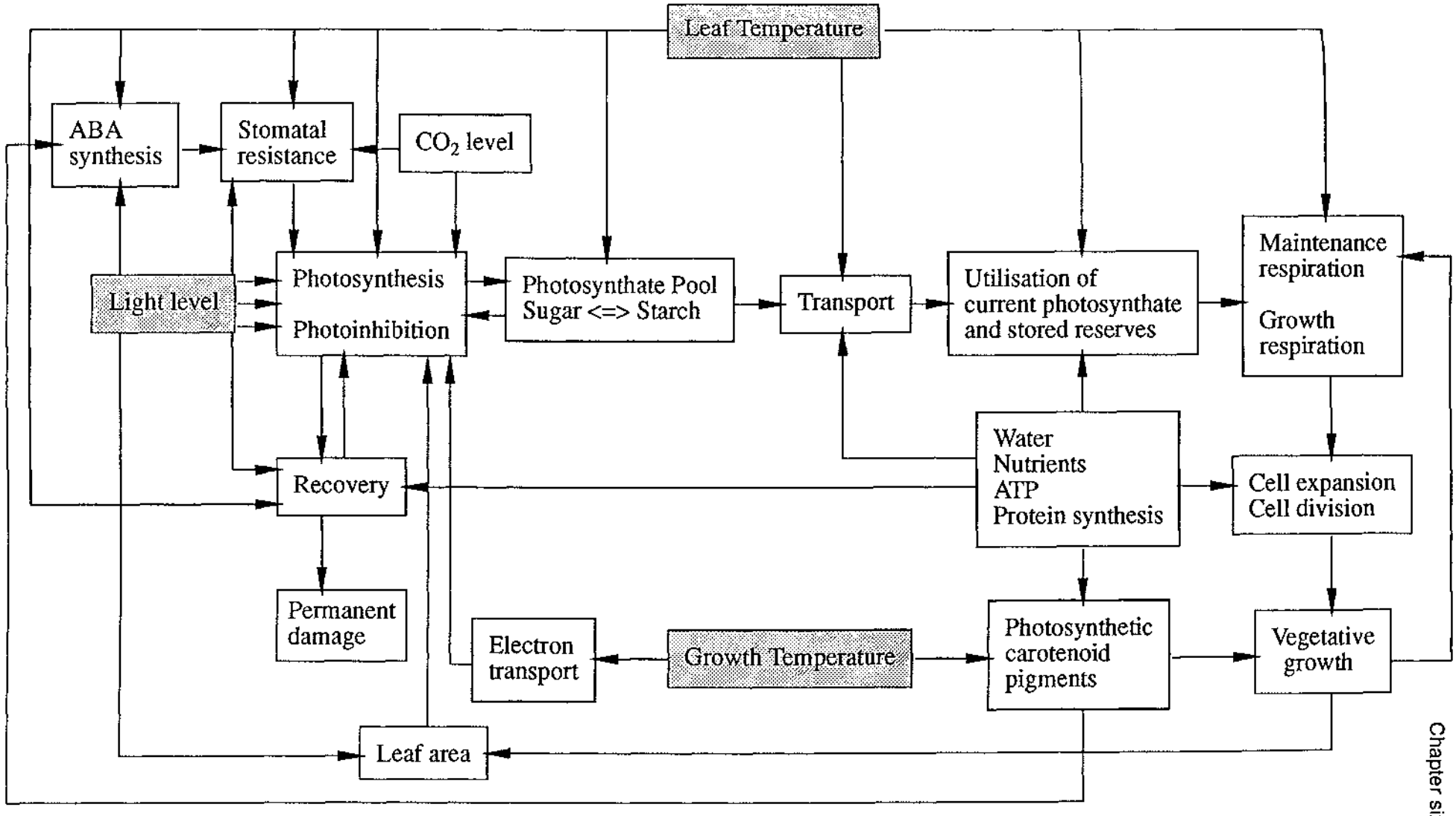


Fig. 6-2. Schematic diagram representing the interaction of light and temperature on growth of Epipremnum and Fatshedera. Major environmental factors studied in this thesis are in the shaded boxes.

growth temperature has a direct effect on development of chlorophyll and probably influences accessory pigments (such as carotenoids) in a similar manner. At low growth temperature chlorophyllous pigments were higher per unit weight than at high temperature . This coincided with increased electron transport capacity compared with plants developed at higher temperatures. In this study it has been observed that plants grown at low temperatures have higher photosynthetic capacity than those grown at higher temperatures. This probably arose from increased density of the photosynthetic apparatus in leaves as a direct consequence of the relatively greater impact of low temperature on leaf expansion than on development of photosynthetic competence (Bunce, 1986).

Protection of the photosynthetic apparatus from damage at low temperature may be related to the higher levels of photosynthetic and accessory pigments in the pigment bed of thylakoid membranes (Araus *et al.*, 1989). Carotenoids may have a specific role in the protection of the thylakoid membranes from photoinhibitory damage. When photoinhibitory conditions predominate, these pigments could confer protection by allowing greater energy dissipation by the interconversion of components of the xanthophyll cycle (Demmig-Adams, 1990; Schreiber and Neubauer, 1990). The presence of zeaxanthin lowered the lumen Ph and promoted the aggregation of the PS II light harvesting complex. Although speculative, this model could provide an efficient channel for non-radiative energy dissipation and is consistent with other findings in this area (Horton *et al.*, 1991).

