Growth and Photosynthesis in Woody Species of the Brazilian Cerrado, with particular reference to *Kielmeyera coriacea* Mart. (Guttiferae)

by

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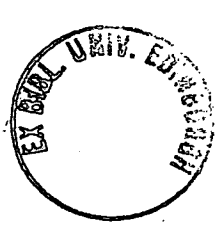

I hereby declare that the work contained in this thesis is my own unless otherwise acknowledged,

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ABBREVIATIONS AND UNITS

Where possible all values are accompanied S.I. units, or equivalents. Chemical elements, when abbreviated, are represented by their recognised chemical symbols.

Table AU1.1 Abbreviation and unit listing for this thesis.

Abbreviation/Unit	Full Version (units)
a, b, c, _ _ _	Equation parameters
A	Area (cm^2)
A_i	Individual leaf area (cm^2)
A_c	Area of leaf in cuvette (cm^2)
antiln	Exponential to the base e
A^z	Leaf azimuth
A_{662}	Absorbance at 662 nm
C_A	'Analysis' line [CO_2]
C_C	Corrected [CO_2] in 'analysis' line
*C.C.*1	First controlled condition experiment
*C.C.*2	Second controlled condition experiment
C_D	'Differential' [CO_2]
CE	Estimated carboxylation efficiency ($mol^{-1}\ m^{-2}\ s^{-1}$)
CEC	Cation exchange capacity
c_i	Sub-stomatal cavity [CO_2]
Cn	Cotyledon number n
c_p	Specific heat at constant pressure ($1.012\ J\ g^{-1}\ K^{-1}$)
C_R	'Reference' line [CO_2]
d	Days
d	Duration of individual leaf expansion (d)
dH_2O	Distilled water
D^i	Leaf dihedral
dn	Day number 'n', *i.e.* d100, day 100
$\delta\theta$	Temperature difference between leaf and cuvette (C)
Dwt	Dry weight (g)
δx	Delta x, the rate of change of x
E	Transpiration rate ($mol\ m^{-2}\ s^{-1}$)
E	Unit leaf rate ($g\ m^{-2}\ d^{-1}$)
e_l	Saturated vapour pressure at leaf temperature
E_{max}	Transpirational correction factor
e_o	Water vapour pressure of air in cuvette (bar)
EP	Unit leaf rate productivity ($g\ m^{-2}\ d^{-1}$)
e_s	Saturated vapour pressure at cuvette temperature (bar)
F	Leaf area ratio ($m^2\ g^{-1}$)
F.C.	First field condition experiment
*F.C.*2	Second field condition experiment

Abbreviation/Unit	Full Version (units)
FH	Frozen-hydrated state
F_M	Mass flow rate of air into cuvette per unit leaf area (mol m^{-2} s^{-1})
Fn	Leaf flush number n
F_V	Volume flow rate of air into cuvette (cm^3 s^{-1})
Fwt	Fresh Weight (g)
g	gramme
G	Force of gravity
G_A	Absolute leaf-area growth rate (cm^2 d^{-1})
g_C	Total conductance to CO_2 transfer
G_i	Individual leaf area growth rate (cm^2 d^{-1})
g_s	Stomatal conductance to water vapour (mol m^{-2} s^{-1})
H	Radiation absorbed by leaf (W m^{-2})
hr	Hour
I^n	Leaf inclination
IRGA	Infra-Red Gas Analyser
K	Allometric coefficient
L_A	Total leaf area (cm^2)
*LGA*1	First controlled condition leaf growth analysis
*LGA*2	Second controlled condition leaf growth analysis
ln	Logarithm to the base e
Ln	Foliar leaf number n
LTSEM	Low-temperature scanning electron microscopy
l_v	Latent heat of vaporisation of water, the program uses $44750-\theta_a/32$ (J mol^{-1})
L_W	Leaf dry weight (g)
LWR	Leaf weight ratio
m	metre
M_a	Molecular weight of air
min.	minute
n	Replicate number
n.d.	No data available
N_L	Emerged leaf number
p	Phyllochron (d)
P	Atmospheric pressure (bar)
P_c	Photosynthetic capacity (µmol m^{-2} s^{-1})
pers. com.	Personal communication
pH	Logarithm to the base 10 of the inverse of the hydrogen ion concentration, *i.e.* $\log_{10}([H^+]^{-1})$
P_n	Net photosynthetic rate (µmol m^{-2} s^{-1})
*PNA*1	Controlled condition primordium number analysis
*PNA*2	Field condition primordium number analysis
PP	Plant photosynthetic productivity (µmol s^{-1} $plant^{-1}$)
PPFD	Ambient photosynthetic photon flux density (µmol m^{-2} s^{-1})

Abbreviation/Unit	Full Version (units)
$PPFD_i$	Incident photosynthetic photon flux density ($\mu mol\ m^{-2}\ s^{-1}$)
p.p.m.	Parts per million volume
$p<0.05$	Probability of the null-hypothesis <5%
Q	Photon flux density incident on cuvette ($\mu mol\ m^{-2}\ s^{-1}$)
θ_a	PLC2-B cuvette temperature (°C)
θ_L	Leaf temperature (°C)
R	Specific or Relative Growth Rate (d^{-1})
$\mathbf{R}_A$	Relative leaf-area growth rate (d^{-1})
r_b	Boundary layer resistance to water vapour transfer ($m^2\ s\ mol^{-1}$)
R_D	Specific respiration rate
R_g	Growth respiration rate
R_i	Estimated plant respiration rate
R_m	Maintenance respiration rate
$\mathbf{R}_{max}$	Maximum potential specific growth rate (d^{-1})
$r_m:r_t$	Main root to root total dry weight ratio
R^o	Leaf rotation
r_s	Stomatal resistance to water vapour transfer ($m^2\ s\ mol^{-1}$)
r:s	Root to shoot dry weight ratio
RuBisCO	Ribulose 1,5 Bisphosphate Carboxylase-Oxygenase
RuBP	Ribulose 1,5 Bisphosphate
r^2	Correlation coefficient
s	seconds
σ	Stefan-Boltzmann constant ($5.7E\text{-}8\ W\ m^{-2}\ K^{-4}$)
S.E.	Statistical standard error of the mean
SF	Estimated supply function ($mol^{-1}\ m^{-2}\ s^{-1}$)
SLA	Specific Leaf Area ($m^2\ g^{-1}$)
sp.	Species
T	time
T_A	Air temperature (°C)
T_D	Dark-period
T_L	Photoperiod
U_L	Unemerged leaf number
V	volt
v/v	Volume per volume
W	Plant dry weight (g)
W_S	Shoot dry weight (g)
w/v	Weight per volume (g per ml)
°C	Degrees Celsius
%	Percent
%RH	Percentage relative humidity
$\%RH_C$	Percentage relative humidity in cuvette
[x]	Concentration of x

CONTENTS

ABSTRACT

Woody species of the Brazilian Cerrado show morphological and functional adaptations to the soil water, soil nutrient and fire stresses of the Cerrado environment. This thesis considers these adaptations in relation to the growth and photosynthesis of Cerrado woody species, and in particular *Kielmeyera coriacea* Mart. (Guttiferae).

Growth of *K. coriacea* and other Cerrado woody seedlings under field conditions is slow, but within the range seen for other late successional woody species. *K. coriacea* displays a limited growth rate plasticity in response to favourable conditions, with a maximum potential specific growth rate of 0.054 d^{-1}. *K. coriacea* has relatively high unit leaf rates, but low leaf area ratios, due to an inherent low specific leaf area (SLA). Low SLA values are compounded by a rapid ontogenic decline in leaf weight ratio (LWR). Declining LWR is due to high biomass partitioning to root development. Within the root and shoot, partitioning is biphasic, with an initial 'establishment' phase of leaf and lateral root favoured development, and a secondary phase dominated by main root, *i.e.* xylopodium, development. The cotyledons have a maximum net photosynthetic rate of 11.0 $\mu mol\ m^{-2}\ s^{-1}$ under favourable conditions, and provide the majority of photosynthate for the 'establishment' phase. Leaf emergence is episodic, or flushing, and individual leaf areas vary depending on their position within the flush. Leaf primordium production parallels leaf emergence, and maintains 4 unemerged primordia at the shoot apex. Adaptations, such as leaf scleromorphy and xylopodium formation, severely limit the growth potential of Cerrado woody species.

Low growth rates under field conditions are primarily due to lower unit leaf rates (E), and are associated with slow leaf-area development. Low E values are associated with lower net photosynthetic rates, and lower carboxylation efficiencies. Slow leaf-area development is due to slower leaf emergence, and primarily, smaller individual leaf areas at full expansion. Slow leaf emergence is associated with slow primordium production at the apical tip.

Photosynthetic capacities for a selection of mature Cerrado trees range from 6.5 to 12.2 $\mu mol\ m^{-2}\ s^{-1}$, with a value for *K. coriacea* of 9.2 $\mu mol\ m^{-2}\ s^{-1}$. Diurnal CO_2-assimilation is principally determined by the diurnal pattern of incident photosynthetic photon flux.

Chapter 1

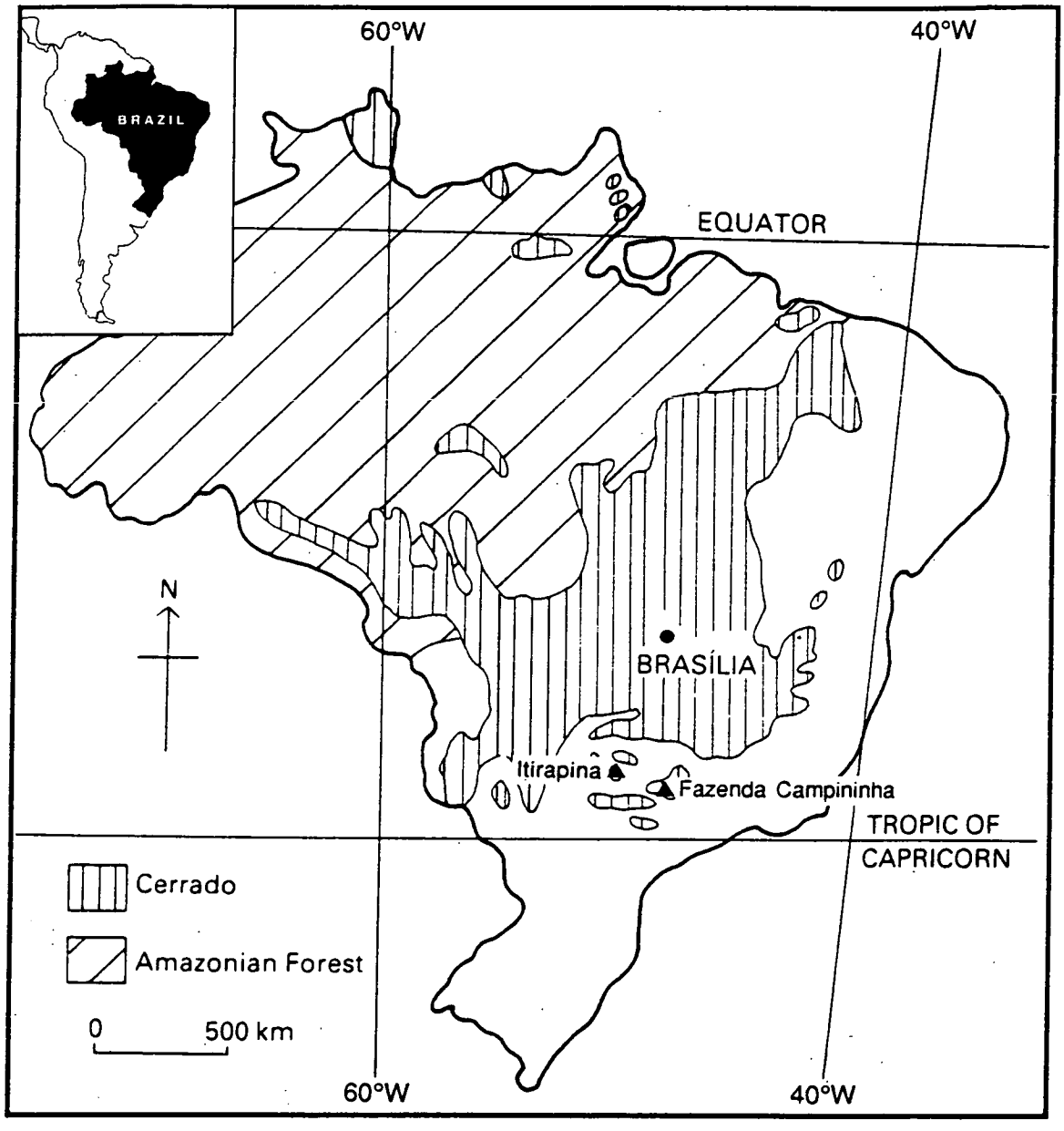
Introduction

The Brazilian Cerrado is the largest South American savanna ecosystem, and is composed of two distinct components, a continuous ground layer of mainly herbaceous grasses, and a varying cover of woody shrubs and trees of low stature. Species show structural and functional adaptations to the distinct ecology of the Cerrado, particularly with respect to the seasonal nature of precipitation, the dystrophic nature of Cerrado soils, and the frequency of vegetation fires. This thesis considers the development and photosynthesis of certain Cerrado woody species, and in particular *Kielmeyera coriacea* Mart. (Guttiferae) an important, characteristic and endemic Cerrado tree.

1.1 The Cerrado

1.1.1 The Cerrado Province

About 23% of the Brazilian territory, some 2 x 10^6 km^2, is naturally covered with a vegetation known as 'Cerrado'. In terms of area it is the second most important vegetation formation of Brazil, exceeded only by the Amazonian forest with 3.5 x 10^6 km^2 (Map 1.1). This 'Cerrado province' as it is known (Eiten, 1972), is a composite of several vegetation forms, namely gallery forest, upland forest, wet campo and 'campo rupestre' (see Eiten, 1978), in addition to the dominant savanna vegetation. A savanna is defined as "all those tropical (and near-tropical) ecosystems characterised by strong seasonality (usually wet summer/dry winter), related to water stress, in which the vegetation consists of a continuous herbaceous cover of mostly C_4 grasses and sedges, and in most of which there is a significant but discontinuous cover of shrubs and trees" (Hills and Randall, 1968; Frost *et al.*, 1986; Walker, 1987) (C_4 describes species exhibiting the C_4-dicarboxylic acid photosynthetic pathway (Lawlor, 1987)). The Cerrado savanna includes a range of vegetation forms from treeless grassland to dense woodland, and represents the climax on the poor, freely draining soils that cover the central Brazilian plateau. Carl Frederick Philip von Martius (Martius *et al.*, 1840-1905) was the first person to classify the vegetations of Brazil and attempt to catalogue its species in his monumental '*Flora Brasiliensis*'. Based on Martius' 5 vegetation divisions of Brazil, the Cerrado province corresponds to the '*Oreades*', that is 'the tropical mountain campo region'. More recently the Cerrado has been reviewed by a number of authors (Ferri, 1963[a]; Labouriau, 1966; Goodland, 1970[a]; Ferri, 1971; Eiten, 1972; Eiten, 1977; Eiten, 1978; Goodland and Ferri, 1979; Eiten, 1982).



Map 1.1 Natural extent of Cerrado and Amazonian forest within Brazil (from Ratter, 1992). The Cerrado covers some 2×10^6 km^2 of the central Brazilian plateau and peripheral areas in states to the east, north-east and south. The field work which formed part of this research project was conducted at two isolated areas of Cerrado in the state of São Paulo, the Estação Ecológica de Itirapina, and the Reserva Biológica de Mogi-Guaçú which forms part of the Fazenda Campininha.

The Cerrado may be separated into two principal areas: the core area, on the central Brazilian plateau, which covers approximately 1.5 x 10^6 km^2 in the states of Goiás, Mato Grosso, Minais Gerais, Bahia, and the Distrito Federal; and peripheral areas in the states of Maranhão, Piauí, southern Rondônia, Pernambuco, south-east Para, Paraná and São Paulo (approximately 0.5 x 10^6 km^2). The field work that formed part of this research project was conducted at two isolated areas of Cerrado in the state of São Paulo (Map 1.1).

Although naturally covering nearly one quarter of the Brazilian territory the present day extent of the Cerrado is very much reduced, particularly in those areas with the greatest population and economic pressures (Furley and Ratter, 1988; Ratter, 1992). Large areas of the original Cerrado province have been altered or cleared for agricultural development (Ferri, 1955[b]; Nogueira Neto, 1977; Ferri, 1974; Furley and Ratter, 1988), although the exact extent of that Cerrado remaining is hard to establish because of the lack of accurate, recent vegetation surveys of the Brazilian territory.

1.1.2 Cerrado Physiognomy and Floristics

The Cerrado, the generic term, has been referred to as a 'wooded-savanna' in respect to the often important role of the woody components of this vegetation (Rizzini, 1963). In fact, Cerrado includes a range of vegetation sub-types from prairie-like grassland to almost closed forest (Eiten, 1972), and although this range of structural forms represents a continuum (Coutinho, 1978), various authors have recognised distinct vegetation classes based on the density of the woody components (Goodland, 1971[a]; Eiten ,1972):

(a) 'campo limpo' (clean field‡) - dry grassland without shrubs or trees;

(b) 'campo sujo' (dirty field‡) - grassland with a scattering of shrubs and trees up to 3 m high;

(c) 'campo cerrado' (closed field‡) - where there are numerous trees and shrubs (up to 4 m high) but still a large area of grassland;

(d) 'cerrado' *sensu stricto* (closed‡, *i.e.*, the vegetation has closed) - when the vegetation is obviously dominated by trees and shrubs (up to 6 m high) but there is still a fair amount of herbaceous vegetation, see Plate 1.1;

(e) 'cerradão' (big/tall 'cerrado'‡) - almost closed woodland made up of trees, often of 8-12 m or even taller, casting a considerable shade so that ground vegetation is much reduced.