Efficient trapping and utilisation of light energy in chloroplast thylakoid membranes requires efficient location and functioning of intermediate components that facilitate photosynthetic electron transport capacity. These two factors have an important function in the overall photosynthetic performance of plants which is ultimately reflected in vegetative growth. Plant growth can only be sustained for an extended period of time when energy expended in respiration is less than the net photosynthetic gain. While not examined in this study, the importance of water and nutrients as primary inputs in energy transduction and in the growth processes of cell division and expansion is recognised. Almost invariably

vegetative growth of plants is dependent upon further leaf area expansion and cell division. Maintenance respiration, which increased in parallel with plant growth, is both temperature dependent and directly related to the catabolic processes of cellular degradation and recycling of structural components (Johnson and Thornley, 1985).

6.2.1.2 Leaf Temperature

Within a normal physiologically-active temperature range, photosynthetic activity is related both to the leaf temperature and to the growth temperature. Increasing leaf temperature up to the optimum temperature decreases stomatal resistance admitting more CO_2 through stomates for fixation in chloroplast activity. Regulation of stomatal activity, although studied for more than a century, is still a rapidly expanding area of investigation (Mansfield *et al.*, 1990). In this model (Fig. 6-2) it is proposed that temperature, light, CO_2, and ABA levels can all participate in stomatal control. Stomates tend to close at high CO_2 and high ABA levels. Closure may also occur when temperature is low or when light is absent.

Leaf temperature influences current metabolic functioning of the plant. Respiration is temperature dependent, the respiratory quotient (Q_{10}) normally doubling for each 10 C rise in temperature (Van't Hoff's Law). In this study no attempt was made to characterise the temperature dependence of the respiratory activity or to partition it into growth and maintenance components as expressed in many plants (Johnson and Thornley, 1985).

Utilisation of current photosynthate or stored reserves for growth or maintenance processes also depends on the supply of other factors required for growth. It is expected that these combined processes would have the same temperature dependence as respiratory activity.

Leaf temperature influences the transport of carbohydrate from the photosynthate pool as transport of assimilates increases with increasing temperature. At low

temperature, the primary and secondary products of photosynthesis tend to accumulate in chloroplasts and in adjacent tissues, particularly in tropical plants (Chatterton *et al.*, 1972; Warrington *et al.*, 1977; Pollock and Lloyd, 1987). This may arise from a direct effect of temperature on transport and utilisation. The activity of sucrose phosphate synthase (SPS) was higher in roses grown at constant rather than alternating day/night temperature and is considered an indicator of the availability of carbohydrate in leaves for export (Kurssanov, 1984). Increased cytokinin levels also promoted SPS activity, probably due to increased sink demand (Rufty and Huber, 1983; Zieslin and Khayat, 1990).

At low temperatures chilling resistance in chilling sensitive plants may be improved by retention of carbohydrates in cells that given higher temperatures would normally have been exported to other plant tissues (Levitt, 1972). This would be in accord with findings of this study that indicated carbohydrates accumulated more in Epipremnum than Fatshedera at low temperatures. Increased carbohydrate concentration contributes to decreased gelling of membrane lipids and increased negativity of cytoplasmic osmotic potential (Siminovitch and Cloutier, 1981). This could increase membrane stability by lowering the gelling temperature and help retain water in plant cells, thereby reducing low temperature-induced water stress.

High concentrations of carbohydrates adjacent to chloroplasts may also accumulate and moderate photosynthetic activity by feedback inhibition. Foyer (1988) suggested that this may involve restricted phosphate availability arising from sequestering of unbound inorganic phosphate from the cytoplasmic pool. This could occur when leaf temperatures were relatively cool and in bright light as photosynthetic activity is less temperature dependent than utilisation. Feedback inhibition of this type has been reported in chilling sensitive species (Bagnall *et al.*,1988).

Gene expression in plants may be altered by changes in light and temperature. The influence of temperature on the expression of the Epipremnum chimera has

not been reported previously. This is reflected in the degeneration of plastids similar to the processes that occur in other photobleaching mutants (Knoth, 1975; Gyurjan *et al.*, 1977; Vaughn *et al.*, 1980). The chlorophyll deficient sectors of Epipremnum leaves possess chloroplasts typical of PS I deficient plastids (Araus *et al.*, 1986). Inability to complete normal electron transport in the chlorophyll-deficient sectors is probably a major factor related to high light-induced damage to these sectors (Plate 5-7).

Above and below the optimum temperature, plant growth rate diminishes as was particularly evident in Fatshedera and to a lesser extent in Epipremnum. Above the optimum temperature the reduction in growth has been attributed to a net increase in respiration coupled with decreased photosynthetic capacity, but enzyme denaturation may also be a contributing factor. In a recent review Vierling (1991) indicated that where plants are acclimated slowly to the higher temperatures they may develop tolerance to high temperatures by the production of heat shock proteins. Although it is possible that heat shock proteins are an adaptive response, there was no evidence of growth rate increasing after a period of adaptation.