(‡ literal English translation)
This continuum represents the increasing stature and density of woody components to the vegetation structure.

Plate 1.1 General view of the Brazilian Cerrado and its physiognomy. This plate shows an area of Cerrado, in fact cerrado *sensu stricto* (see section 1.1.2), from the Reserva Biológica de Mogi-Guaçú which forms part of the Fazenda Campininha, São Paulo State, Brazil.

Work by Moreira (1990) suggests that woody species from the more open forms of Cerrado show greater root development than those from the more closed forms of Cerrado. This suggests an inverse subterranean physiognomic gradient which parallels that seen in the aerial parts of the vegetation. Floristic composition gradually changes along this gradient, with some species occuring over the whole range of densities but in different proportions, while other species are absent in the densest or in the most open stands (Eiten, 1963; Rizzini, 1963; Goodland, 1969; Silberbauer-Gottsberger and Gottsberger, 1984; Oliveira-Filho *et al.*, 1989). *Kielmeyera coriacea* Mart. (Guttiferae), has been reported in all these structural categories, but is usually best represented in intermediate forms such as campo cerrado and cerrado *sensu stricto* (Goodland, 1969; Ratter, 1980; Ribeiro *et al.*, 1985; Ratter *et al.*, 1988; Felfili and Silva, 1992). As well as these physiognomic/floristic relationships, marked differences in floristic composition are seen in the Cerrados of different regions (Goodland, 1972), and studies have shown differences in structural dominants from region to region (Gibbs *et al.*, 1983; Ratter *et al.*, 1988). A few species occur over the whole province, but widely separated areas may have only one-fourth of the species in common, with gradients of floristic similarity connecting the two extremes (Sarmiento, 1983).

The rich flora of the Cerrado is estimated to be composed of some 800 woody species, and a greater number of herbaceous and semi-herbaceous species (Rizzini, 1963; Goodland, 1970; Rizzini, 1971; Ratter, 1986). Even small areas may have rich and diversified floras as shown by Warming (1892), Ratter (1980), Silberbauer-Gottsberger and Gottsberger (1984), and Heringer (1971). The latter author recorded more than 300 species in one hectare of protected Cerrado near Brasília.

The following families of woody species are well represented in the Cerrado: Anacardiaceae, Annonaceae, Apocynaceae, Bombacaceae, Bignoniaceae, Caryocaraceae, Connaraceae, Dilleniaceae, Erythroxylaceae, Guttiferae, Leguminosae (Papilionoideae, Caesalpinioideae, Mimosoideae and Indeterminata), Malpighiaceae, Melastomataceae, Myrtaceae, Ochnaceae, Proteaceae, Rubiaceae, and Vochysiaceae (Rizzini, 1963; Goodland, 1970[b]; Rizzini, 1971). Many of these families are large with many species, however the Annonaceae, Bignoniaceae, Malpighiaceae, Melastomataceae and Vochysiaceae are not, and are therefore more characteristic of the Cerrado (Goodland, 1970[b]).

Plate 1.2 *Kielmeyera coriacea* Mart. (Guttiferae) a charateristic and endemic tree of the Brazilian Cerrado. This tree, photographed in the Reserva Biológica de Mogi-Guaçú, was approximately 3.5 m high.

The genus *Kielmeyera*, family Guttiferae, is reported to be one of the most characteristic genera of the Cerrado (Goodland, 1970[b]), and exhibits a remarkably high percentage of species endemism, with 33 of the 47 member species described, endemic to limited geographical areas mainly within Brazil (Saddi, 1982). *Kielmeyera coriacea* Mart. has the widest distributional range within the genus (Saddi, 1982), and is often locally dominant (Goodland, 1970[b]).

1.1.3 Physiognomy of Individual Trees and Shrubs

The woody plants of the Cerrado have a characteristic morphology that distinguishes them from the mesophytic woody plants of the gallery forests (Eiten, 1972; Ferri, 1983), and other major tropical ecosystems (Sarmiento *et al.*, 1985). This morphology includes: short stature (typically 3-8 m tall); large, thick and entire leaves which are either stiff and glabrous or very hairy and mesomorphic (except for leguminous species which often have compound leaves); thick, corky and ridged bark; inclined and twisted boughs and trunks, giving a tortuous growth form; and substantial underground development, often producing subterranean woody organs known as 'xylopodia' (Ferri, 1978). The term xylopodium is preferable to 'lignotuber', which implies a stem-tissue origin or formation from a lateral rhizome, not the main root or hypocotyl derived structures seen in Cerrado species (Eiten, 1972). Xylopodium formation may be obligatory or induced by specific environmental conditions, such soil nutrient deficiencies or fire (Rawitscher and Rachid, 1946; Rachid-Edwards, 1956). The tortuousity of Cerrado woody species is thought to be accentuated by the increasing frequency dry-season fires (Eiten, 1972). The leaves of many species have considerable longevity, thick cuticles, sunken stomata, and greatly lignified and sometimes silicified tissues (Furley and Ratter, 1988).

1.2 The Cerrado Environment

1.2.1 Climate

The Cerrado province covers a large number of geological formations, types of topography, and a range of altitudes, and consequently its distribution must be due to the only factor which is essentially consistent, that is macro-climate (Eiten, 1972; Nix, 1983). Although the local climate does vary from region to region (Ferri, 1977), there are a number of well-defined characteristics common to the Cerrado climate as a whole: (i) a pronounced wet season generally from about late September to April, and a dry season coincident with the coldest months of the year, annual precipitation averages approximately 1400 mm; (ii) mean annual temperatures from 20°C to 26°C;

and (iii) a mean annual evaporating transpiration deficit (Thornthwaites method) of 4-491 mm (Lopes and Cox, 1977[a]). The climate, in general, is in the transition between Köppens Savanna (Aw) and Monsoon (Am) subtypes (Carmargo, 1963; Carmargo, 1968; Reis, 1971).

Although mean annual temperatures of the Cerrado region typically range from 20°C to 26°C, in southern São Paulo State they may be as low as 18°C, and extremes of minimum temperature vary from 14°C to -4°C in parts of São Paulo (Eiten, 1972). The average variation in temperature extremes within a year is from 22°C in Piauí and 26°C in central Maranhão, to 44°C in southern São Paulo. The very southern edge of the Cerrado, that occurs at high altitude in south-western São Paulo, experiences 1-2 (-4) frost days per year, and Cerrados in the rest of São Paulo and southern Minais Gerais occasionally suffer from slight frosts.

Cerrado occurs in areas which receive mean annual rainfall levels of between 750 mm in northern São Paulo, to 2000 mm at the Amazonian forest boundary. Rainfall levels outside this range result in alternative vegetation formations. Drier vegetations, like the Caatinga and Chaco, generally form in areas with rainfall levels below 750 mm. Mesophytic forest, like Amazonian or Atlantic forest, forms in areas with precipitation levels of more than 2000 mm, or possibly less in the southern states. In the state of São Paulo continuous evergreen forest forms in areas with annual rainfall levels of as little as 1300 mm, owing to the lower mean temperatures and evapotranspiration rates in these areas. Patterns of rainfall are highly seasonal, with the driest months July or August, typically having only 10 mm to 30 mm of rain. Annual evaporation ranges from 600 mm to 1400 mm.

1.2.2 Cerrado Soils

Cerrado soils are very old, estimated to have existed from the early Cenozoic, Cretaceous, or even Jurassic, and are consequently highly weathered. Cerrado soils are typically dark-red latosols or red-yellow latosols, with low base status, low nutrient availabilities, and low pH with consequent high aluminium availability (Ranzani, 1963; Lopes and Cox, 1977[a]; Goedert, 1983). Soils are characteristically very deep, often more than 20 m, and freely draining (Ferri, 1944). Cerrado soils range in composition from very sandy to very clay-rich (Ranzani, 1963; Lopes and Cox, 1977[a]).

Cerrado does not develop on lithosols, that is, soils which are appreciably less than 1 m deep, and where soils abruptly change to very shallow depths, Cerrado

vegetation often shows an equally abrupt transition to an alternative vegetation type. Cerrado does not occur on soils with any long term accumulation of water. This is in strong contrast to the hyperseasonal savannas of northern South America (Beard, 1953).

Cerrado is a vegetation of nutritionally-poor dystrophic soils, and where more fertile soils occur in the Cerrado region they are occupied by deciduous and semi-deciduous mesophytic forests (Denevan, 1968). These nutritionally-poor soils may be either, relatively young soils derived from rocks of low nutrient content, or older soils which have been leached of all major nutrient ions, particularly sulphates and bases (Ca^{2+}, Mg^{2+} and K^{+}). This soil leaching, as well as depleting soil nutrients, results in: a reduction in cation exchange capacity (the ability to retain mineral nutrient ions); and a decrease in soil pH which results in an increase in aluminium availability. The latter combination, of low pH and high aluminium availability, rapidly occludes phosphorus in iron-aluminium-phosphates, which are unavailable to plants. The total amount of organic matter in the soil-plant-leaf litter cycle is low, and soil organic matter is rapidly mineralised producing a constant low humus content. Typical characteristics of Cerrado soils, as summarised by Furley and Ratter (1988), are shown in Table 1.1.

Table 1.1 Range and median values of soil properties in the Brazilian Cerrado (from Furley and Ratter, 1988).

Soil Property	Median	Range	Comment
pH (H_2O)	5.0	4.3-6.2	nearly 50% have high acidity (<5)
Ca (meq/100ml)	0.25	0.04-6.81	96% classified as low
Mg (meq/100ml)	0.09	0.00-2.02	90% classified as low
K (meq/100ml)	0.08	0.02-0.61	85% classified as low
Effective CEC* (meq/100ml)	1.1	0.35-8.1	84% <2 meq/100 ml, indicative of highly weathered soils
Al (%)	59	1.1-89.4	79% over 40% saturation, the level toxic to most crop species
Organic matter (%)	2.2	0.7-6.0	Contributes little to the effective CEC*
N (%)§	0.1	0.01-0.2	low to very low levels
P (µg/ml)	0.4	0.1-16.5	>90% with less than 2 µg/ml
Zn (µg/ml)	0.6	0.2-2.2	80% below 0.8 µg/ml
Cu (µg/ml)	0.65	0.0-9.7	70% below 1.0 µg/ml
Mn (µg/ml)	7.6	0.6-92.2	37% below 5.0 µg/ml
Fe (µg/ml)	32.5	3.7-74.0	No deficiency or toxicity, but levels influence P fixation
Clay (%)	33.5	4.5-72.4	High clay contents related to P fixation and water holding capacity.

CEC* is the cation exchange capacity of the soil, § Data from Ranzani (1963).

1.2.3 Topography

The Cerrado vegetation is characteristic of the Brazilian plateau, but occurs at altitudes from 100 m (Porto Velho, Rondônia) to 1240 m above sea level (Capitólio, Minais Gerais). Cerrado is only found in areas that show seasonal drying out of the upper soil layers, and this restricts Cerrado to broad, gently sloping upland interfluvial areas, and prevents it from forming on valley bottoms and steeper hillslopes which suffer out-flushing from lateral water flow.

1.3 Ecology of the Cerrado: Climate, Soils, and Fire

The savannas of northern South America are thought to be in a steady state, regulated by a fire-water interaction on a background of low nutrient availability (Medina and Silva, 1990). The Brazilian Cerrado may be similarly regulated. Reviews of the general ecology of the Cerrado have been provided by Ferri (1977) and Goodland and Ferri (1979), and a specific review of the ecology of neotropical woody species has been provided by Sarmiento *et al.* (1985).

The Cerrado has been described as a xeromorphic vegetation (Eiten, 1972; Eiten, 1978). During the dry season the upper layers of the soil dry out, usually below the wilting point, and the aerial parts of most of the herbaceous plants dry up and die back (Rawitscher *et al.*, 1943; Sarmiento *et al.*, 1985). Indeed, the functioning of the herbaceous vegetation is closely coupled to the availability of soil moisture (Medina, 1982), and most species show adaptations to the winter drought and fire stress (Eiten, 1972). Growth is triggered by the availability of soil moisture, and stomatal behaviour, which is highly sensitive to ambient conditions, is closely controlled in many graminaceous species (Rachid, 1947; Goldstein and Sarmiento, 1987).

In contrast, the woody species of this savanna ecosystem often remain green and active during the dry season, rarely showing any signs of wilting, and showing leaf flushing and/or flower production in advance of the first wet-season rains (Ferri, 1983). This has lead to a re-appraisal of the use of the term xeromorphic to describe the woody strata, and instead the term 'pseudo-xeromorphism' has been favoured (Ferri, 1963[b]; Ferri, 1972; Ferri, 1983). Ferri has contrasted the morphology and behaviour of the woody species of the Caatinga (considered to be a truly-xeromorphic vegetation) and the Cerrado to illustrate this point (Ferri, 1955[a]; Ferri, 1961; Ferri, 1978). Many Cerrado woody species show high stomatal conductances throughout the day and the dry season (Ferri, 1944; Coutinho and Ferri, 1956; Coutinho and Ferri, 1960; Válio *et al.*, 1966; Grisi, 1971), and possess large or pinnate leaf forms which

are not typically xeromorphic features. As a consequence of the generally deep soils on which Cerrado forms, the soil water table is correspondingly deep, usually 10-30 m below the soil surface (Schubart, 1959). However soil horizons below 2 metres are generally moist, even in the dry season, and these horizons contain water reserves equivalent to 3 years precipitation (Rawitscher *et al.*, 1943; Rawitscher, 1948). As most woody species show extensive root development with many, including *K. coriacea*, forming roots reaching up to 5-10 m in depth (Rawitscher, 1948), most are in contact with soil-water throughout the year, and are thus able to freely transpire even in the dry season (Ferri, 1963[b]; Ferri, 1978).

However, although not exhibiting truly xeromorphic characters the leaves of many Cerrado woody species commonly show sclerophylly, having thick cuticles, sunken stomata, and greatly lignified and sometimes silicified tissues (Morretes and Ferri, 1959; Beiguelman, 1962[a-d]; Morretes, 1967; Morretes, 1969; Furley and Ratter, 1988). Arens (Arens, 1958[a,b]; Arens, 1963) has put forward a theory of oligotrophic scleromorphism (pseudo-xeromorphism), and proposed that the scleromorphic habit is due to soil nutrient difficiencies. The deficiency of nitrogen is considered particularly important, although deficiencies of P, Ca, B, Zn, and other nutrients could be locally important. Arens suggests that the high stomatal conductances permit the maintenance of high photosynthetic rates which result in an excess of fixed carbon. This fixed carbon cannot be combined with nitrogen, phosphorus and sulphur to form protein, as these elements are deficient in the soil, and is therefore consumed in the production of carbohydrate-based scleromorphic structures.

Allied to this nutritional interpretation of scleromorphism is Goodlands (Goodland, 1971[b]) suggestion that it is a result, at least in part, of the high levels of available aluminium within Cerrado soils. As indicated in Table 1.1, typical levels of available aluminium are so high as to be toxic to most cultivated plants. All Cerrado species must be adapted to these high aluminium availabilities, and indeed a number of important species actively accumulate aluminium (Haridasan, 1982). Important aluminium-accumulator species are found in the following families (genera), Melastomataceae (*Miconia*), Rubiaceae (*Palicourea*), and Vochysiaceae (*Qualea*, *Vochysia*). *K. coriacea* is not an aluminium-accumulating species (Haridisan, 1982).

The concentrations of elements such as N, P, K and Ca in the leaves of savanna trees are known to be relatively low (Sarmiento *et al.*, 1985). This reduced nutrient accumulation in response to low soil availability, is a common physiological response to a nutrient-deficient medium, but is particularly apparent in evergreen woody

species (Chapin, 1980). For savanna trees foliar concentrations of N, P, and K peak in young leaves, and decline steadily throughout the wet season reaching minimal values immediately before abscission (Montes and Medina, 1977; Medeiros and Haridasan, 1985). These declines are not thought to represent losses, such as those from leaching (Tukey, 1970), but rather to result from an internal recycling process. Indeed, the recuperation of mineral nutrients from senescent leaves is known to be particularly efficient in savanna woody species (Medina, 1984).

The seasonal nature of Cerrado rainfall results in the accumulation of large quantities of combustible herbaceous dry-matter during the dry winter period. Today this is ignited to recycle nutrients and improve vegetative regrowth for cattle-grazing (Coutinho, 1982; Frost and Robertson, 1987), although occasional natural fires must have been an environmental factor throughout the long history of the Cerrado (Van der Hammen, 1983). Consequently the Cerrado vegetation, both herbaceous and woody components, is highly adapted to the occurrence and ecology of fire (Eiten, 1972; Coutinho, 1980; Coutinho, 1990), and indeed the flora has features typical of pyrophytic savanna vegetation (Coutinho, 1982; Furley and Ratter, 1988). Graminaceous species have a clumped growth form (tunic-graminoids), which insulates the central basal meristems from the heat of the fire, and trees frequently have thick, corky, fire-resistant bark around trunks and branches, even in those of the last order. Most forbs, shrubs and semi-shrubs, and many trees have thick woody subterranean xylopodia (Warming, 1892; Rizzini and Heringer, 1961; Rizzini and Heringer, 1962; Rizzini, 1965[a]; Rizzini, 1965[b]; Rizzini and Heringer, 1966; Silva and Heringer, 1979). As well as being proof against the fire, these organs contain latent meristems and stored reserves for regrowth (Rachid-Edwards, 1956; Coutinho *et al.*, 1978; Figueiredo-Ribeiro, 1981; Figueiredo-Ribeiro *et al.*, 1986). Indeed, Dionello (1978), and Raw and Hay (1985) described adventitious bud formation and regrowth from xylopodia of *K. coriacea* and *Simarouba amara* Aubl. (Simaroubaceae) juveniles respectively, after shoot removal/death by burning. Nutrients in the ash residue, left after burning, are quickly recycled by shallow roots of the woody and herbaceous strata. However, as the vegetation burns part of its nutrient content (N, P, S) is lost to the atmosphere as gaseous oxides, and part as finely divided particles (Ca, K, Mg) (McClung and Martins de Freitas, 1959; Frost and Robertson, 1987). Although some of these loses may be returned by gravity or in solution in rainfall (Coutinho, 1979), this process may further reduce soil nutrient levels. In addition to being well adapted to the occurrence of fire, many herbaceous species may be considered fire-dependent, since their vegetative and reproductive vigour depends on the physical or chemical effects of fire (Coutinho, 1978; Coutinho, 1980).

1.4 Determinants of Cerrado Structure

There are four principle determinants of savanna structure and functioning, these are soil moisture availability, soil nutrient availability, herbivory, and fire (Huntley and Walker, 1982; Sarmiento, 1984; Walker, 1987). Soil moisture and nutrient status are generally considered to be key factors, affecting both the balance between grasses and woody plants, and the patterns of primary productivity and plant quality (Frost *et al.*, 1986; Solbrig, 1986). Annual rainfall levels and patterns determine plant available moisture, that in turn regulates the growth rate of the vegetation. This affects the light regime within the canopy, and the amount of standing live and dead biomass, which in turn affects the probability of fire. The rhythm of the wet and dry seasons regulates the rhythm of growth and reproduction of the herbaceous and woody vegetation. Soil water dynamics in northern South American savannas are highly correlated with community structure and composition along moisture gradients (Silva, 1972; Silva and Sarmiento, 1976[a,b]), and this also appears to be true for the Cerrado (Goldsmith, 1974). The effects of variation in rainfall are compounded by differences between soils in permeability and moisture retention properties (Young, 1976; Montgomery and Askew, 1983). In areas of low precipitation, or very good drainage, trees are absent or restricted to depressions where water accumulates (Sarmiento and Monasterio, 1971). At the other extreme, in wet areas with poor drainage, trees are found only on high elevations. The spatial heterogeneity of savanna soils is marked. Substantial differences in species composition and abundance can readily be observed over short distances in relation to this heterogeneity, suggesting that optimal sites for different species are generally limited to one or a few sites along an edaphic gradient.

Walker (1987) has suggested that the vegetation structure and the primary productivity of the Brazilian Cerrado is principally determined by soil nutrient status and fire, although many other authors have attributed the origin, distribution and form of the Cerrado to a variety of climatic, topographic, edaphic, and anthropogenic factors (Alvim and Araujo, 1952; Hueck, 1957; Cole, 1960; Beiguelman, 1963; Ferri, 1973[a,b]; Sarmiento and Monasterio, 1975; Eiten, 1978; Oliveira-Filho *et al.*, 1989). In reality Cerrado is probably a function of any one or more of these factors, the relative importance of each dependant on local conditions (Furley and Ratter, 1988; Oliveira-Filho *et al.*, 1988).

The distribution of Cerrado, and variations in Cerrado physiognomy have been correlated with variations in edaphic factors such as soil depth, aluminium availability, pH, and soil nutrient availabilities, particularly for phosphorus. Eiten (1972) reported

the dwarfing of Cerrado physiognomy over lithosols (shallow rocky soils), and Goodland (1971[b]) stressed the importance of aluminium to Cerrado structure. Goodland and Pollard (1973), and Lopes and Cox (1977[b]) correlated increasing density of the woody components of the vegetation with an increasing soil fertility gradient. However other workers have shown distinct differences in Cerrado structure in the absence of significant differences in soil fertility (Gibbs *et al.*, 1983; Ribeiro, 1983; Oliveira-Filho *et al.*, 1989). Gibbs *et al.* (1983) indicated that local gradients of Cerrado physiognomy may be due to, localised burning, differential frost exposure, drainage differences, or man-made disturbances.

Soil moisture is another factor which controls many of the most obvious differences in vegetation in the Cerrado province. Swampy gallery forest forms where the water table is permanently high, while wet campo grassland (not campo limpo) forms where the soil is inundated for part of the year but dries up during the dry season (Furley, 1985). At its extreme, soil saturation leads to a pure grassland such as that of the 'pantanal' of south west Brazil, or 'murundus' (hummocks) where woody species are restricted to small raised islands of drier soil. A number of important Cerrado tree species, including *Kielmeyera coriacea*, have been shown to be intolerant of inundated soils (Joly and Crawford, 1982), and therefore within the Cerrado increasing seasonal water saturation opens out the woody layer and selects for tree species which are most tolerant of soil waterlogging, such as *Curatella americana* L. (Dilleniaceae) and *Byrsonima crassifolia* H.B.K. (Malpighiaceae).

Fire is reported to be extremely important in determining the density of the Cerrado woody species (Furley and Ratter, 1988). Cerrado vegetation is adapted to resist burning, however, excessively frequent burning favours the herbaceous as opposed to the woody component of the vegetation, and when this occurs savanna woodlands are transformed into grasslands. Conversely, protection from fire often results in an opposite effect, and a dense savanna woodland with considerable shade and only a very sparse ground layer is established (Frost and Robertson, 1987). Today the lower and more open forms of the Cerrado are often a result of clearing and annual burning of taller, denser forms (Furley and Ratter, 1988).

The regeneration phase of the forest cycle is a highly stochastic process, and is recognised to be the phase most sensitive to change and variability (Harper, 1977; Shugart *et al.*, 1982). Therefore some of the differences seen in Cerrado structure may reflect processes operating primarily during regeneration. Successful seedling establishment is a critical component of forest (*i.e.* tree) regeneration. Local woody

species floristic composition, and therefore site physiognomy, may be strongly influenced by the differential survival of woody seedlings under local soil moisture, soil nutrient and fire conditions. Since smaller seedlings are generally the most sensitive to environmental stresses and disturbance, in terms of resistance and resilience, limitations to seedling growth and therefore dry weight accumulation will increase the risk of seedling mortality (Frost *et al.*, 1986). Thus limitations to woody seedling growth may influence Cerrado structure.

1.5 Cerrado Woody Species Growth

The often hard and dry soils of the Cerrado, in conjunction with seasonal fires and competition from taller vegetation, were originally thought to reduce the occurrence of regeneration from seed, and therefore explain the paucity of Cerrado annual species (Warming, 1892). Indeed, Warming declared that the multiplication of Cerrado plants by seed was a pure exception. Ferri later supported this conclusion, by noting the lack of seedlings of Cerrado species observed in the field (Ferri, 1961; Ferri, 1963[b]). However later work (Labouriau *et al.*, 1963; Labouriau *et al.*, 1964[a]; Válio and Moraes, 1966[b]) suggests that seedling regeneration by woody species is more common than previously thought. The work of Labouriau *et al.* (Labouriau *et al.*, 1964[a]) demonstrated the role of regeneration from seed for 50 different Cerrado species, including *Kielmeyera* species; and that species such as *Caryocar brasiliense* Camb. (Caryocaraceae) were capable of surviving the dry season following germination. Numerous germination studies of Cerrado woody species have since established the potential for regeneration by this means (Labouriau *et al.*, 1963; Melhem, 1975[a]; Dionello, 1978; Melo *et al.*, 1979; Joly and Felippe, 1979[a]; Joly and Felippe, 1979[b]; Felippe and Silva, 1984; Arasaki and Felippe, 1987; Moreira, 1990; Godoy, 1991; Sassaki, 1991; Sassaki and Felippe, 1992; Oliveira and Silva, 1993). However, with the exception of a small number of recent studies, there is a paucity of studies on the growth of seedlings of Cerrado woody species (Labouriau, 1963). Indeed, this is true of tropical savannas in general (Frost *et al.*, 1986), and particularly those of West Africa (Menaut pers. com., 1992), northern South America (Medina pers com., 1992), and Australia (Landsberg pers. com., 1992; Leishman pers. com., 1992). Detailed studies of woody seedling growth and establishment, both in the Cerrado (Labouriau, 1966) and in savannas in general (Frost *et al.*, 1986), are required for a better understanding of savanna structure and functioning.

Early considerations of the growth of Cerrado woody species were largely descriptive, and being visual, usually involved descriptions of shoot development.

Most authors inferred from the (relatively) low stature of Cerrado trees that growth rates were slow (Warming, 1892). Later studies continued this theme considering the quantitative increase in root and shoot length (Rizzini and Heringer, 1962; Rizzini, 1965[a]; Melhem, 1975[b]). These studies recognised the often substantially greater development of roots over shoots in terms of length, and the formation of xylopodia. Only recently has the growth of Cerrado woody species been quantitatively determined on a dry weight basis (Poggiani, 1971; Poggiani, 1973; Arasaki, 1988; Self, 1989; Arasaki and Felippe, 1990; Felippe and Dale, 1990; Moreira, 1990; Paulilo, 1991; Godoy, 1991; Sassaki, 1991; Arasaki and Felippe, 1991; Mendes, 1991; Godoy and Felippe, 1992). These studies, although considering important Cerrado woody species, are limited to a small number of species, particularly in view of the tremendous diversity of the Cerrado woody flora. Species studied to-date include, *Dalbergia miscolobium* Benth. (Leguminosae); *Dimorphandra mollis* Benth. (Leguminosae); *Kielmeyera coriacea* Mart.; *Qualea cordata* (Spreng.) (Vochysiaceae); *Qualea grandiflora* Mart. (Vochysiaceae); *Stryphenodendron adstringens* (Mart.) Coville (Leguminosae); and *Sweetia pseudelegans* Mohlenbr. (Leguminosae). These investigations have established the high variability in growth rate and the relatively slow dry weight accumulation of Cerrado woody species under field conditions compared with other temperate and subtropical/tropical woody species, and the developmental increase in root to shoot dry weight ratio. However, the bases of these slow growth rates, and the consequences of this partitioning have hitherto not been considered. In particular, growth potential (maximum potential relative growth rate, *sensu* Grime and Hunt (1975), that is maximum possible growth rate under productive conditions) of Cerrado woody species has been little investigated, and the importance of sub-processes such as leaf area development and the development of leaf assimilatory capacity, which may limit whole plant growth, have not been investigated. Research of the growth of Cerrado woody seedlings under natural and favourable environmental conditions is required to establish, the inherent and environmental limitations to plant growth, and the limitations of leaf area and assimilatory capacity to plant growth under these conditions.

Válio (1990) stated that the growth rate of *Dimorphandra mollis* Benth. (Leguminosae) seedlings is conditioned more by internal genetic controls than by environmental factors. However, studies of *Kielmeyera coriacea* (Self, 1989), and an aluminium-accumulating Cerrado shrub species, *Miconia albicans* (Sw.) Triana. (Melastomataceae) (Haridasan, 1988), have indicated that Cerrado woody species do respond positively to increased soil fertility. In the latter case these positive responses included significant increases in plant height, the number of leaf pairs, and individual

leaf size, and therefore one assumes plant dry weight. Similar responses are reported for another important aluminium-accumulating Cerrado species, *Vochysia thyrsoidea* Pohl. (Vochysiaceae) (Machado, 1985). Haridasan's study (Haridasan, 1988) suggested that an absence of free aluminium in the growing medium limits the growth of *M. albicans*, as this element has some specific function in the metabolism of the species. Thus, for *Qualea grandiflora* Mart. (Vochysiaceae) seedlings, the lack of enhanced growth with nutrient feeding (Paulilo, 1991) and the failure of seedlings to develop in full-strength Hoaglands solution (Felippe and Dale, 1990); and for *Qualea cordata* Spreng. (Vochysiaceae) seedlings, the reduced growth seen with increasing nutrient feeding (Godoy and Felippe, 1992), may be a consequence of an aluminium requirement. Such aluminium-accumulating species may have an aluminium requirement for vigorous growth under nutrient rich conditions, deficiency resulting in calcium-induced iron chlorosis, or manganese toxicity.

Plant primary production is ultimately dependent on photosynthetic CO_2 uptake. However, photosynthate production also depends on the amount of photosynthetically active tissue constructed by the plant, and on many aspects of carbon use (expenses and investments) (Mooney, 1972). Körner (1991) describes those important factors which co-determine carbon balance during vegetative growth as,

(i) metabolic factors (photosynthetic, and respiration rates),

(ii) developmental factors (including cell division and differentiation rates, and ontogenetic status),

(iii) allometric factors (including plant dry mass compartmentalisation, specific leaf area, and leaf weight ratio),

(iv) biomass losses (including fine root turnover, and above-ground mortality),

(v) time factors (including leaf duration, and the duration of vegetative plant activity).

All these factors apply to Cerrado woody seedling growth. However allometric, metabolic, and time factors may be particularly important, in view of the substantial subterranean development of seedlings, and the extreme mineral nutrient depletion of Cerrado soils. In the longer term, biomass losses, such as above ground mortality from fire damage, could also prove to be particularly important.

Xylopodium formation represents an adaptation to the Cerrado soil moisture, soil nutrient, and particularly fire environment, and enhances tree seedling survival. However xylopodium development places a demand on accumulated resource pools of fixed carbon and mineral nutrients. This demand diverts these resources from shoot

(in particular leaf area), and fine-root development. The greater the xylopodium development, the greater the resource diversion. Resource allocations (investments) to shoot and fine root development result in greater resource capture, of fixed carbon through increased leaf area and nutrient uptake through increased absorbing root surface respectively, and thus these investments produce returns in the resource economy of the plant (Figure 1.1(A)). This model involves the balanced partitioning of accumulated resources to shoot and fine roots for resource capture, to maintain the required mineral nutrient/carbon balance within the plant. Even allocation to structural organs such as the stem, petioles and main roots provides returns in terms of maintaining efficient light interception for carbon fixation or mineral nutrient uptake. However unlike these sinks, to which allocation may therefore be considered to be cyclical, biomass allocation to xylopodium development produces no short term return, and may therefore be considered to be linear (Figure 1.1(B)). In the absence of xylopodium development these resources could be allocated to shoot and fine root development, to increase resource capture, to increase shoot and fine root development, and so on, as is the compound nature of growth. The importance of allocation is clearly illustrated by models described by Körner (1991), and reference to the growth of wild and cultivated radish (Mooney and Chiariello, 1984). In the latter example, after only 5 weeks of synchronous growth wild radish had double the total biomass of cultivated radish, purely because a greater fraction of photosynthate was allocated to new leaf tissue rather than storage tissue. Thus, xylopodium development can reduce leaf area development by reducing leaf weight ratio (LWR), the ratio of leaf dry weight to whole plant dry weight. However, allocation to the xylopodium must not be considered as wasteful, but rather as an investment providing a return at critical stages during the seedling establishment phase, *i.e.* immediately after shoot loss by disturbance such as fire, and therefore enhancing the long-term survival of the individual (Frost and Robertson, 1987).

The sclerophyllous nature of the leaves of savanna trees results in them having particularly low specific leaf areas (SLA), the ratio of leaf area to leaf dry weight (Sarmiento *et al.*, 1985). Medina (1982) for a selection of northern South American savanna species, and Rizzini (1976) for a selection of Cerrado species described means and ranges of SLA substantially below those of non-savanna evergreen species, and well below those of deciduous species from other ecosystems. These low SLAs can also reduce leaf area development, as leaf area is the product of leaf weight ratio and specific leaf area.

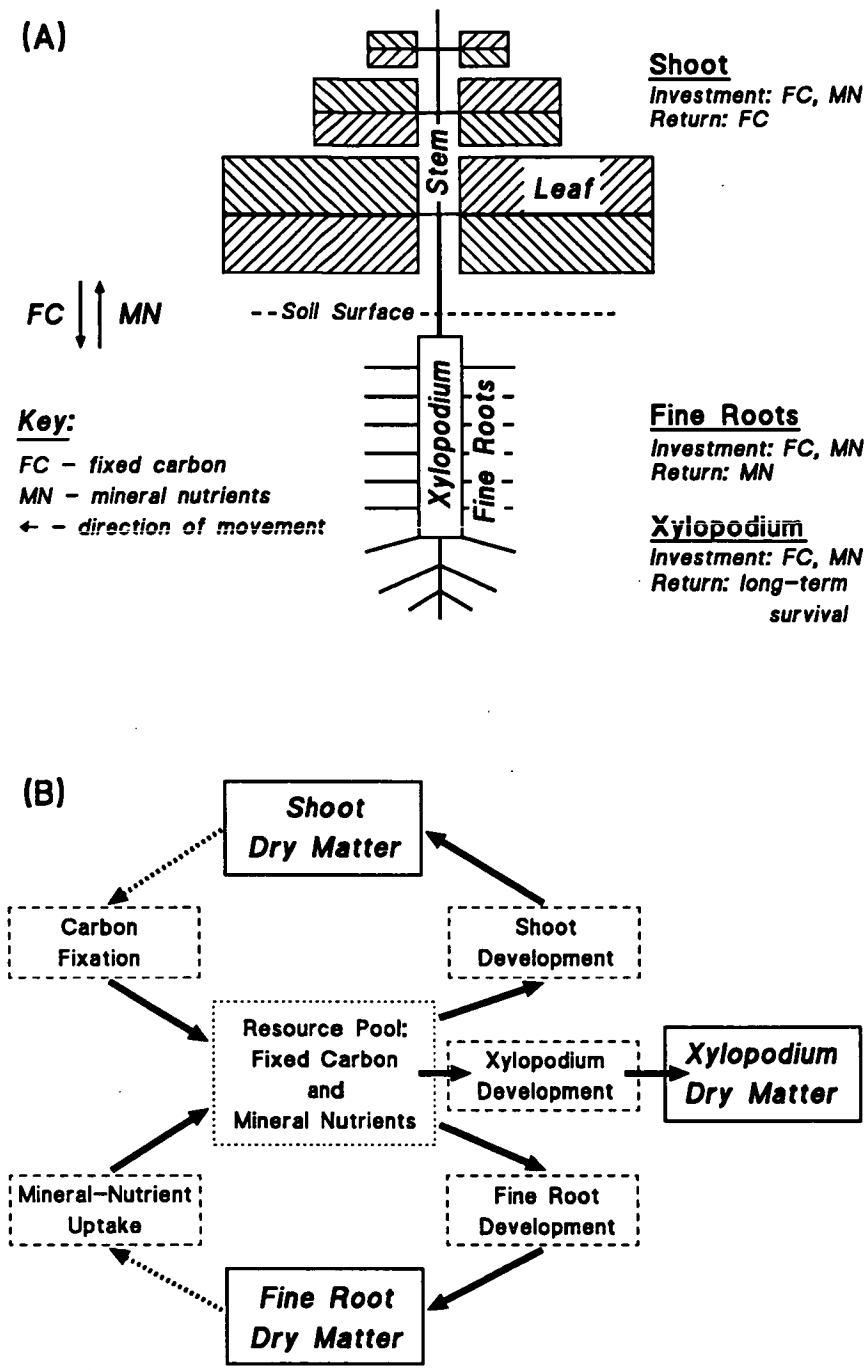


Figure 1.1 **(A)** Schematic diagram showing Shoot, Fine Roots and Xylopodium resource investments and returns, for a typical xylopodium-forming Cerrado woody seedling. 'Shoot' includes all leaves (including cotyledons) and stem material to maintain efficient light interception. 'Fine Roots' includes absorbing roots and structural roots to maintain efficient mineral nutrient uptake. 'Xylopodium' is the non-absorbing subterranean perennating and storage organ.