Below the optimum temperature, photosynthesis may be reduced, particularly following exposure to chilling temperatures. In this study using chilling-sensitive Epipremnum and chilling-resistant Fatshedera the period of chilling required for a marked effect on plant growth was related directly to their respective chilling sensitivity. Within each species, plants grown at high temperature were more prone to chilling injury and inhibition of photosynthesis than if they had developed at low temperature. In a related study of tomatoes the major contribution to inhibition of photosynthesis originated in the chloroplast, with a component arising from reduced stomatal conductance (Ort and Martin, 1982). The current work was unable to distinguish between the effects of stomatal and non-stomatal contributions to chilling impairment of photosynthesis. This would be both a profitable and an interesting aspect to investigate in the future.

Prolonged exposure to high PFD, particularly at low temperature, initially results in photoinhibition. If this stress is not relieved, further light energy is trapped and must be dissipated from the reaction centre. This energy may be dissipated without causing permanent damage. However, if the photoinhibitory stress is not discontinued, and the capacity to dissipate the absorbed energy diminished, then photo-oxidation may cause potentially permanent damage to thylakoid membranes. Bleaching of leaves is an external manifestation of intracellular photo-oxidative damage, initially occurring within chloroplasts and finally causing cell death (Sagar and Briggs, 1990). In this model (Fig. 6-2) damage of this type is considered virtually irreversible.

Transport of photoassimilates to sink organs is severely curtailed at low temperature (Shishido and Hori, 1979; Ho, 1988). Coupling of the translocation and transpiration rate has also been correlated with plant water status (Lang and Thorpe, 1986). Low temperatures will have a direct effect on transpiration and will contribute to the accumulation of photoassimilates in leaves. Recent studies in phloem transport suggest that loading of sucrose into the sieve tubes in leaves of a some species may be controlled by an energy requiring proton/sucrose co-transport process in the plasmalemma of the sieve tube/companion cell complex (Giaquinta, 1983). The factors controlling the unloading of sucrose from the sieve tube in the sink are not known for certain, there could be either an active energy dependent process located in the plasmalemma, or permeability may be sensitive to turgor pressure in the apoplast (Thorne, 1986).

6.2.2 Effect of Light

Plants respond to the amount and duration of light. Plant growth is ultimately dependent upon photosynthesis which is regulated by temperature, light, stomatal resistance, CO_2, photosynthate pool size and balance between photoinhibition and recovery. High rates of net photosynthesis and plant growth can occur in

bright light when other essential factors such as water and nutrient supply are not limiting (Thompson *et al.*, 1992).

Photosynthetically active radiation is the most important single factor determining the rate of photosynthesis. At PFDs below the light compensation point (LCP) there is no net photosynthesis. Above LCP this increases with increasing PFD up to a maximum value at light saturation. In leaves exposed to high PFD, light trapping capacity of the reaction centre may exceed the transport capacity of the electron transport system causing photoinhibition of photosynthesis. One of the major causes of photoinhibition is the interruption of electron transport caused by dysfunctioning of the Q_B protein. This interferes with normal non-cyclic electron transport from PS II to PS I. Restoration of normal electron transport requires energy and protein synthesis for reconstruction and reinsertion of the Q_B protein into the damaged reaction centres (Greer *et al.*, 1986; 1991).

Data collected in this thesis indicated restoration of normal photosynthetic activity from a previously photoinhibited state was enhanced by growth at low temperature and with exposure of leaves to warm temperatures during the recovery phase. These conditions would favour protein synthesis and are congruent with reports by Greer and Laing (1988, 1989). Low PFD also promotes recovery, suggesting that there is a photomorphological requirement for light in the restoration of inactivated reaction centres. Recovery proceeds very slowly in the dark and in bright light recovery may be severely curtailed. The net rate of recovery is markedly less than the rate of photoinhibition (Greer and Laing, 1988,) or may not even occur during photoinhibition. Mechanisms operating during photoinhibition and recovery are still subject to debate in this rapidly developing area (Krause and Weis, 1991).

Although not examined in the present study, the role of light during recovery presents an interesting physiological problem for photoinhibited plants (Greer and Laing, 1988). Where environmental conditions do not favour the processes

required for recovery, the photoinhibited state may persist from one photoperiod to the next. The physiological consequences of this condition have not been examined elsewhere. If recovery from photoinhibition is prevented by further exposure to bright light, particularly at low leaf temperature, then photo-oxidative damage results. Initially this causes swelling of thylakoid membranes, but if the damage continues unabated the damage becomes irreparable, finally causing cell death. In this study (Chapter five) Epipremnum leaves were permanently damaged during exposure to bright light (Plate 5-7) while Fatshedera leaves were able to quench chlorophyll fluorescence without damage.

Light is important in the development of new leaf area. Leaf expansion ceased at 3-4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ but resumed quickly at 250 - 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In white light an ATP-mediated proton pump was activated and proton secretion was directly correlated with leaf growth (Van Volkenburgh and Cleland, 1980; Dale, 1988). Although the absolute amount of dry matter production generally increased with higher PFD and higher temperatures, there was no direct effect of PFD or temperature on the partitioning of dry matter between leaf, stem and root tissue in both species. Allocation of dry matter into reproductive growth was not considered as part of this model as neither Epipremnum or Fatshedera developed flowers during this study. The lack of flowering is not surprising in view of the infrequent reports of flowering in both species (Beckett, 1987; Dehgan, 1987).

While it was beyond the scope of this study, at high PFD the production and activity of ABA could be enhanced by concurrent exposure to low temperatures as reported in stress related studies (Rikin *et al.*, 1981), and be a contributing factor in the photoinhibition of photosynthesis. In this situation ABA may be acting as a long distance signalling molecule as proposed by Davies *et al.* (1990). Abscisic acid permeates biomembranes almost exclusively in the protonated form from within chloroplasts. Small pH shifts arising during stress facilitate rapid redistribution of ABA (Slovik and Hartung, 1992a,b). Abscisic acid may be responsible for the rapid transmission of the stress signal to stomates from the chloroplasts in the palisade layer where high light stress will first be perceived.

This may arise from increased synthesis in the chloroplasts or from a change in membrane permeability allowing ABA escape into the cytosol (Hartung *et al.*, 1992). Rapid decrease in stomatal conductance would reduce water loss and CO_2 uptake, this would be related to the concentration of unbound ABA and the sensitivity of the particular processes being regulated (Hetherington and Quatrano, 1991). Reduced capacity for CO_2 fixation at high PFD could contribute to the accumulation of an excess of reduced NADP required to fix the CO_2 available from photorespiration and the limited CO_2 that may enter the laminar by direct cuticular diffusion.

6.3 Consequences for greenhouse management

In this section the practical consequences of the results from this study will be considered with particular reference to split night and day/night differential temperature and PFD regimes. It is important to distinguish between plant growth and crop growth as a single leaf or individual plant systems give different responses to PFD (unlike temperature) compared with plants growing in closed canopy of a crop. This is not a significant consideration in greenhouses where plants are adequately spaced to minimise interplant competition.

6.3.1 Inverted temperature treatments

The practice of growing greenhouse crops at higher day than night temperature has often been accredited to Went (1944, 1945), although it has been common practice for much longer (Schimper, 1898). It has been suggested this more closely resembles the conditions occurring in an uncontrolled environment or natural habitat and therefore should be close to the biological optimum.
More recently these practices have been advocated to minimise fuel consumption or produce more compact plants rather than attempting to maximise dry matter

accumulation by growing crops at the optimum temperature for physiological activity.

Comparison of Epipremnum and Fatshedera growth at constant temperature and alternating day/night temperature treatments showed that growth and development was maximised in the constant temperature treatments. In this study there was no definitive evidence of thermoperiodicity resulting from increased growth using alternating day/night temperatures compared with optimal constant temperature regimes with the same mean temperature. The activity of enzymes linked with soluble sugar transport was higher in roses grown at constant rather than alternating day/night temperature (Kurssanov, 1984; Zieslin and Khayat, 1990). This suggests a substrate limitation could occur in plants not developed at constant temperature and could be a key factor explaining the enhanced growth in constant rather than variable temperature regimes.

The leaf unfolding rates using inverted day/night temperature regimes were similar, but substantially less than those in constant temperature treatments. In both Epipremnum and Fatshedera, as daily mean temperature increased the disparity between the inverted temperature treatments and the constant temperatures decreased. Dale (1964) reported similar findings with chilling-sensitive bean plants. This is compatible with evidence found in Chapters three and four where time spent at 10 C markedly reduced growth and development.

Growth of plants at higher night than day temperatures has been a strategy proposed to make greenhouse plant production more energy efficient. This may be possible particularly when combined with thermal screens in winter. However, plant growth in inverted day/night temperature treatments is probably impaired in some species by reduced chlorophyll concentration in the leaves. In this thesis the reduction in chlorophyll concentration was exacerbated where leaves were exposed to 10 C in the light period. Similar results have been reported where plants were grown at higher night than day temperature (Heins *et al.*, 1988; Erwin, 1992) and may result from high light mediated destruction of chlorophyll

(M°Williams and Naylor, 1967). In a related study, chlorophyll content in leaves developed in normal or inverted day/night temperature regimes were similar provided the PFD was low (Armitage and Carlson, 1981). This suggests that the destruction of chlorophyll was mediated by high light.

Net chlorophyll breakdown may arise from a shift in the balance achieved in normal pigment turnover between synthesis and degradation (Thomson and Whatley, 1980). However, this is difficult to reconcile with constant temperature treatments where chlorophyll was not depleted from leaves at any temperature.

The effect of environmental factors and growth regulators on the development of chromoplasts does not appear to have been thoroughly investigated (Thomson and Whatley, 1980;). Gibberellins may participate in dedifferentiation of chromoplasts to chloroplasts (Thomson *et al.*, 1967). However the situation is far from clear as some *in vitro* studies indicate gibberellins may inhibit chloroplast development while cytokinins may have the opposite effect (Stetler and Laetsch, 1965). Presumably when *in vivo* either the production of gibberellins *per se* may influence plastid formation or factors controlling the expression of genes that regulate chloroplast formation are also linked to gibberellin synthesis. The photo-oxidative destruction of chloroplasts and its effect on nuclear gene expression and extra-plastidic enzyme activity has been reported by Oelmüller (1989). Gibberellin levels are probably highest in Epipremnum when exposed to high light and high temperature. This would coincide with the environmental conditions that favoured maximum extension growth and lowest chlorophyll development.

In the context of this study, reduced endogenous gibberellin and cytokinin biosynthesis or activity would be in accord with reduced shoot and leaf growth in the inverted day/night temperature treatments relative to growth at constant temperature.