(B) Flow diagram showing the pattern of resource allocation for a typical xylopodium-forming Cerrado woody seedling. Note cyclical nature of 'Shoot' and 'Fine Root' development, and linear nature of 'Xylopodium' development.

To date studies of the growth of mature Cerrado trees have been largely phenological (Sarmiento and Monasterio, 1983), although recent studies have made quantitative investigations of the increase in plant height (Barros and Caldas, 1980; Caldas and Coutinho, 1991) or leaf growth (Santos and Silva, 1972; Silva, 1976; Nascimento *et al.*, 1990; Paulilo, 1990; Arasaki and Felippe, 1992; Arasaki, 1993). Phenological behaviour during the early stages of growth of any savanna tree has yet to be investigated (Medina, 1982).

The nutrient-stressed and fire-disturbed nature of the Cerrado, is apparent in the structural and functional traits characteristic of Cerrado woody species. Of primary importance to successful establishment in this type of environment is the conservation of captured resources (Grime *et al.*, 1988). As most plant activities depend upon the level of supply of mineral nutrients, it seems likely that conservative mechanisms of mineral nutrient capture and utilization will invariably be associated with constraints upon carbon assimilation (Chapin, 1980). It is well documented that a restriction in nitrogen supply during plant growth causes a strong reduction in the photosynthetic capacity per unit leaf area (Medina, 1984). Thus, the low availability of mineral nutrients in Cerrado soils, especially nitrogen and phosphorus, may strongly influence metabolic factors, such as photosynthetic rate.

1.6 Cerrado Woody Species Photosynthesis

Transpiration rates are reported to be high in many savanna woody species (Medina, 1982; Goldstein and Sarmiento, 1987). Some authors (Medina, 1986) have suggested that, as stomatal conductance correlates with photosynthetic capacity (Körner *et al.*, 1979; Wong *et al.*, 1979), such transpiration rates and therefore leaf conductances may be taken as an indication of relatively high photosynthetic capacities in these species. Certainly some inferences can be made about possible stomatal limitations to net photosynthetic rate from studies of stomatal conductance and transpiration rate under field conditions (Ferri, 1944; Rawitscher, 1948; Coutinho and Ferri, 1956; Coutinho and Ferri, 1960; Valio *et al.*, 1966; Foldats and Rutkis, 1975). These studies, using rapid weighing and/or infiltration techniques, have indicated that most Cerrado woody species maintain stomata open and freely transpire throughout the day, in both wet and dry seasons, unless subject to root or shoot damage. Rawitscher (1948) described the 'wide' stomatal apertures of *K. coriacea* as, 'remaining open the entire day, even at the end of the dry season', and indeed Medina (1982) has calculated that large leaves, such as those possessed by *K. coriacea*, would be liable to overheat under typical savanna conditions unless leaf stomatal resistances

were low, to allow substantial transpirational cooling. However, species such as *Annona coriacea* Mart. (Annonaceae) (Ferri, 1944), *Byrsonima coccolobifolia* Spr. (Kunth.) (Malpighiaceae) (Ferri, 1944), *Curatella americana* L. (Dilleniaceae) (Foldats and Rutkis, 1975), and *Terminalia argentea* Mart. and Zucc. (Combretaceae) (Válio *et al.*, 1966) are reported to show some midday stomatal closure leading to reduced transpirational rates, and therefore possibly reduced net photosynthetic rates. Although nocturnal stomatal opening has been reported for a small number of woody species from the Cerrado (Labouriau *et al.*, 1964[b]), with the exception of a single cactus species, no Cerrado species show nocturnal CO_2-fixation (Válio and Moraes, 1966[a]).

Medina (1982) reported that, 'there is very little information about the photosynthetic capacity of savanna plants under natural conditions', and with the exception of a few recent studies (Tuohy and Choinski, 1990; Tuohy *et al.*, 1991) this statement remains true. Almost all net photosynthetic rate measurements of savanna woody species have been made on mature plants, values for seedlings are almost nonexistent. Photosynthetic studies using Infra-Red Gas Analysers (IRGA) on Cerrado woody species are few, and concern a limited number of species: *Byrsonima crassifolia* H.B.K.† (Malpighiaceae) (Medina, 1982); *Caryocar brasiliense* Camb. (Caryocaraceae) (Pereira Netto and Hay, 1985; Pereira Netto and Hay, 1986); *Curatella americana* L.† (Dilleniaceae) (Medina, 1982); *Didymopanax macrocarpum* (C. & S.) (Leguminosae) (Franco, 1983; Johnson *et al.*, 1983); and *Ouratea hexasperma* (St. Hil.) Baill. (Ochnaceae) (Johnson *et al.*, 1983) († indicates laboratory measurements made on branches collected from specimens of the Venezuelan Llanos). These studies indicated: interspecific variations in net photosynthetic rate on an area basis (P_n); ontogenic and seasonal variations in P_n; that incident photosynthetic photon flux density, as determined by solar position and leaf orientation, is the principal environmental determinant of P_n; and that net photosynthetic rates for these species are low, but comparable with those reported for woody species of other savanna ecosystems. Assimilation rates appear to decline with leaf age, and this correlates with the decreasing concentrations of foliar nutrients, particularly nitrogen, reported for savanna trees (see section 1.3). The low net photosynthetic rates of savanna woody species have been attributed to morphological and functional traits imposed by soil nutrient deficiencies (Sarmiento *et al.*, 1985). Using Gaastras (Gaastra, 1959) electrical analogy, resistances to the assimilation of CO_2 may be separated into those that are associated with CO_2 conduction to the intercellular spaces (leaf boundary layer and stomatal resistances), and that associated

with CO_2 transfer to the sites of carboxylation and the carboxylation process itself (mesophyll resistance: r_m). Medina (1982) has suggested that high r_m values are the primary limiting resistances for savanna woody species. These are thought to be a consequence of the low activities of Ribulose 1,5 Bisphosphate Carboxylase-Oxygenase (RuBisCO) due to low concentrations of RuBisCO, and leaf structural characteristics due to sclerophylly. These conclusions are supported by the fact that mesophyll resistances decrease considerably with decreasing oxygen partial pressures, and the fact that a substantial r_m remains even at very low oxygen partial pressure, respectively. Further measurements of net photosynthetic rates of Cerrado woody species in the field using IRGAs are required for a better understanding of photosynthetic behaviour and productivity of Cerrado woody species.

1.7 *Kielmeyera coriacea* Mart.

Kielmeyera coriacea Mart. (Guttiferae) is known by the vernacular names 'Saco de Boi', 'Pau de São José', and most frequently 'Pau-Santo', that is 'good/holy wood', as a result of its reputed medicinal properties (Dionello, 1978; Ratter, 1980).

K. coriacea was chosen as the principle species for this investigation for the following reasons: (1) *Kielmeyera* is a phyto-sociologically important Cerrado genus (Ribeiro *et al.*, 1985; Oliveira-Filho *et al.*, 1989; Felfili and Silva, 1992), and one of the most characteristic genera of the Cerrado (see section 1.1.2); (2) *K. coriacea* is the most abundant and widespread species of the genus, and is occasionally locally dominant (see section 1.1.2); (3) *K. coriacea* exhibits many features characteristic of Cerrado woody species, namely epigeal germination, extensive root development with xylopodium formation, large coriacous and entire leaves, thick corky bark, and a short tortuous growth form (Rizzini, 1965[a]; Saddi, 1982; Oliveira, 1986); (4) the genus *Kielmeyera* and specifically *K. coriacea* is one of the most thoroughly studied species of the Cerrado, and a modest pool of background information on the species already exists, including work completed at Edinburgh; and (5) *K. coriacea* regularly produces large quantities of seed, which germinates readily (Dionello, 1978; Oliveira, 1986; Moreira, 1990) and under favourable controlled conditions establishes well (Self, 1989).

Previous studies of the genus *Kielmeyera* have been taxonomic (Saddi, 1982; Saddi, 1988 and references therein), chemical (Gottlieb *et al.*, 1966[a,b]; Barros Corrêa, 1966), anatomical (Ferri, 1944; Paula, 1974[a,b]), ecological (Dionello, 1978; Dionello and Basta, 1980; Martins, 1980; Oliveira, 1986; Oliveira *et al.*, 1989; Oliveira and

Sazima, 1990; Oliveira and Silva, 1993), and physiological (Ferri, 1944; Rizzini and Heringer, 1962; Barros and Caldas, 1980; Joly and Crawford, 1982; Arasaki, 1988; Self, 1989).

1.8 Rationale and Aim of the Research

Although broad determinants of savanna floristic composition and structure have been identified, specific mechanisms are, as yet, poorly understood (Frost *et al.*, 1986; Walker, 1987). It is likely that many of these determinants have their primary effects on the processes of woody species regeneration, and particularly seedling establishment. Morphological and functional adaptations to savanna stresses and disturbances are probably key to woody seedling survival under natural conditions, however individual plant size/weight may be important in enhancing plant resilience. This may be particularly important as savanna environments impose fixed constraints on development and many adaptations incur costs or involve compromises in themselves.

Research into savanna woody seedling establishment is required for a better understanding of the ecology of these ecosystems, and the eco-physiology of their woody species. In particular, an understanding of the inherent and environmental limitations to development (intrinsic and extrinsic constraints, *sensu* Grime *et al.*, 1988), and the costs of adaptations to the savanna environment are needed.

The work of this thesis attempts to address, at least in part, some of these needs through an investigation of the growth of a characteristic Cerrado woody species. Developmental studies under favourable controlled conditions were used to establish inherent limitations (intrinsic constraints) to development, and to provide a baseline against which field studies were compared (work by Self (1989) and this author established the favourability of the growing environment, with respect to the growing medium, growing temperatures, and nutrient-feeding and watering regimes). Developmental studies under 'field conditions' were used to determine seedling performance in the field, and to determine the additional environmental constraints to establishment found in the field. Thus the aim of this work was to determine the inherent and environmental limitations to development of Cerrado woody species, with reference to *Kielmeyera coriacea* Mart. (Guttiferae).

1.9 Objectives

The aim of this work was achieved by a sequential, reductive analysis of whole plant growth, attempting to determine the mechanistic limitations to growth rate. In asking what limits the rate of growth, we are not so much interested in the immediate cause, as in the underlying limitation which prevents growth from going faster. The following objectives were thus established:

(1) For *Kielmeyera coriacea* Mart. seedlings grown under productive controlled conditions:

(i) determine the ontogenic patterns of dry matter accumulation and specific growth rate;

(ii) determine the ontogenic patterns of unit leaf rate, and leaf area ratio (and its components, leaf weight ratio and specific leaf area), and their influence on specific growth rate.

(iii) determine the consequences of xylopodium formation on whole plant development, particularly in the context of a competitive sink for photosynthate.

(iv) determine the ontogenic pattern of leaf area development, and in particular the associated rates of leaf primordia production and individual leaf expansion.

(v) determine the ontogenic patterns of individual leaf photosynthesis, and thereby the development of whole plant carbon assimilatory capacity.

(2) Determine 1 (i), (ii), (iii), (iv), and (v) for *K. coriacea* seedlings grown under field conditions.

Foliar development of *K. coriacea* trees in the field was investigated by Arasaki (1993). To complement this work, and to provide an indication of longer-term developmental changes in photosynthetic rate and productivity, a study of photosynthetic behaviour for *K. coriacea* trees in the field was also needed.

(3) Determine the photosynthetic behaviour of mature *K. coriacea* trees in the field.

In order to place the results of (3) in context, and to expand the small pool of existing photosynthetic study, similar investigations for other Cerrado woody species were also required.

Chapter 2:

Materials and Methods

This chapter describes those materials, species and sources, and methods, equipment and techniques, employed in the experimental work of this research. Further details of weather conditions at the field site during the period of field work, and details of the calibration of the Infra-Red Gas Analyser may be found in Appendix 2.1 and Appendix 2.2, respectively.

2.1 Materials

Experiments were conducted on two types of material: *Kielmeyera coriacea* Mart. seedlings grown under controlled environment or field conditions, and on mature *K. coriacea* and other Cerrado woody species in the field.

All controlled environment experiments using *K. coriacea* seedlings were conducted in growth rooms in the Daniel Rutherford Building, University of Edinburgh, Edinburgh, Scotland, U.K.. Seedlings were grown under field conditions at the viveiro (nursery) of the Reserva Biológica de Mogi-Guaçú (Decreto Estadual No. 12.500 de 07/01/42), which forms part of the Fazenda Campininha, São Paulo State (S.P.), Brazil. Members of the Departamento de Fisiologia Vegetal, UNICAMP, Campinas, S.P. kindly provided all seed for experimentation, from collections at the Reserva Biológica de Mogi-Guaçú in the spring of 1988 and 1990.

Field measurements were made at two sites, the Reserva Biológica de Mogi-Guaçú, and the Estação Ecológica de Itirapina (Decreto No. 22.355 de 07/06/84), S.P., Brazil. The following species were selected because of their local abundance, lack of previous field photosynthetic measurements, and their entire leaf shape: *Anacardium humile* St. Hil. (Anacardiaceae); *Annona coriacea* Mart. (Annonaceae); *Bauhinia holophylla* Steud. (Leguminosae); *Byrsonima coccolobifolia* (Spr.) Kunth (Malpighiaceae); *Kielmeyera coriacea* Mart. (Guttiferae); *Kielmeyera variabilis* Mart. (Guttiferae); *Ouratea spectabilis* (Mart.) Engl. (Ochnaceae); *Xylopia aromatica* Lam. (Annonaceae). All measurements, except those for *B. coccolobifolia* which were made at the Estação Ecológica de Itirapina, were made at the Reserva Biológica de Mogi-Guaçú.

2.2 Methods

2.2.1 Seedling Culture Methods

2.2.1.1 Controlled Conditions

Controlled conditions were used to establish growth rates under very favourable conditions, and thereby the near-maximal potential growth rate of *K. coriacea* seedlings. Although impracticable to determine truly optimal growing conditions, environmental conditions were designed to be, as far as possible, non-limiting for temperature, water availability, nutrient availabilities, and incident photosynthetic photon flux.

Healthy seed was initially surface-sterilised by immersion in a 5% (v/v) aqueous solution of sodium hypochlorite, containing a little Tween 80 as a wetting agent. The seed was then imbibed for 12 hr in a continuously flowing current of lukewarm (25°C) water. After imbibition the testa and tegma were removed and the seed transferred to dH_2O-moistened filter paper in petri-dishes (day 1). The petri-dishes were placed in the growth-room environment under shading, and the filter papers kept moist. Germination (day 6-7) was followed by sowing in 10 cm diameter × 12 cm deep pots containing a mixture of equal volumes of peat and sand, and transfer to the growth-room table surface. The 24 hr growth-room cycle consisted of a 12 hr 30°C light period with a 12 hr 20°C dark period. Mean irradiance at plant height on the table surface was 300 $\mu mol\ m^{-2}\ s^{-1}$, provided by a combination of fluorescent metal halide and tungsten lighting. Together these provided a mean red:far-red ratio (660 nm:730 nm) of 1.2. Although not controlled directly, relative humidity was maintained in the range 50-80%. Pots were watered (dH_2O) as required, to maintain the growing-medium moist. Over-watering led to brown necrotic patches on emerging leaves, which was thought to be a symptom of the species flood intolerance (Joly and Crawford, 1982), and was avoided. Each pot was given 50 cm^3 of nutrient solution every 7 days from day 14 onwards. The nutrient solution composition is described in Table 2.1, and is a modification of that used by Hoagland and Arnon (1938).

Table 2.1 Nutrient solution composition for *K. coriacea* culture in controlled conditions.