Plant growth in the diurnal temperature regimes 30/10 and 10/30 C led to significant reductions in RGR and LER compared with plants at 20/20 C, whereas

the temperature regimes 30/20 and 20/30 were similar to the constant 25 C treatments. Similar findings were reported by Dale (1964) using identical temperature treatments. The large difference in growth may be related to either the size of the temperature differential, or exposure of leaves to 10 C had a deleterious and persistent effect on metabolic activity.

The results of this investigation are in agreement with the evidence accumulated by Friend and Helson (1976), Klapwijjk and Wubben (1978), De Jong and Smeets (1982) and Heuvelink (1989) who showed that the vegetative growth of young plants was lower in inverted day/night temperature regimes. Only rarely have investigations using higher night than day temperature resulted in growth equivalent to or better than constant temperature treatments (Calvert, 1964; Hussey, 1965; Krug and Liebig, 1980). To accommodate the inconsistent nature of these findings in the general body of evidence, it is clear that other factors need to be considered. These may include the magnitude of the temperature differential, the absolute temperatures used and the duration of the experiment. The particular species or cultivar may interact with these factors to produce this response (Krug and Liebig, 1980).

Using chilling sensitive species Wolfe (1991) reported substantial reduction in net photosynthesis and leaf water potential at low temperature (DT/NT 8/4 C). This work suggested chilling stress in some species may be water stress related. Reduced water uptake by chilled roots has been linked to changes in the endodermal plasmalemma of roots (Markhart *et al.*, 1979). Slow stomatal closure has been reported in chilling sensitive plants while chilling resistant plants retained normal stomatal function (Emaus and Wilson, 1983). Stomatal operation during photoinhibition studies was monitored on attached leaves in the leaf chamber, but did not show any evidence of chilling-related impairment.

Although photoinhibition increased in water stressed plants (Powles, 1984; Björkman, 1989) this has been discounted as the primary cause of reduced photosynthetic activity in chilled tomato leaves (Brüggemann *et al.*, 1992). There

is evidence for a chilling-induced limitation in the Calvin cycle. This is believed to cause accumulation of NADPH causing feedback inhibition in the light-dependent electron transport pathway.

More than one factor seems implicated in chilling induced reduction of photosynthesis. Labate *et al.* (1990) and Brüggemann *et al.* (1992) suggest this may be explained by a limitation in inorganic phosphate, although in the longer term Rubisco activity will be more important in determining photosynthetic capacity. Rubisco activase is both chilling sensitive and light dependent (Grafflage, 1990; Sassenrath and Ort, 1990; Sassenrath *et al.*, 1990).

Data from this thesis indicates that in Epipremnum, and to a lesser extent in Fatshedera, net photosynthetic activity was impaired by exposure of whole plants to low temperature in either the light or the dark as evident from the dry weight increases of the plants. Leaf chamber studies showed no evidence of reduced photochemical efficiency after exposure at 10 C in the dark. However reduced plant growth occurred in low temperature regimes irrespective of whether plants were exposed to low temperatures in the light or the dark. It may be concluded that reduction in plant growth was not directly mediated by or dependent on light. The evidence points towards inhibition of growth being related to a reduction in inorganic phosphate or Rubisco activity.

6.3.2 Effect of day/night differential on shoot growth

Regulation of shoot growth is a focus of economic importance in commercial production of pot plants and cut flowers (Larsen and Gertsson, 1992; Erwin, 1992). Control of shoot growth in most crops can be accomplished using chemical growth regulators [estimated to cost 10-20 c/plant (R. Heins pers. com. 1990)]. There is however increasing uncertainty about how long these chemicals will remain registered for use (Moe *et al.*, 1991). This has stimulated interest in manipulation of shoot growth by exposing plants to appropriate light and

temperature treatments. This has had a direct effect on the profile of environmental physiology studies as postulated mechanisms controlling shoot growth are evaluated (Erwin *et al.*, 1991; Moe *et al.*, 1991).

Shoot extension growth of Epipremnum and Fatshedera were influenced by the daily mean temperature and in these studies was maximal in constant temperature treatments. The effect of PFD on shoot length was generally small compared with temperature as reported recently in *Lilium longiflorum* (Erwin *et al.*, 1989) and *Campanula isophylla* (Moe, 1990). These authors suggest reconsideration of the day/night temperature differential and the difference between day and night temperature (DIF) may be instructive when examining the underlying factors controlling shoot growth in flowering plants. They report many instances of thermomorphogenic responses, claiming internode growth in different day/night temperature treatments was promoted by the difference between the day and night temperature. Plant height increased and leaf orientation became more erect as the differential between day (DT) and night temperature (NT) increased.

In the current study leaves were paler when DT<NT, but no change in leaf orientation was observed in foliage plants. The only shoot growth data conforming remotely to the DIF hypothesis occurred at 15 C when both species were growing very slowly. This is contrary to the findings of Moe (1990) and others who reported DIF was most useful in quantifying shoot growth when plants were actively growing, and gibberellin activity was probably high.

Growth regulators that interfere with gibberellin biosynthesis or action may also contribute repression of stem elongation when DT>NT (Tangerås, 1979; Moe, 1990). The predominant gibberellins known to have a significant role in stem elongation include GA_1, GA_{19} and GA_{44} (Zevaart, 1985). Although interconversion of gibberellins is recognised (Jones and MacMillan, 1984), inhibition of these specific GAs may be an important factor determining the shoot elongation in plants grown with DT>NT.