Macro Nutrients	Concentration	
Calcium Nitrate, $Ca(NO_3)_2.4H_2O$	5.9038×10^{-1}	kg m^{-3}
Potassium Di-hydrogen Orthophosphate	6.8×10^{-2}	kg m^{-3}
Potassium Nitrate, KNO_3	2.5275×10^{-1}	kg m^{-3}
Magnesium Sulphate, $MgSO_4.7H_2O$	2.4625×10^{1}	kg m^{-3}
Ferric EDTA	6.25×10^{-4}	kg m^{-3}
Micro Nutrients	**Concentration**	
Boric Acid, H_3B_3	7.15×10^{-4}	kg m^{-3}
Manganese Chloride, $MnCl_2.4H_2O$	4.525×10^{4}	kg m^{-3}
Zinc Sulphate, $ZnSO_4.7H_2O$	5.5×10^{-5}	kg m^{-3}
Copper Sulphate, $CuSO_4.5H_2O$	2×10^{-5}	kg m^{-3}
Molybdic Acid, H_2MoO_4; MoO_3	2.25×10^{-5}	kg m^{-3}

2.2.1.2 Field Conditions

Field conditions were used to determine growth rates under near-natural conditions, and thereby realistic approximations of growth rates in the field. Growth analysis of *K. coriacea* seedlings under field conditions was conducted from September 1990 to December 1990. All other seedling material was grown during the period December 1990 to March 1991.

For seedlings grown under field conditions, seed was surface sterilised and imbibed as in Edinburgh, and germinated in a 25°C illuminated incubator. Once germinated seed was sown in 10 cm diameter × 30 cm deep plastic bags containing riddled Cerrado soil. The soil was collected from a site within the Reserva Biológica de Mogi-Guaçú under cerrado *sensu stricto* vegetation at a depth of between 5 cm and 50 cm below the soil surface. Riddling the soil helped to homogenise it and remove unwanted debris. Results of a chemical analysis of the soil used, are provided in Table 2.2.

Table 2.2 Results of chemical analysis of soil used for *K. coriacea* culture under field conditions (analysis by Instituto Agrinomico de Campinas, No. 113928).

Phosphorus	1 µg/cm^3
Percentage Organic Material	1.1
pH in $CaCl_2$	3.9
Potassium	0.05 meq/100 cm^3
Calcium	0.1 meq/100 cm^3
Magnesium	0.1 meq/100 cm^3
Hydrogen + Aluminium	3.8 meq/100 cm^3
Sum of Bases (Ca + Mg + K)	0.3 meq/100 cm^3
Cation Exchange Capacity	4.1 meq/100 cm^3
Percentage Saturation of Bases	7

Seedlings were watered daily, with tap water in the absence of rainfall, and grown under nylon mesh shading. The latter was considered necessary (Arasaki pers. com., 1992) to achieve reasonable seedling establishment, and reduced photosynthetic photon flux density (PPFD) by 55%-80% depending on the time of day. A typical day's PPFDs and air temperatures beneath the shading are shown in Figure 2.1.

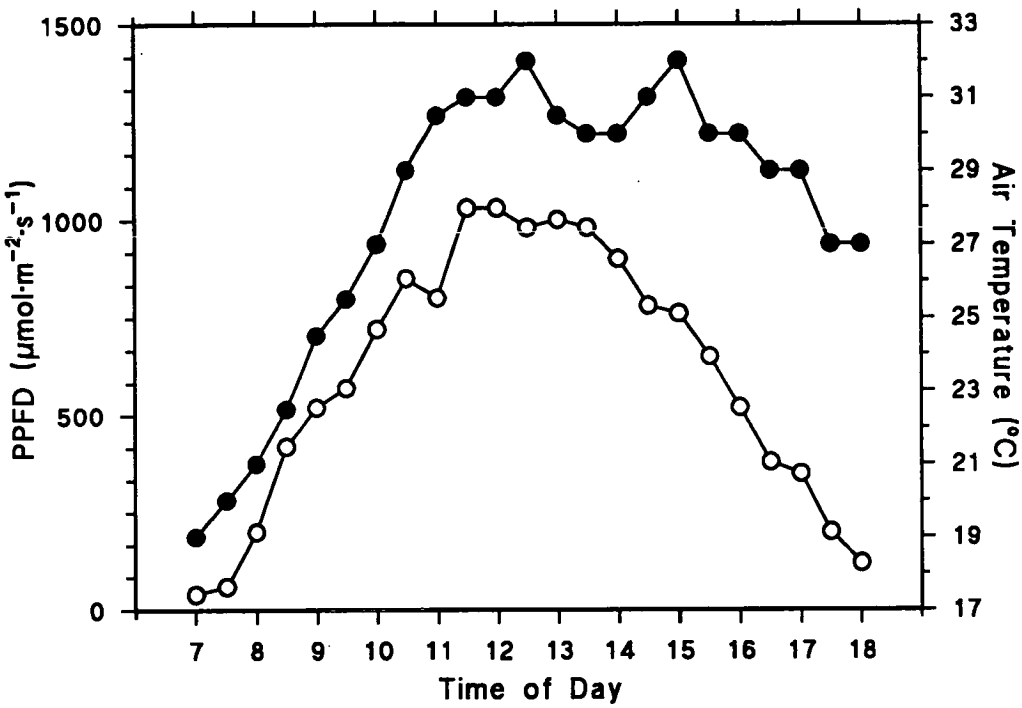


Figure 2.1 Changes in photosynthetic photon flux density (PPFD) below artificial shading (○) and air temperature (●) with time of day, on a typical day at the viveiro, Reserva Biológica de Mogi-Guaçú.

Weather conditions at the Reserva Biológica de Mogi-Guaçú during the period September 1990 to March 1991 are described in Appendix 2.1, however a summary is provided in Table 2.3. The freely draining soil and perforations in the plastic bag base ensured there was no accumulation of standing water.

Table 2.3 Summary of weather conditions at the Reserva Biológica de Mogi-Guaçú during the period September 1990 to March 1991.

Month (year)	Temperature (°C) Min.	Max.	Mean	Sunshine hr Total (daily)	Rainfall mm Total (daily)
September (90)	4.5	33.5	18.3	195 (6.5)	67 (2.2)
October (90)	11.6	35.5	22.7	227 (7.3)	107 (3.5)
November (90)	14.3	36.1	24.4	213 (7.1)	61 (2.0)
December (90)	10.5	34.7	23.7	234 (7.5)	128 (4.1)
January (91)	12.3	33.6	23.4	186 (6.0)	187 (6.0)
February (91)	13.8	32.7	22.9	177 (6.3)	207 (7.4)
March (91)	15.3	32.7	22.1	139 (4.5)	459 (14.8)

2.2.2 Harvesting

Seedlings were collected intact and immediately after organ separation, fresh weights and leaf areas were recorded.

Leaf areas were recorded by photocopying, along with a template of known area, using a Xerox model 1038 ZAF Reduction/Enlargement Copier. Photocopied leaf silhouette areas were calculated using a Quantimet Image Analyser (Cambridge Instruments Ltd.) running a purpose made program written by Jeffree (1990). This technique allowed rapid recording of leaf areas with a high degree of accuracy. In the field, leaf areas were determined by, tracing round leaves on to paper of known specific weight, and cutting out and weighing the drawn leaf shapes. From the weights of the paper leaf shapes and knowing the paper specific weight, leaf shape areas were calculated.

Tissue destined for dry weight measurement was placed in a ventilated 80°C oven until constant mass was achieved. Material was weighed to the nearest milligram, and to the nearest 0.1 mg when practicable. No continued mass loss was detected up to 14 days, the maximum drying period.

2.2.3 Leaf Area Estimation

For the non-destructive leaf growth analyses, leaf and cotyledon dimensions were measured and areas calculated according to previously established regressions.

Leaf areas were calculated according to,

$$\text{Leaf Area} = a + b \cdot \text{Leaf Length} + c \cdot (\text{Leaf Length})^2$$

where: $a = -66.9$; $b = 4.51$; $c = 0.269$; $n = 302$; $r^2 = 0.963$.

Cotyledon dimensions (length and breadth) were measured, and areas were calculated according to,

$$\text{Cotyledon Area} = a + b\cdot(\text{Cotyledon length}\cdot\text{Cotyledon breadth})$$

where: $a = 23.8$; $b = 0.694$; $n = 245$; $r^2 = 0.985$.

2.2.4 Cell Number Estimation

Total leaf cell number was estimated using a modification of the technique used by Brown and Rickless (1949) for root tissues.

After area and fresh weight determination leaves were transferred to a known volume of 5% Chromic Acid (5% w/v chromium trioxide in water). A fresh weight to volume ratio of 1:20 (g/cm^3) was typically used. The tissues were then incubated for 48 hr at room temperature. Maceration of the tissue was achieved by repeated perturbation using a pasteur pipette, to produce a fine cell suspension. The resultant macerates were diluted by known volumes of distiled water and aliquots removed from each for counting on a haemocytometer slide (Hawksley Crystallite, modified Fuchs Rosenthal). A dilution which produced approximately one cell per grid square was used to make the final counting. For each sample six 3 x 3 mm replicate fields were counted, each having a volume of 1.8 mm^3. From the original volume and dilution of the solution and cell number per grid, total cell number was calculated.

2.2.5 Leaf Photosynthetic Pigment Assay

After leaf homogenization pigments were extracted with 100% acetone and concentrations determined spectrophotometrically according to Holm (1954).

The more widely used technique of using 80% acetone (Arnon, 1949) was not employed as this produced a distinct opaqueness to the resultant solution which interfered with the spectrophotometric assay. This was thought to be a consequence of the precipitation of leaf latex in the aqueous medium.

After fresh weight and area measurement, leaves were ground thoroughly with a little liquid nitrogen to produce a fine powder. This was then extracted with 100% acetone, and incubated at 65°C for 3 minutes. After centrifugation (1 min., 1250 G) to sediment all cell debris the supernatant was poured off and collected. The sedimented pellet was resuspended in further 100% acetone and incubated again. This was

repeated 3 times and the accumulated supernatant made up to a known volume. A final fresh weight to volume ratio of 1:20 was typically used.

From absorbance values at 440.5 nm, 644 nm and 662 nm determined against an acetone blank (using a Phillips PU8625 spectrophotometer) pigment concentrations (mg 1×10^3 cm^{-3}) for chlorophyll *a* ([Chl *a*]), chlorophyll *b* ([Chl *b*]) and a composite group of 'carotenoids' were calculated as follows:

$$[\text{Chlorophyll } a] = 9.78 \cdot A_{662} + 0.99 \cdot A_{644}$$

$$[\text{Chlorophyll } b] = 21.4 \cdot A_{644} - 4.65 \cdot A_{662}$$

$$[\text{Carotenoids}] = 4.69 \cdot A_{440.5} - 0.267 \cdot ([\text{Chl } a] + [\text{Chl } b])$$

When assaying large leaves, leaf discs were punched from the lamina surface, avoiding the midrib, and assayed as normal after fresh weight determination. When extrapolating to calculate total leaf chlorophyll levels a correction factor was employed to allow for the large achlorophyllous midrib:

$$\text{Leaf Lamina Fresh Weight} = a + b \cdot \text{Total Leaf Fresh Weight}$$

where: $a = 0.00722$; $b = 0.804$; $n = 115$; $r^2 = 0.996$.

This relationship holds true for leaves from leaf emergence to full leaf expansion.

2.2.6 CO_2-Assimilation and Transpiration Measurement

2.2.6.1 Introduction

Leaf CO_2 assimilation and transpiration rates were measured with an A.D.C.™ LCA-2 Field Analytical System. The LCA-2 was operated as an 'Open-System', with the leaf enclosed in the leaf chamber and exposed to a measured flow of air of known [CO_2] and water vapour content. Modification of the air by the leaf is measured by the analyser and with additional inputs, photosynthetic and transpirational variables are calculated.

2.2.6.2 The LCA-2 Field Analytical System

This consists of an A.D.C.™ Portable Infra-Red Gas Analyser (LCA2), an A.D.C.™ Mass Flow Air Supply Unit (ASU(MF)), an A.D.C.™ Parkinson Broadleaf Chamber (PLC2-B), and an A.D.C.™ Data-Logger type DL2.

The instrumentation was organised as in Figure 2.2.

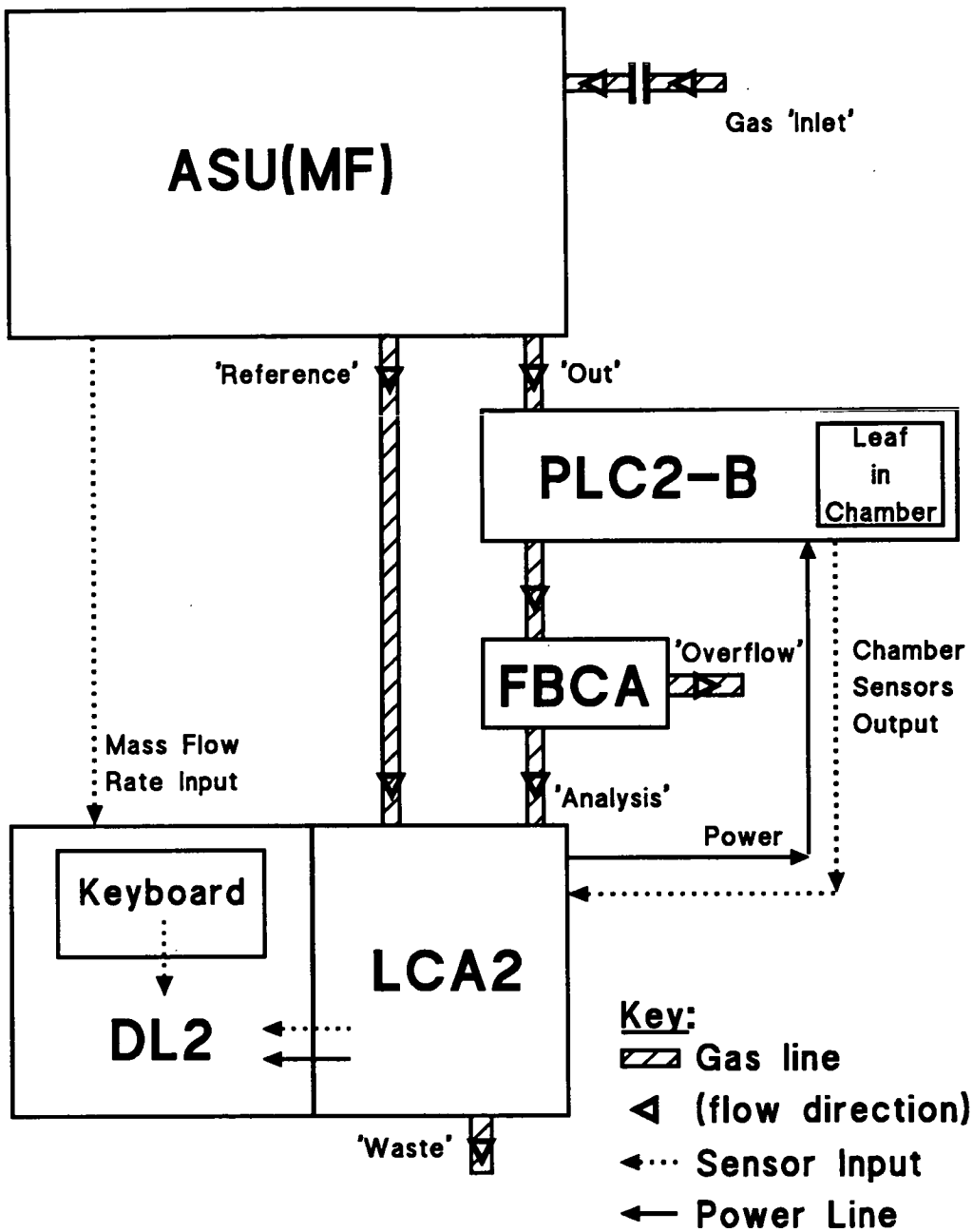


Figure 2.2 Diagrammatic Representation of the organisation of the LCA-2 Field Analytical System operated as an open system. Components: Mass Flow Air Supply Unit (ASU(MF)); Parkinson Leaf Chamber (PLC2-B); Flow Balance Control Assembly (FBCA); Infra-Red Gas Analyser (LCA2); and Data Logger (DL2).

A description of the various system components and their operation is provided below:

(1) Mass Flow Air Supply Unit (ASU(MF)). This unit provides a precise flow of dry air to both 'out' and 'reference' gas lines. An analogue output relays flow rates instantaneously to the DL2 Data-Logger (A.D.C.™, 1985a).

(2) Parkinson Broadleaf Chamber (PLC2-B). The chamber consists of an external Photosynthetic Photon Flux Density (PPFD) sensor (a filtered selenium photocell) and a chamber cuvette, containing a temperature sensor (a Fenwal LTN precision thermistor), a humidity sensor (a Coerci element), and a 12 V stirring motor (A.D.C.™, 1985[b]). Dry air from the 'out' gas line of the ASU(MF) enters the unit which is powered-up by the LCA2 analyser. Outputs to the LCA2 are from the three sensors and the chamber 'analysis' gas line. To minimise temperature differences between the chamber cuvette and the ambient air, the chamber base has a heat exchanger and an outer acrylic window absorbs a significant fraction of incident infra-red radiation.

(3) Infra-Red Gas Analyser (LCA2). The LCA2 analyser provides: CO_2 analysis of 'reference' and 'analysis' gas samples; power supply for the PLC2-B; digital display for the all sensory data, and data outputs for the DL2 (A.D.C.™, 1986[a]).

The absorption of a single non-dispersive optical beam by CO_2 in the sample gas is recorded. The analyser was operated in the 'differential' mode alternately measuring [CO_2] from 'reference' and 'analysis' gas lines. Light emitted by a low voltage sealed infra-red source passes through the sample cell (0.75 cm^3) to an interference filtered window (wavelength of 4.3 μm only) and onto a solid state energy detector. The analyser operates on a 4 s analysis cycle sequentially comparing the sample gas (2 s) and a CO_2-free air source (2 s), provided by pumping the sample through an external soda-lime column. The internal pump flushes the sample cell every half cycle ensuring no flow rate sensitivity. In the 'differential' mode the cycle is 8 s, the analyser alternately measuring 'reference' and 'analysis' samples to produce a differential value.

(4) Flow Balance Control Assembly (FBCA). This consists of a gas line throttle and overflow pipe. The throttle is adjusted to ensure an equal flow rate for 'reference' and 'analysis' gas lines to the LCA2 and thereby maximise analyser accuracy (A.D.C.™, 1986[b]).

(5) Data-Logger (DL2) running program version 3.3. This processes data inputs and stores the accumulated raw and calculated variables for later retrieval (A.D.C.™, 1986c). Data inputs are from the LCA2 analyser, the front panel keyboard and ASU(MF) air supply. The DL2 may be operated in 1 of 4 'options' each providing differing degrees of data processing and storage. The DL2 was operated in 'option 2' which required inputs for:

(a) Chamber Temperature (θ_a), Relative Humidity (%RH), 'Analysis' [CO_2] (C_A), 'Reference' [CO_2] (C_R), Differential [CO_2] (C_D), and PPFD, all from the LCA2;

(b) Keyboard entries for Chamber Leaf Area (A_c), Atmospheric Pressure (P), Transpiration Correction Factor (E_{MAX}), and Boundary Layer Resistance (r_b);

(c) Mass Flow Values from ASU(MF).

From this information, the following physiological values are calculated (according to Appendix 2.2): net photosynthetic rate (P_n) μmol m^{-2} s^{-1}; stomatal conductance (g_s) mol m^{-2} s^{-1}; sub-stomatal cavity [CO_2] (c_i) μbar; and leaf temperature (θ_L) °C.

2.2.6.3 System Operation

The LCA-2 Analytical System was operated as an 'open-system', as described in the A.D.C.™ Manual (1985c).

In the Edinburgh growth room, measurements were taken with the chamber placed horizontal, perpendicular to the incident light source. In the field, measurements were taken with the chamber positioned 'around the leaf', so that the leaf was kept 'in-position', unless otherwise specified.

Young leaves and cotyledons were often of insufficient area to completely occupy the 25 × 25 mm cuvette area. In these instances a tape mask was carefully and quickly applied to the leaf or cotyledon surface to produce an artificial sealed straight edge. This was then positioned in the cuvette so that the exposed leaf surface covered exactly half the cuvette area. After re-adjustment of the DL2 A_c value (to 313 mm^2) the system was operated as normal. The validity of this technique was tested by comparing the photosynthetic and transpirational values for unmasked (area = A) and masked (A/2) leaves and the effect of the mask only in the cuvette. There was no

significant difference between predicted and experimental values for masked leaves, and the presence of the mask had no effect on cuvette performance, while kept clean and dry.

The LCA2 was operated with a flow rate of between 150-200 cm^3 $min.^{-1}$. The ASU(MF) was operated at a flow rate of 6.25 cm^3 s^{-1}, 1 cm^3 s^{-1} cm^{-2} of chamber leaf area as recommended (A.D.C.™, 1985c). This results in a slight over-pressure in the chamber cuvette, excess air being dumped in the FBCA overflow. Vigorous stirring of the cuvette volume by the chamber motor, in conjunction with the slight over-pressure means that 100% sealing of the cuvette is not necessary for accurate measurement (A.D.C.™, 1985c).

Despite various means to reduce the effect (see PLC2-B description, section 2.2.6.2 (2)), when exposed to any high radiation the cuvette temperature increases above ambient air temperature. As a consequence leaf enclosure times were kept as short as possible, and between measurements the PLC2-B was cooled to ambient air temperature, as determined by a shaded mercury bulb thermometer. In the growth room this was achieved by shading the chamber and placing it in the rooms circulating air current. In the field this was accomplished by placing the chamber in a polystyrene ice-box containing a number of pre-frozen 'freeze-packs'.

Minimal disturbance was made to the leafs immediate environment prior and during gas-exchange measurement. Elevation of local CO_2 levels by operator exhalation was often encountered. This was a particular problem in the enclosed growth room with its recycling air flow. As a result the LCA-2 system was installed in the growth room well in advance of use, and was operated while wearing a safety gas-mask which dumped exhaled air, via a connecting pipe, outside of the growth room. In the field, the stillness of the early morning air together with the enclosed nature of the vegetation often led to locally elevated [CO_2]. Precautions included making measurements in discrete locations and taking the systems air, for the 'in' gas line, from a height of 4 m above ground level.

2.2.7 Stomatal Density and Dimension Measurement

Leaf stomatal numbers and dimensions were determined using commercial nail varnish replicas of the leaf surface.

Typically, replicas were taken in 3 locations per lamina surface: alternately on either side of the midrib in the acropetal, central and basipetal thirds of the leaf; or in 3 random locations for cotyledons. Firstly an adhesive paper annulus (such as those used as ring binding supports) was firmly attached to the leaf surface, and then the aperture and adjacent areas of the annulus were coated with thin layer of nail varnish. When fully dry the replica was removed and stomatal numbers and dimensions measured under a light microscope. The annulus serves to aid replica removal and more importantly protect the replica from distortion on removal. Generally six 1 mm^2 fields were counted per replica, and the mean of 3 replicas used to provide a stomatal density. Stomatal complex and guard cell dimensions were determined from pole to pole using a calibrated eye-piece graticule. This was done as only small changes can occur in this dimension during stomatal movement, owing to the guard cells tangential walls (Meidner and Mansfield, 1968). Replicas made of electron microscope mounting grids (50×50 µm lattice) have shown there is no significant replica distortion or shrinkage using this method.

2.2.8 Low-Temperature Scanning Electron Microscopy (LTSEM)

2.2.8.1 Introduction

All LTSEM work was conducted using a Cambridge Instruments Stereoscan S250 Scanning Electron Microscope with an attached EMscope SP2000 Sputter-Cryo Cryogenic-Preparation System. A detailed description of the SP2000 system components and their basic operation is provided by Robards and Sleytr (1985), and Beckett and Read (1986). The major advantages of the LTSEM procedure are that it allows *very* rapid specimen fixation in the frozen-hydrated state (FH) and avoids the artifacts of chemical preparation. This means the specimen may be observed and recorded in a fully-hydrated and chemically unmodified form (Jeffree and Read, 1991).

LTSEM involves 3 operational phases: rapid freezing (quench-freezing) of the mounted specimen; specimen fracturing, etching and coating; and specimen observation at low temperature.

2.2.8.2 Specimen Mounting and Fixation

LTSEM was used to observe and record: the anatomy of adaxial and abaxial leaf surfaces and the primordia of the apical meristem; leaf structure in transverse section; and leaf structure in paradermal section. Depending on the intended type of analysis different specimen preparation techniques were necessary:

(1) Surface examination. Lamina pieces (5 × 10 mm) or seedling embryos were mounted on a blank copper stub using a little Tissue-Tek II OCT compound, a cryoadhesive.

(2) Leaf transverse section examination. Leaf lamina pieces (5 × 5 mm) were mounted vertically on a parallel grooved copper stub using a little Tissue-Tek.

To observe *K. coriacea* leaves in paradermal section it was necessary to devise a sheer-fracturing technique to divide the tough coriacous lamina. Previously established paradermal fracturing methods involving either separating a V-shaped copper gauze mount or opening a silver stub mounted hinge (Jeffree *et al.*, 1987) were tried without success. This was thought to be the result of the inherent toughness of the species leaves, and also the numerous lactiferers which were thought to form a reinforcing network when cryofixed.

(3) Leaf paradermal section examination. Leaf discs were punched from the leaf lamina and mounted on modified blank copper stubs into which a 0.3 mm-0.8 mm cylinder had been drilled. The leaf disc was mounted proud within the bore with a little Tissue-Tek. A brass washer was placed around the leaf disc and also adhered with a little Tissue-Tek. The object of this exercise was to ensure that the thickness of the leaf transversed the cylinder rim/washer base boundary.

Once mounted specimens were quench-frozen by plunging into subcooled nitrogen, and maintained in a dry argon atmosphere below -130°C.

2.2.8.3 Specimen Fracturing, Etching and Coating

Again depending on the intended purpose differing procedures were followed:

(1) Surface examination. Specimens were not fractured, but examined prior to coating to determine the need for etching. When necessary the sample was heated to -80°C in the Stereoscan under continuous observation until the surface was sufficiently clear of ice-crystals. The specimen was then recooled to -178°C, transferred to the SP2000 and coated.

(2) Leaf transverse section examination. After quench freezing the specimen was transferred to the SP2000 preparation chamber and fractured transversely using the chamber macro-manipultor. The specimen was struck laterally to fracture the upper exposed edge of the lamina and leave a clean undisturbed transverse section.

(3) Leaf paradermal section examination. The leaf disc was fractured by striking the covering brass washer using the macro-fracture device to sheer fracture off the upper layers of the specimen disc.

All prepared specimens were gold sputter coated at 20 milli-amps for 1 min., which was found to be ideal for the magnifications used.

2.2.8.4 Specimen Observation and Record

Specimens were observed in the Stereoscan S250 under vacuum at -178°C, accelerating voltages of 5 kV-6.5 kV and magnifications ranging from 50×-2000×. All images were recorded on Kodachrome Tmax 120-format print film.

2.2.9 Light Microscopy

2.2.9.1 Primordium Number Determination

Leaf primordia numbers were determined by dissection of the shoot apex under a binocular microscope.

Fresh shoot apices were carefully examined under low (×10) and medium (×30) magnifications, and when possible leaves and leaf primordia dissected out for measurement. Leaf primordia were identified as clear protuberances from the apical dome, with a radial heights greater or equal to half their basal diameter. Using this technique it was possible to identify primordia with radial heights down to 100 μm.

2.2.10 Growth Indices Estimation

The following section describes the methodology for the calculation of the growth indices: specific or relative growth rate (**R**), unit leaf rate (**E**), leaf area ratio (**F**), specific leaf area (SLA), and leaf weight ratio (LWR). The notation of Evans (1972) is used for all growth analysis equations and expressions.

Specific growth rate (**R**) is defined as the increase in plant weight per unit plant weight per unit time. The instantaneous specific growth rate may be expressed as,

$$\mathbf{R} = \delta(\ln W)/\delta T \quad (2.1)$$

Mean specific growth rate (**R**) determined in 'classical' growth analysis may be calculated by substitution into the following derived equation,

$$\mathbf{R}_{1\text{-}2} = (\ln W_2 - \ln W_1)/(T_2 - T_1) \quad (2.2)$$

An alternative procedure for the calculation of specific growth rate and other growth descriptors, is that referred to as the 'dynamic' (Radford, 1947) or 'functional' (Hunt, 1982) approach. In this, curves of best-fit are applied to the raw data, such as plant dry weight and plant leaf area, and values for the growth descriptors are derived from the equations for these curves. This has a number of advantages over the classical approach (Hunt, 1982), and was the approach used in this investigation. The only assumption necessary for the adoption of this approach is that the fitted growth curves adequately describe the trends in the raw data. However regression analysis may only be performed on data with a constant variability (homoscedacity). In using logarithmic functions, heteroscedasticity (non-uniform variability) of the data may be avoided, and is therefore not a problem to curve fitting.

Measurements were made of the rates of growth attained in the phase of exponential growth which follows germination (Grime and Hunt, 1975). Since in this phase growth is normally most rapid in the life history of the plant (and since controlled conditions were designed as far as possible to present non-limiting environmental quantities) these measurements may be regarded as estimates which approximate to the 'maximum potential specific growth rate', $\mathbf{R}_{max}$ (after Evans, 1972).

From equation 2.1 it is clear that the slope of the plot of natural logarithms of plant dry weight with time, is the specific growth rate. Thus the specific growth rate

may be calculated by differentiating the equation of best-fit for ln (plant dry weight) with time,

$$\ln W = f(T) \quad (2.3)$$

The exact form this function will naturally have profound effects on the pattern and values derived from it. Solving the differentiated function of the natural logarithm of dry weight for the time period considered, provides instantaneous specific growth rates for this interval.

Leaf area ratio (**F**) (Briggs *et al.*, 1920) is defined as the ratio of total leaf area to whole plant dry weight, and is an index of the leafiness of the plant on an area basis,

$$\mathbf{F} = L_A/W \quad (2.4)$$

$$= \text{antiln}\,(\ln L_A - \ln W) \quad (2.5)$$

By substituting calculated values for ln (leaf area) and ln (plant dry weight) into equation 2.5, values for leaf area ratio (**F**) may be obtained.

Unit leaf rate (**E**) (Briggs *et al.*, 1920) is defined as the 'net gain in weight per unit leaf area' (Gregory, 1918), and is an index of the carbon assimilatory capacity of the leaves,

$$\mathbf{E} = (1/L_A)\cdot(\delta W/\delta T) \quad (2.6)$$

By definition

$$\mathbf{R} = \mathbf{E}\cdot\mathbf{F} \quad (2.7)$$

By substituting values for the specific growth rate (**R**) and leaf area ratio (**F**) into equation 2.8, values of unit leaf rate (**E**) may be obtained.

Leaf area ratio may be separated into two components, specific leaf area (SLA) and leaf weight ratio (LWR).

$$L_A/W = (L_A/L_W)\cdot(L_W/W) \quad (2.8)$$

$$i.e.\ \ \mathbf{F} = \mathrm{SLA} \cdot \mathrm{LWR} \quad (2.9)$$

Specific leaf area is the mean leaf area displayed per unit leaf weight, and is as an index of leaf density or leaf thickness. Leaf weight ratio is the unit leaf weight per unit plant weight and is an index of the leafiness of the plant on a weight basis.

2.2.11 Computer-Based Data Processing and Presentation

Data processing was accomplished using Minitab (Version 7) statistical package, and Fig-P graphics package (Version 4.1) curve fitting facility. Data presentation was achieved using Fig-P graphics package. Text processing and presentation was completed using Microsoft Word (Version 5.0)

For all figures the following conventions were followed, unless otherwise specified:

(1) controlled condition data is represented by filled symbols (*i.e.* ●);

(2) field condition data is represented by open symbols (*i.e.* ○);

(3) whole plant and cotyledon data is represented by circular symbols (*i.e.* ○);

(4) foliar leaf data is represented by square symbols (*i.e.* ❑);

(5) raw data for functional data sets is omitted for clarity;

(6) error bars represent standard errors of the mean.

Chapter 3

Growth of *Kielmeyera coriacea* Mart. Seedlings.

3.1 Introduction

This chapter describes the results of growth analyses conducted on *Kielmeyera coriacea* Mart. plants grown from seed under controlled environment and field conditions. The aim of these analyses was to investigate growth under 'natural', and near-optimal conditions, and thereby consider environmental and inherent limitations to development. Objectives were: (1) to determine the patterns of change of specific growth rate (**R**), and its maximum value under controlled and field conditions; (2) to compare patterns of leaf area ratio (**F**) and unit leaf rate (**E**) change under controlled and field conditions; (3) to establish patterns of biomass partitioning between and within root and shoot systems, as a background to a consideration of the way in which allocation limits growth. Although the development of *K. coriacea* has previously been described by Self (1989) and Arasaki and Felippe (1990), a more detailed analysis was required of growth under favourable, and 'natural' conditions.

Three separate growth analysis experiments, involving destructive harvests at regular intervals, were used to investigate plant growth. The first considered the longer term growth of *K. coriacea* seedlings under favourable controlled conditions from imbibition (day 0) to day 112 (*C.C.*1). The second and third analyses followed the first, with more detailed considerations of seedling development during the first 70 days of growth under controlled (*C.C.*2) and field conditions (*F.C.*). Results of the *C.C.*2 experiment support those of the *C.C.*1 experiment, and provide a comparison for development in the field (*F.C.*). Harvest frequencies for *C.C.*1, *C.C.*2 and *F.C.* were sufficient to justify functional analyses of the data.

3.2 Plant Development Under Controlled Conditions

The naked seed of *K. coriacea* consists of two fleshy kidney shaped cotyledons (area = 1.5 cm^2) connected to a short (2 mm) embryo. The cotyledons are closely appressed, and enclose the apical tip and one, rarely two, leaf primordia (see Plate 4.1). From a mean dry weight of 0.126 g the naked seed rapidly hydrates to a mean fresh weight of 0.299 g (day 0). Germination, seen as a positive geotropic response of the hypocotyl, occurs about day 6-7 and is immediately followed by a more general elongation of the radicle and hypocotyl. It was at this point that the seed was transferred to the growing-medium, positioned with the cotyledons just breaking

the soil-surface. Hypocotyl elongation began at germination and continued, generally increasing the hypocotyl to 20 mm in length, to raise the cotyledons above the soil-surface, while the cotyledons themselves began to separate. The cotyledons were generally unfolded by day 14, and Leaf 1 was usually visible soon after (day 14-day 21). Although separate, the cotyledons maintained an acute angle between themselves, only diverging further as foliar leaf development continued. The main root continued to grow rapidly downwards, with the first lateral roots visible soon after day 21. Leaf 1 developed between the cotyledons, initially over the shoot apex, and expanded upwards and radially outwards. The opposite decussate positioning of Leaf 1 and Leaf 2 ensured that even at full expansion there was minimal shading of the cotyledons by these leaves. Leaf 1 and Leaf 2 expansion was staggered in time and rapid, beginning around day 28 and finishing about day 56. There followed a short phase of apparently little leaf development before Leaf 3 and subsequent leaves progressively expanded with a spiral phyllotaxis. Internode development was minimal, with usually only a 1-2 mm increase in stem length per leaf, leading to a rosette growth form. As a consequence of the lack of substantial stem elongation and the plants phyllotaxis, Leaf 3 and Leaf 4 expanded over the two cotyledons, and Leaf 5 expanded over Leaf 2. This self-shading effect was reduced by the progressively more acute angles the younger leaves subtended from the stem axis. Occasionally, with particularly fast growing individuals, a period of stem elongation was seen, during which the stem increased in length by 30-80 mm, however this was rare. From about day 42 xylopodium formation began, seen as a radial thickening and development of brown suberised outer layers in the main root. A description of xylopodium development is given by Self (1989).