Stem elongation in many crops tends to be greatest at the time immediately preceding and after sunrise (R. Heins pers. com. 1990), and is greatly depressed by lowering the temperature in the early morning. Several factors could contribute to this response: it may be a critical period for GA biosynthesis/activity, or related to reduced water availability in roots at low temperature (Crookston *et al.*, 1974) that limits cell expansion. The reduction in shoot growth could also be interpreted as evidence of a photoinhibitory response caused by bright light acting on leaves at low temperature, as shown in the current study.

Moe (1990) has recently speculated that internode extension may be under phytochrome control. Shoot growth in *Campanula* sp. is enhanced by far-red light as is internode extension of many other photoperiod sensitive that respond to DIF treatments (Moe *et al.*, 1991). The photoperiodic response of most foliage plants is unknown (Conover and Poole, 1981).

Although it was outside the scope of the present study to assay phytochrome activity in Epipremnum and Fatshedera it is considered unlikely that this growth regulator plays a significant role in shoot growth and development as in photoperiodic plants (Vince-Prue, 1975) and proposed by Moe (1990). This could explain the lack of shoot extension growth in foliage species when grown at DT>NT compared with DT = NT or DT<NT (Fig. 3-21). Plant response to DIF treatments may depend on a physiological receptor or growth stage. Hemming (1992) reported that Mortensen in Norway had found geranium seedlings responded well to DIF treatments, but not those grown from cuttings and concluded that the physiological age, or the plant material could influence the results.

The chlorophyll fluorescence studies indicated growth in bright light should always be accompanied with warm temperature so that photoinhibition of photosynthesis will be minimised. Recovery from photoinhibition is both a temperature and light mediated process. Recovery increases with increasing temperature, but may be

slowed considerably by even moderate PFDs preventing complete restoration of photosynthetic competence.

When plants are exposed to bright light in the early morning (following a cold night), leaves may not be warm enough to allow processing of the intercepted light with negligible photoinhibition. This could be an important moderator of plant growth as photoinhibition early in the day could severely depress CO_2 fixation for the remainder of the day. This could directly influence dry weight accumulation.

A practical consequence of using differential temperature regimes as recommended in DIF studies is that the environmental variables must be set and calibrated using more than simple temperature control, requiring more than simple thermostats to implement.

There could be a philosophical problem reconciling evidence indicating that plant growth is related to the temperature integral during growth, with the rapidly growing body of evidence suggesting that it is the difference between the day and night temperature that is controlling plant growth.

When a plant is operating within an appropriate temperature range it may be functioning as a temperature integrator. In this situation it is responding additively to the changes in the environment on a moment by moment basis, and shoot growth represents the sum of the growth rates at each temperature during the integration period. The dilemma concerning plant response to a temperature differential is that growth rate at any instant in time is not based on the present environmental conditions, but on a comparison between the present and a previous situation.

6.3.3 Foliage plant growth with variable night temperature regimes.

Growth and development of many species is regulated more by the temperature integral than diurnal temperature fluctuations. Langhans *et al.*, (1981) using young lettuce and tomato plants in a CE study showed that plant growth was directly related to the night temperature integral when the day temperature was held constant.

Many plant growth studies have set out to compare treatments with environmental conditions resembling the commercial production environment and have successfully demonstrated that plant growth was related to a function of the growth temperature. However, it is difficult to compare treatments within experiments and between experimenters as the environmental conditions have varied widely.

Instances where growth and development were compared on the basis of equivalent energy input are rare, although a few investigators in CE studies have compared plant growth with the same temperature integral where night temperature regimes were changed (Langhans *et al.*, 1981; Langhans and Albright, 1981; White and Warrington, 1984).

The current studies showed that with a constant day temperature equivalent plant growth occurred using the same night temperature integral. All other reported split or sliding night temperature studies have used control treatments that were not equivalent on a heatsum or temperature integral basis. The relatively small delays in development and retardation of growth in these investigations are evidence of the plant's ability to accommodate change in temperature.

In greenhouse studies plant growth rate (and precocious fruiting) were also related to the night temperature integral (Calvert and Slack, 1977; Hand and Hannah, 1978).

This has been extended to temperature integration during both the day and night (Krug and Liebig, 1980; Cockshull *et al.*, 1981; Hurd and Sheard, 1981; Miller and Langhans, 1985; Van den Berg, 1987) including temperature integrations across periods up to 2 weeks (Hurd and Graves, 1984). The upper limits of this integration period have not yet been fully explored (Koning, 1988). This could be a fruitful area of investigation as any attempt to optimise the greenhouse environment will impact on the specifications and functioning of the environment controller.

Results from this study (Chapter four) confirm the hypothesis that, provided variation in night temperature did not adversely influence Epipremnum and Fatshedera, their growth and development would reflect the temperature integral they received irrespective of how this was achieved.

The differences in growth between Epipremnum and Fatshedera at mean night temperature treatments of 15 and 20 C reflect the different temperature optima for each species and respective sensitivity to incipient chilling injury.

Rather than lowering the night temperature in greenhouses this study suggests that it would be more energy efficient to allow the day temperature to rise above the normal set-point. The temperature should then be permitted to decline slowly during the later part of the day and in the early part of the night to a minimum set-point temperature determined by the chilling sensitivity of the crop. Greenhouse heating would then be programmed to ensure chilling damage did not occur with further lowering of temperature and to adjust the temperature back to an acceptable predawn level, thereby preventing photoinhibition induced by bright light in susceptible leaves. The greenhouse heating system could be used to adjust the instant when the minimum temperature was expected so that the capacity of the heating system could be matched to total energy demand prior to the dawn.

Several studies have examined the effect of night temperature on plant growth and development. Most investigators used high value greenhouse vegetable or flowering crops and reported delayed production particularly when small plants were exposed to low night temperatures. Production delays in split-night regimes have been reported widely with reduced night temperature (Parups, 1978; Bonaminio and Larson, 1980; Tsujita and Craig, 1980), particularly when the PFD was relatively low (Heins and Wilkins, 1981; Hicklenton and McRae, 1984). Production delays in low night temperature regimes could be offset by root zone heating (Shedlosky and White, 1987), indicating that comparisons between growing regimes should be made on the basis of equivalent inputs. Only rarely has vegetative growth been promoted using split-night regimes (Hanan, 1979; Parups, 1978), this may be related to the size or age of the plant material used in these studies (Kohl and Mor, 1981; Merrit and Kohl, 1989).

6.3.4 Validation of findings

Validation of results in a commercial environment is vital if the transfer of information from the theoretical to the practical is to take place. Testing of models can be a controversial topic, and it has often been remarked that validation in an absolute sense is not possible. A useful model will enable a little progress to be made towards a quantitative understanding of plant growth, but its fate is usually to be incorporated into more powerful theories or models, of which it is just a special case (Cooper and Thornley, 1976). The present qualitative model appears to work quite well when compared with the data currently available, although its inadequacies will be revealed in the light of more comprehensive data and as the precision of analytical procedures improve.

If the following provisos are satisfied it would be possible to compare the relative cost of production of each foliage plant (on an energy basis) in different areas of New Zealand (Table 6-1).

Table 6-1. Effect of production area on energy requirement for greenhouse heating and time to produce Epipremnum and Fatshedera plants of a marketable size using fixed set point temperatures.

			Species			
			Epipremnum		Fatshedera	
Location (Latitude)	Set point temp. (C)	Energy demand[z]	Days of growth to 30 cm[y]	Energy to produce 30 cm[x]	Days of growth to 30 cm[y]	Energy to produce 30 cm[x]
Auckland	15	0.4	320	128	280	112
(37°S)	20	1.4	88	123	38	53
	25	3.1	45	140	36	112
	30	4.8	37	178	68	326
Levin	15	0.7	320	224	280	196
(41°S)	20	2.1	88	185	38	80
	25	3.8	45	171	36	137
	30	5.5	37	204	68	374
Christchurch	15	1.8	320	576	280	504
(43°S)	20	3.8	88	334	38	144
	25	6.2	45	279	36	223
	30	8.7	37	322	68	592

[z] Mean energy requirement ($MJ \cdot m^{-2} \cdot day^{-1}$) to maintain a constant set point temperature over a year. Assuming a heat transfer coefficient U = 8 $W \cdot m^{-2} \cdot °C^{-1}$ (day and night) and solar transmission = 0.7 (Based on data supplied by C. Wells pers. com. (1992)).

[y] Growing time (days) to produce plants 30 cm high based on functions fitted to growth data.

[x] Energy input required to produce plants 30 cm high.

Assuming the following:

> All the fixed and variable costs related to production of foliage plants, except energy used for greenhouse heating were constant in Auckland, Levin and Christchurch. Rental on greenhouse space ≈ $\$10 \cdot m^{-2} \cdot yr^{-1}$ was considered as a fixed cost at all locations.
>
> Constant temperature is maintained in a greenhouse with a heat transfer coefficient of 8 $W \cdot m^{-2} \cdot °C^{-1}$ and solar transmission coefficient of 0.7.
>
> Incident PFD has a mean value of 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and *ceteris paribus.*
>
> Each crop of foliage plants is marketable at the same height.
>
> The value of each crop is not subject to seasonal fluctuations in price.
>
> Greenhouse productivity is economically most efficient when the product of greenhouse occupancy time and heating requirement is minimised.

The time to produce Epipremnum and Fatshedera plants of a marketable size (30 cm high) has been calculated from the constant temperature treatment data. Inspection of Table 6-1 indicates energy requirements within New Zealand increase with decreasing latitude, more than doubling between Auckland and Christchurch. The required production time for Epipremnum decreased markedly as greenhouse temperature increased up to 30 C, there was a concomitant increase in energy requirement per crop of these plants. The optimum temperature for minimising energy production is location-dependent. Fatshedera shoot growth was most rapid between 20 and 25 C, outside this temperature range production times were considerably extended. Energy requirement for this crop was minimised at 20 C in each area; at 25 C the reduction in production time by 2 days was more than offset by doubling the energy requirement per crop in Auckland and a slightly lower proportion in other areas.

It is clear from this study that where production of Epipremnum and Fatshedera in the same greenhouse is envisaged; the environmental conditions will be a compromise as it will not be possible to produce each crop at its biological optimum.

6.4 Further research

In the course of this study more questions have been raised than answered confirming the visionary comment of Goethe who aptly stated "Any solution to a problem is a new problem". Some issues arise through experience gained in hindsight and relate particularly to experimental procedures, while others have arisen spontaneously from this study.

The range of temperature treatments investigated did not allow precise characterisation of plant response, particularly at high temperature over short or longer periods.