3.3 Plant Growth

3.3.1 Ontogenic Changes in Plant Dry Weight

Changes in seedling dry weight with age under controlled conditions (*C.C.*1) are shown in Figure 3.1. Initially, as the seedlings germinated and the embryo began to develop, there was little or no change in plant dry weight with time, although at harvest six (day 17; marked "α" on Figure 3.1) dry weight was significantly ($p<0.05$) lower than the original seed weight.

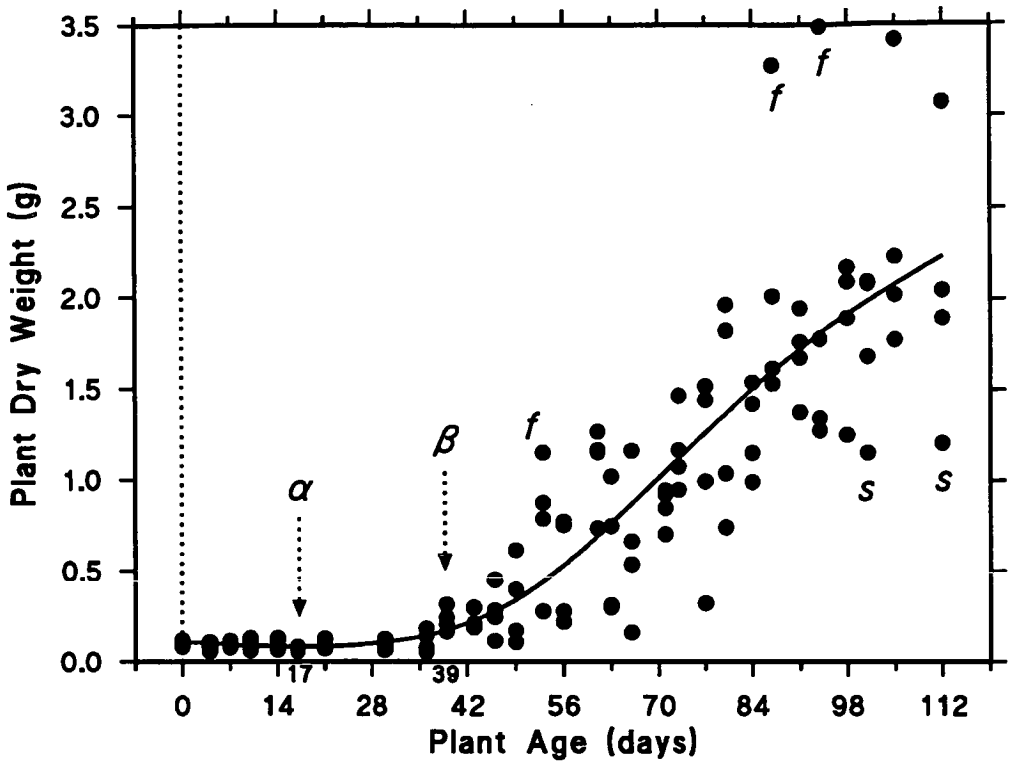


Figure 3.1 Changes in plant dry weight with age for *K. coriacea* seedlings grown under controlled conditions (*C.C.*1). The line is a free-hand curve of the *C.C.*1 data. "α" and "β" mark the points of significant ($p<0.05$) decrease and initial increase in dry weight, respectively. "*f*" and "*s*" indicate some suggested faster and slower growing individuals.

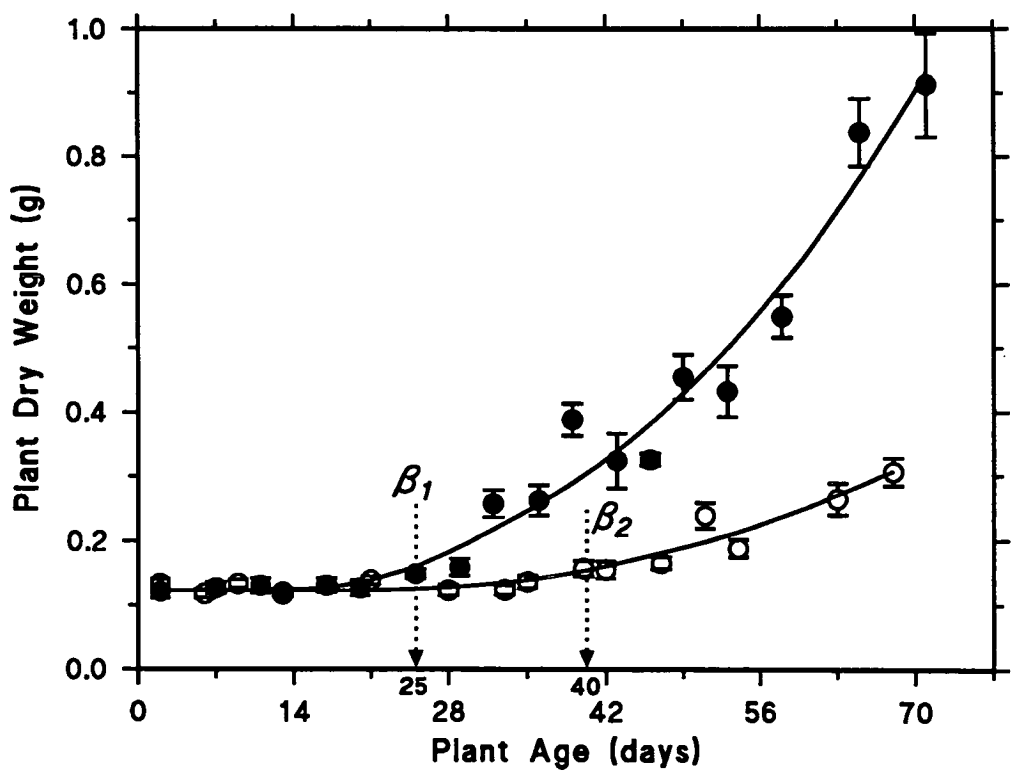


Figure 3.2 Changes in plant dry weight with age for *K. coriacea* seedlings grown under controlled (●; *C.C.*2), and field (○; *F.C.*) conditions: each point is the mean of 7 and 10 replicates respectively; error bars represent standard errors of the mean. Free-hand curves describe the *C.C.*2 and *F.C.* data. "β_1" and "β_2" mark points of initial significant ($p<0.05$) dry weight increase for *C.C.*2 and *F.C.*, respectively.

From day 39 ("β" on Figure 3.1) there was a significant ($p<0.05$) and continued increase in plant dry weight to the end of the study period, with seedlings reaching dry weights of 1 g and 2 g by day 68 and day 102, respectively. Some individuals with relatively high dry weights (marked "*f*" on Figure 3.1) suggest inherently faster growth rates, whereas others with relatively low dry weights ("*s*") suggest later development and/or inherently slower growth rates (Benjamin and Hardwick, 1986). This indicates the large degree of variation seen in growth which is typical of *K. coriacea* plants under controlled (Self, 1989), and field conditions (Arasaki, 1988).

A comparison of changes in dry weight for seedlings grown under controlled (*C.C.*2) and field (*F.C.*) conditions is provided in Figure 3.2. *C.C.*2 seedlings showed an earlier significant ($p<0.05$) increase in dry weight at day 25 ("β_1"), with a relatively rapid increase in values thereafter. This earlier significant increase compared with *C.C.*1 seedlings was thought to be due to the differing methodologies used (*C.C.*2 involved a higher replicate number and a slightly higher harvesting frequency). In contrast, *F.C.* seedlings showed a much slower rate of dry weight increase after initial significant ($p<0.05$) dry weight increase on day 40 ("β_2"). Consequently *C.C.*2 seedlings had doubled their original seed weight by day 35 and reached 0.5 g and 0.9 g, by day 52 and day 70 respectively, whereas the slower-growing *F.C.* seedlings doubled their seed weight at around day 60, but failed to reach 0.5 g within the study period. The logarithmically transformed dry weight data are shown in Appendix 3.1.

3.3.2 Ontogenic Changes in Plant Leaf-Area

Changes in seedling leaf-area with age under controlled conditions (*C.C.*1) are shown in Figure 3.3. Leaf-area increase was initially due to cotyledon expansion, followed from day 28, by foliar leaf expansion. The absolute rate of foliar leaf expansion was greater than the rate of cotyledon expansion, resulting in a more rapid increase in area from day 28. Plant leaf-area increased from 3.0 cm^2 in the seed, to 50 cm^2 by day 52, and 150 cm^2 by day 100.

Comparison of leaf-areas for seedlings grown under controlled (*C.C.*2) and field (*F.C.*) conditions (Figure 3.4) showed that *C.C.*2 seedlings reached leaf-areas of 10 cm^2 and 50 cm^2 by day 28 and day 56 respectively, while *F.C.* seedlings showed the initial increase in area as the cotyledons expanded, but failed to continue this increase with foliar leaf expansion until later, around day 56.

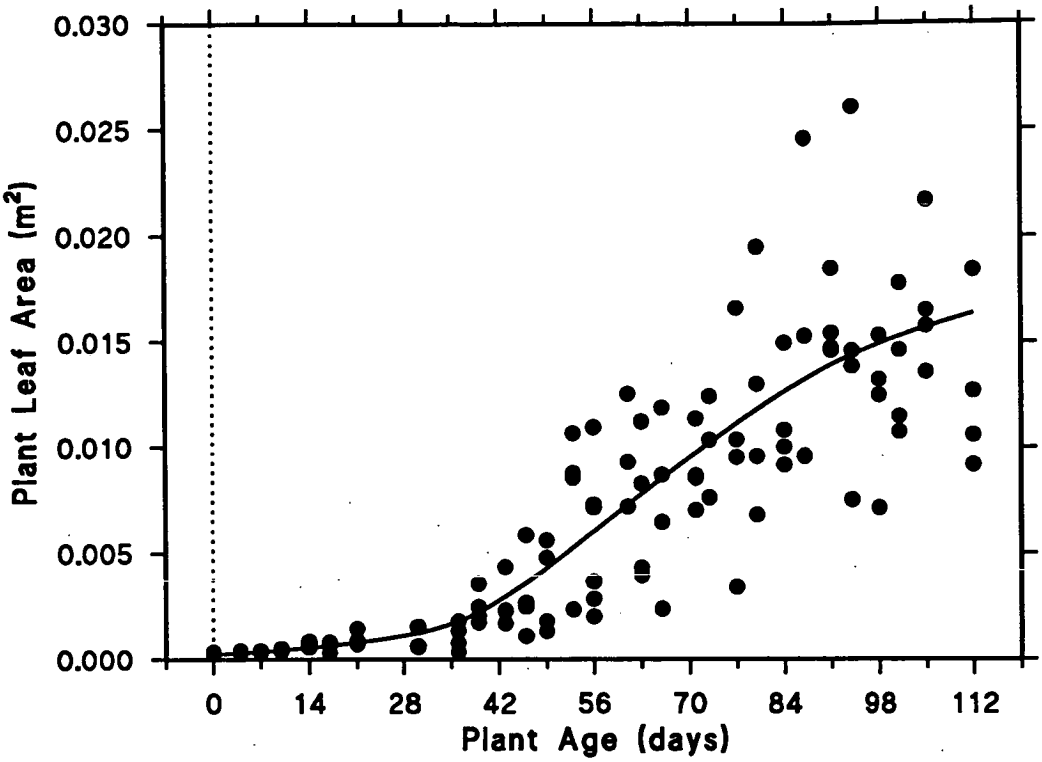


Figure 3.3 Changes in plant leaf area with age for *K. coriacea* seedlings grown under controlled conditions (*C.C.*1). The line is a free-hand curve of the *C.C.*1 data.

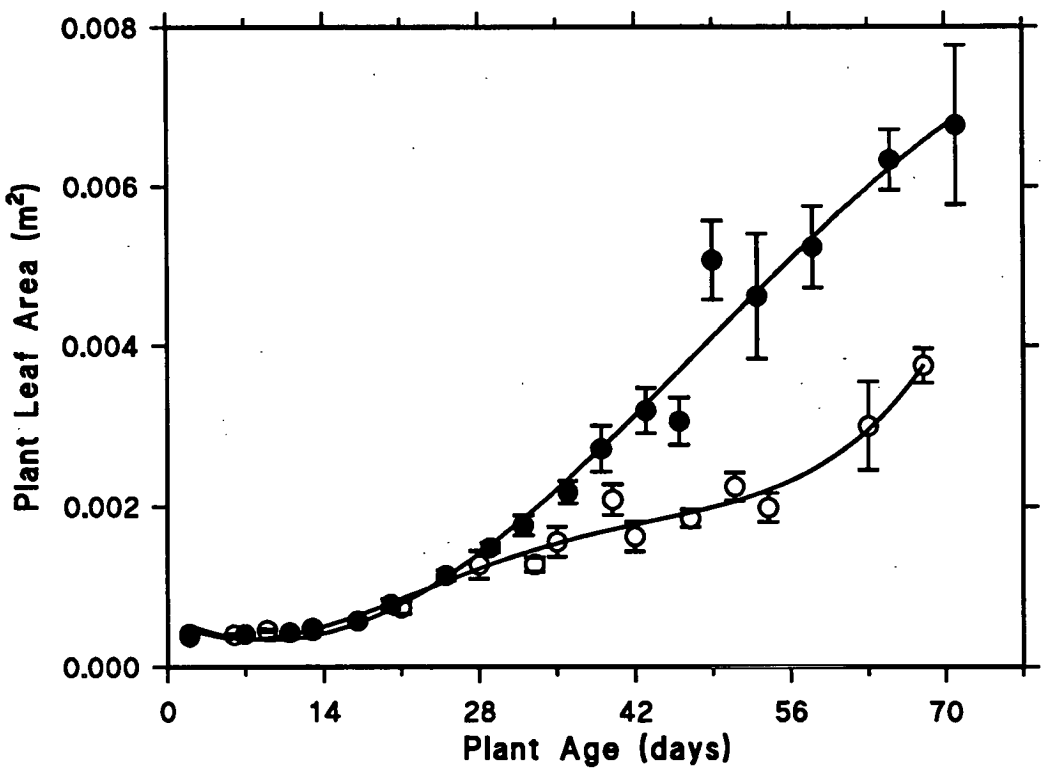


Figure 3.4 Changes in plant leaf area with age for *K. coriacea* seedlings grown under controlled (●; *C.C.*2), and field (○; *F.C.*) conditions: each point is the mean of 7 and 10 replicates respectively; error bars represent standard errors of the mean. Free-hand curves describe the *C.C.*2 and *F.C.* data.

This resulted in *F.C.* leaf-areas of 10 cm^2 by day 28, but only 20 cm^2 by day 56. The logarithmically transformed leaf-area data are shown in Appendix 3.1.

3.3.3 Ontogenic Changes in Specific Growth Rate, Unit Leaf Rate, and Leaf Area Ratio

3.3.3.1 Introduction

The growth indices, specific growth rate (**R**), unit leaf rate (**E**) and leaf area ratio (**F**) for the controlled and field condition grown seedlings were calculated using best-fit functions of ln (dry weight) and ln (leaf-area) data (see section 2.2.10). All functions were polynomials of the form,

$$y = a + b \cdot x + c \cdot (x)^2 + d \cdot (x)^3 + e \cdot (x)^4 \_ \_ \_$$

where: y is ln (plant dry weight) or ln (leaf-area); x is plant age; and *a*, *b*, *c*, *d*, *e* are equation parameters.

Equation parameters of the best-fit curves for the appropriate logarithmic transformed dry weight and area data are shown in Appendix 3.1. As these functions describe the data from day 0 onwards, derived growth indices occasionally show anomalies at their extremities which do not accurately represent the data.

3.3.3.2 R, E and F Under Controlled Conditions

The changes in **R**, **E** and **F** with plant age for *K. coriacea* seedlings grown under controlled conditions (*C.C.*1) are shown in Figure 3.5. Specific growth rate increased rapidly to a peak of 0.0545 d^{-1} (R_{max}) at day 48, thereafter gradually declining with plant age to a value of 0.01 d^{-1} at 100 days. The initial pattern of rapid dry weight increase seen in Figure 3.1 is reflected in this peak of high **R** values. The declining rate of increase is similarly seen as the steady decline in **R** values to the end of the study period.

Leaf area ratio showed a similar pattern to **R**, sharply increasing from a value of 0.0034 $m^2 g^{-1}$ at day 0, to a peak of 0.0110 $m^2 g^{-1}$ at day 45. Thereafter **F** declined steadily to a value of 0.0075 $m^2 g^{-1}$ by day 100. The initial increase in **F** values up to day 45 is a consequence of the rapid increase in plant leaf-area from imbibition (Figure 3.3), with a much later increase in plant dry weight (Figure 3.1).