Propagation of plants in growth rooms using the experimental conditions that would occur during the growth study would ensure their entire development was directly attributable to the environmental conditions imposed on them and not to something that may have occurred previously.

Further harvests would allow more precise curve fitting procedures to be applied, particularly where plants could be grown beyond the early exponential growth phase. Extending the growth temperature range would enable more accurate definition of plant growth response at high temperature. This information could become increasingly more relevant if projected global warming eventuates.

The case for normal replication of experimental treatments (between rooms) in standardised conditions still worries statisticians, but is of less concern to pragmatists, or commercial operators who will frequently make management decisions based upon information drawn from very simple trials or experience. The probability levels associated with these events may be several orders of magnitude smaller than generally accepted by the wider scientific community.

While it could be of commercial advantage to investigate other species in detailed environmental studies of this type, it would be more profitable to develop the use

of the sensitive non-intrusive environmental stress probe available in chlorophyll fluorescence studies to accomplish some aspects of this task. This could be complemented with a limited selection of constant temperature treatments in a plant growth study. It would also be of interest to study the anatomy of leaves in greater detail, tracing the sequence of events that lead to permanent disabling and destruction of the chloroplasts. Investigation of the early signs of membrane disruption using electron microscopy would help to ascertain what determines the threshold point between repairable damage and permanent damage. This would extending our understanding of how plants adjust to large changes in their environment, in particular evaluation of the adjustment rate of greenhouse-grown plants to seasonal changes in PAR and their disposition to photoinhibition.

The precise details of the events occurring in photoinhibition and recovery are still not fully resolved, particularly in the relationship between photoinhibition and plant growth. Is there a general response that occurs widely throughout the plant kingdom? Does each species have a similar underlying environmental response controlling the mechanisms used for protection from high PFD-induced damage? Further investigation of the protective mechanisms operating within chilling sensitive and chilling resistant species is warranted, followed by extrapolation to general principles applying to all plants.

The influence of PFD and temperature on the expression of the chimeral structure in Epipremnum leaves provides an interesting opportunity to investigate the interaction of environmental factors on the development of green and nongreen plastids. Epipremnum could have value in fundamental studies investigating environmental effects on chloroplast development and chimeric expression. This has not been reported elsewhere. It would also be useful to examine the effects of photo-oxidative stress in leaves developed in contrasting light environments. This would enhance our understanding of the adaptive strategies used by plants to protect the photosynthetic system from damage.

Why is chlorophyll 'degraded' or produced at a lesser rate in plants where the night temperature is greater than day temperature, but not when plants are grown at constant temperatures? Is the observed photoinhibitory response a cause or an effect?

Relatively few studies have compared the different techniques available for measurement of photoinhibition at room temperature and at 77K. Close study of this is warranted as the processes occurring at each temperature may be different or may be indicating different aspects of the same phenomena.

How important is photoinhibition in the greenhouse environment? Does it occur in the commercial greenhouse or is an artifact of the method of treatment? Although minimising photodamage is probably a priority of plants, it is not known how important photoinhibition of photosynthesis is in terms of providing an adaptive mechanism for regulation of photosynthesis and plant productivity.

Studies investigating relationships between photosynthetic activity and plant growth frequently face a dilemma in that while these two factors are by definition intimately related, they are often only poorly correlated. The high rates of photosynthesis observed in plants grown at low temperature relative to high temperature was not directly related to plant growth. This will require further biochemical work to establish a basis for conversion of photoassimilates into plant growth. Investigation of the target-point in metabolism most sensitive to exposure to low temperature, although an attempt to unify some of the factors influenced by chilling has been proposed recently (Brüggemann *et al.*, 1992). This deserves evaluation in other species to enlarge our understanding of factors controlling photosynthetic function.

Growth control in flowering plants requiring a low temperature period at dawn to minimise shoot elongation should have this practice coordinated with solar screens to manage the PFD to minimise photoinhibition, thereby maximising the opportunity for photosynthesis and minimising shoot growth. This requires further

evaluation to identify how important inhibition of photosynthesis is in the control of plants experiencing the predawn chill.

Appreciation of the mechanistic basis for plant response to stress improves our perception of whether the response is adaptive or if it is a consequence of stress injury. The verification of results obtained from controlled environment studies in real world production situations is essential if plant breeders or genetic engineers are going to be supplied with the relevant information that will allow the productive efficiency of economically important plants to be enhanced by genetic manipulation of metabolism.

To conclude...

This thesis has examined the effects of temperature and light on the growth and development of Epipremnum and Fatshedera, through the use of controlled environment facilities and noninvasive techniques, to study these species as whole plants down to processes taking place at the sub-cellular level. While experiments conducted in this study did not allow complete definition of the factors that explain the differential temperature and light response of Epipremnum and Fatshedera, the evidence presented here makes a useful contribution to our understanding of the environmental physiology of foliage plants and could provide a useful springboard for further investigations in this area.

Epilogue

If someone tells me that in making these conclusions I have gone beyond the facts I reply: "This is true, that I have put myself freely among ideas which cannot be rigorously proved. That is my way of looking at things. Every time a [horticulturist or plant scientist] concerns himself with these mysterious phenomena and he has the luck to make an important step forward he will be led instinctively to attribute their prime cause to a class of reactions in harmony with the general results of his own researches. That is the logical course of the human mind, in all controversial matters".

Louis Pasteur, 1857

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