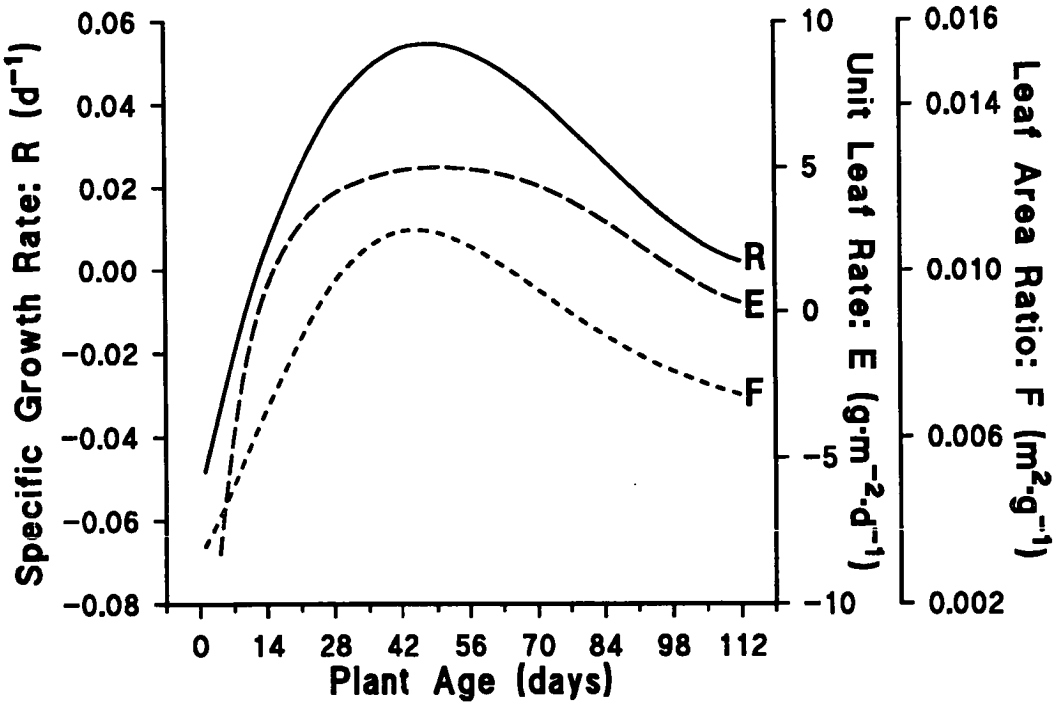


Figure 3.5 The relationships between specific growth rate (R), unit leaf rate (E), leaf area ratio (F) and plant age for *K. coriacea* seedlings grown under controlled conditions (*C.C.*1).

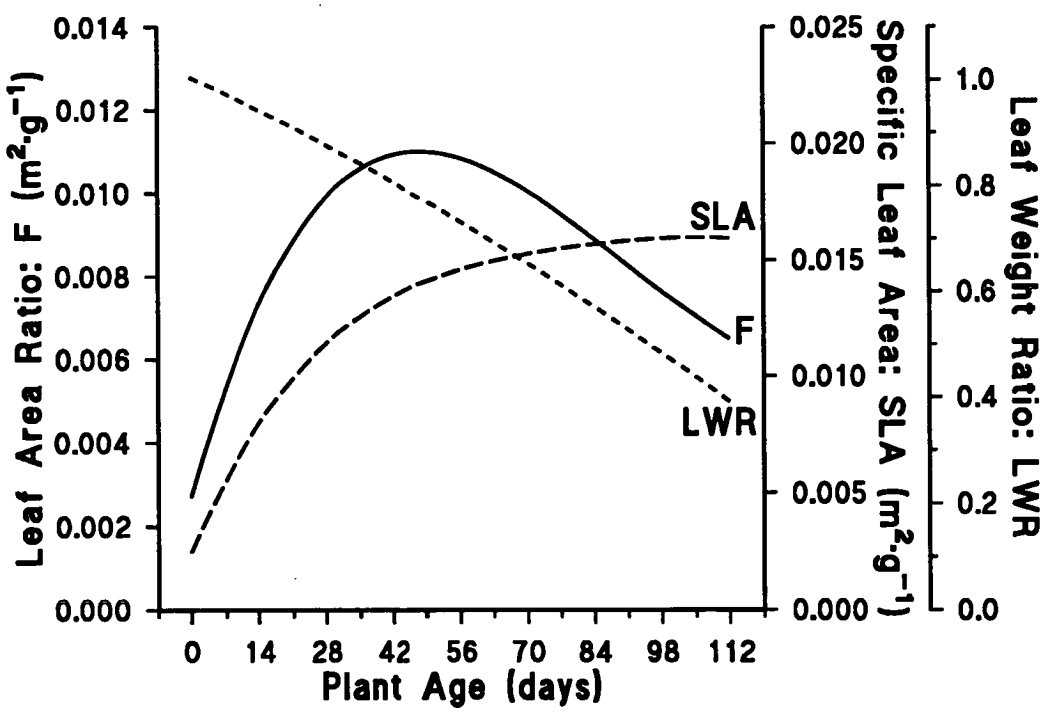


Figure 3.6 The relationships between leaf area ratio (F), specific leaf area (SLA), and leaf weight ratio (LWR) and plant age for *K. coriacea* seedlings grown under controlled conditions (*C.C.*1).

Despite leaf-area continuing to increase beyond day 45, the phase of maximal **R** values and so dry weight increase, resulted in the decrease in **F** values seen.

Unit leaf rate initially increased very rapidly to a value of 4 g m^{-2} d^{-1} at day 28. **E** then remained almost constant until day 77, rising slightly to 5 g m^{-2} d^{-1} around day 50. After day 77, unit leaf rate declined gradually to a value of 1.3 g m^{-2} d^{-1} by day 100. The relative constancy of unit leaf rate from day 28 is interesting in view of the transition from the cotyledons to the foliar leaves as the main source of leaf-area.

Patterns of change of specific leaf area (SLA) and leaf weight ratio (LWR) for controlled environment grown seedlings (*C.C.*1) are shown in Figure 3.6. SLA was initially low at a value of 0.002 m^2 g^{-1} at day 0, and rapidly increased to a value of 0.013 m^2 g^{-1} by day 42. Thereafter SLA increased more slowly, so that by day 100 SLA was 0.016 m^2 g^{-1}. This initially rapid increase in plant SLA was a consequence of the expansion of the thick, fleshy cotyledons, and of the increasing domination of leaf-area by the foliar leaves with their higher specific leaf areas.

Leaf weight ratio showed an almost linear decline with plant age from a value of almost 1 at day 0, to a value of 0.45 by day 100 (Figure 3.6). This decline in LWR was responsible for the decline in leaf area ratio values beyond day 45, as progressively less biomass was allocated to leaf development.

The patterns of change of **R**, **E** and **F** for *C.C.*2, shown in Figure 3.7, agreed closely with those seen in *C.C.*1 (Figure 3.5), although the exact timing and magnitude of peaks are slightly different.

3.3.3.3 R, E and F Under Field Conditions

The patterns of change of **R**, **E** and **F** with plant age for *K. coriacea* seedlings grown under field conditions (*F.C.*) are shown in Figure 3.8. Specific growth rate increased from an initially negative value to a maximum value of 0.0262 d^{-1} at day 56, before declining thereafter. The late attainment of positive **R** values reflects the much later point at which significant dry weight increase was seen (Figure 3.2). Similarly the slow rate of dry weight increase is shown by these lower **R** values under field conditions.

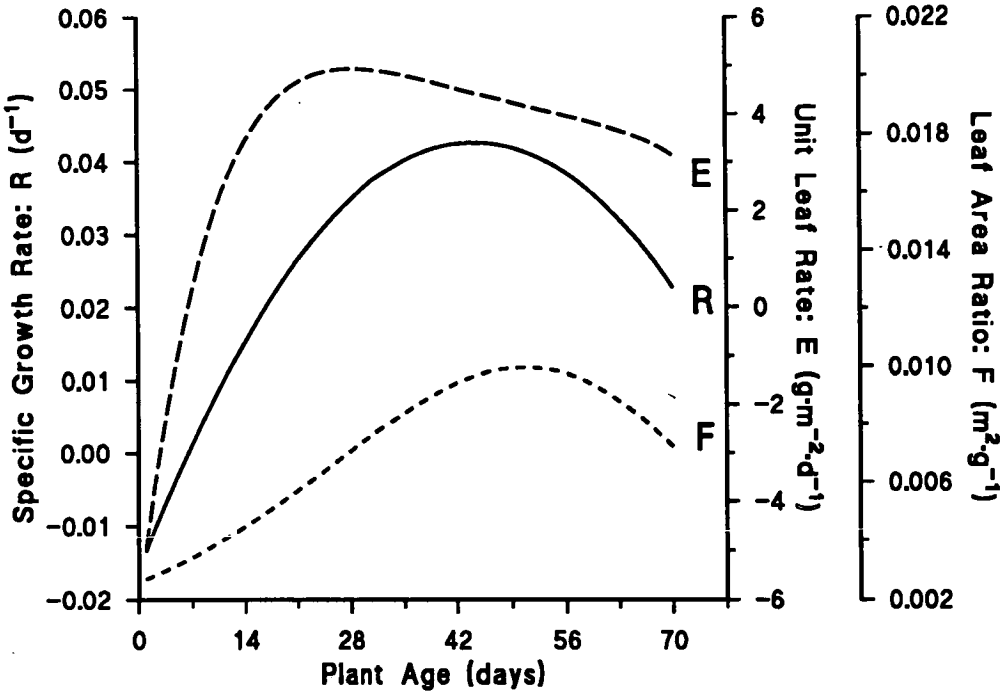


Figure 3.7 The relationships between specific growth rate (**R**), unit leaf rate (**E**), leaf area ratio (**F**) and plant age for *K. coriacea* seedlings grown under controlled conditions (*C.C.*2).

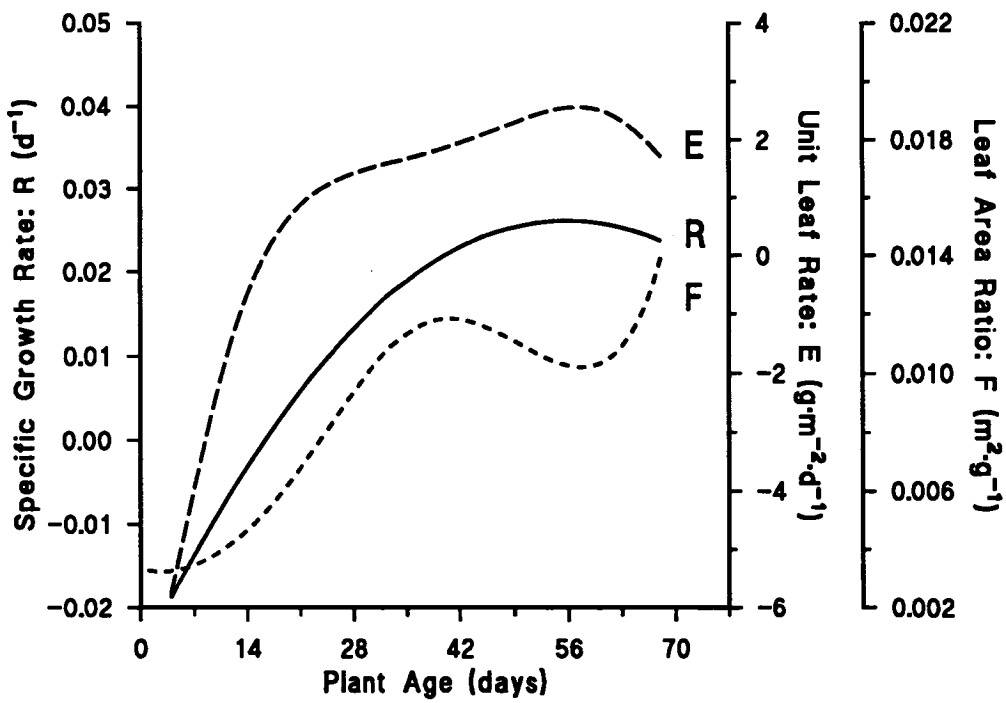


Figure 3.8 The relationships between specific growth rate (**R**), unit leaf rate (**E**), leaf area ratio (**F**) and plant age for *K. coriacea* seedlings grown under field conditions (*F.C.*).

Leaf area ratio increased steadily from a value of 0.0033 $m^2 g^{-1}$ at day 0 to a first peak of 0.0116 $m^2 g^{-1}$ at day 42. Values then decreased slightly to 0.0099 $m^2 g^{-1}$ by day 60, before increasing again to the end of the study period (0.0122 $m^2 g^{-1}$ at day 68). This pattern of change in **F** is a reflection of the very distinct pattern of leaf-area increase seen in Figure 3.4. Expansion of the cotyledons was seen as the initial rapid increase in values to a peak on day 42, with values higher than those seen for *C.C.*2 because of the minimal accompanying increase in plant dry weight seen in *F.C.* seedlings. Thereafter as plant dry weight increased without foliar leaf development, **F** declined, before increasing a second time as the delayed foliar leaf expansion began.

Unit leaf rate initially increased from a negative value to 1 g $m^{-2} d^{-1}$ at day 22, steadily increasing thereafter to 2.7 g $m^{-2} d^{-1}$ by day 56.

3.3.4 Ontogenic Changes in Organ Dry Weights

As a prelude to an consideration of an allocation determined limitation to the rate of growth, rates of dry weight increase for the root and shoot were considered.

Shoot dry weight values for controlled (*C.C.*2) and field (*F.C.*) condition grown seedlings (Figure 3.9) were initially similar. However, from day 25 (marked "β_1" on Figure 3.9) *C.C.*2 seedlings showed an earlier and more rapid increase in dry weight, reaching 0.2 g and 0.5 g by day 33 and day 66, respectively. In the longer term *C.C.*1 experiment (inset, Figure 3.9), this increase continued to day 95, when shoot weight reached 1.0 g, after which point growth slowed. In contrast *F.C.* seedlings showed a much later and reduced rate of shoot dry weight increase beginning on day 40 ("β_2"), seedlings reaching a dry weight of only 0.2 g by day 66.

Comparing root dry weight in *C.C.*2 and *F.C.* seedlings (Figure 3.10) divergence between conditions appeared to occur much later than for the shoot. Root dry weight in the seed is negligible, and although root development was extensive from germination overall root weight remained low until day 35. From this point, *C.C.*2 seedlings showed a relatively rapid increase in dry weight reaching 0.05 g and 0.34 g by day 42 and day 68, respectively. The longer term *C.C.*1 experiment (inset, Figure 3.10) showed that this rapid increase continued beyond day 70, to at least day 112, with a root dry weight of 1.0 g at 100 days. This substantial and continued dry weight increase represents the development of an extensive root system, and in particular the main root xylopodium.

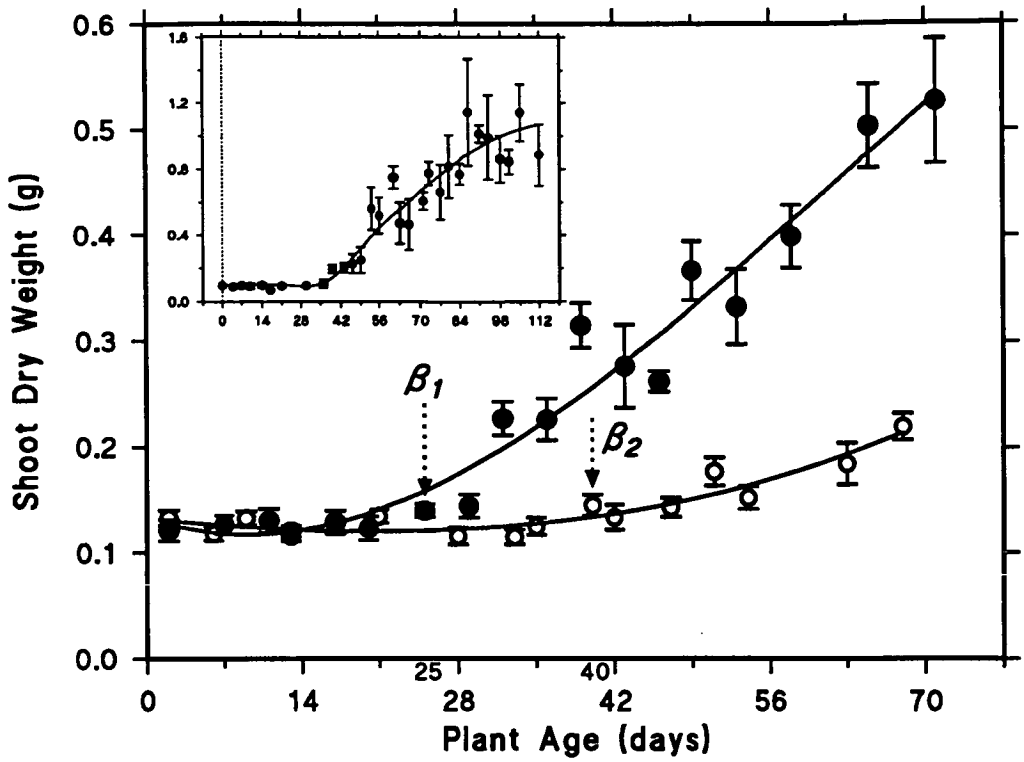


Figure 3.9 Changes in shoot dry weight with age for *K. coriacea* seedlings grown under controlled (●; *C.C.*2) and field (○; *F.C.*) conditions: each point is the mean of 7 and 10 replicates respectively; error bars represent standard errors of the mean. The inset shows *C.C.*1 data. Free-hand curves describe the *C.C.*1, *C.C.*2 and *F.C.* data. "β_1" and "β_2" mark points of initial significant ($p<0.05$) dry weight increase for *C.C.*2 and *F.C.* data, respectively.

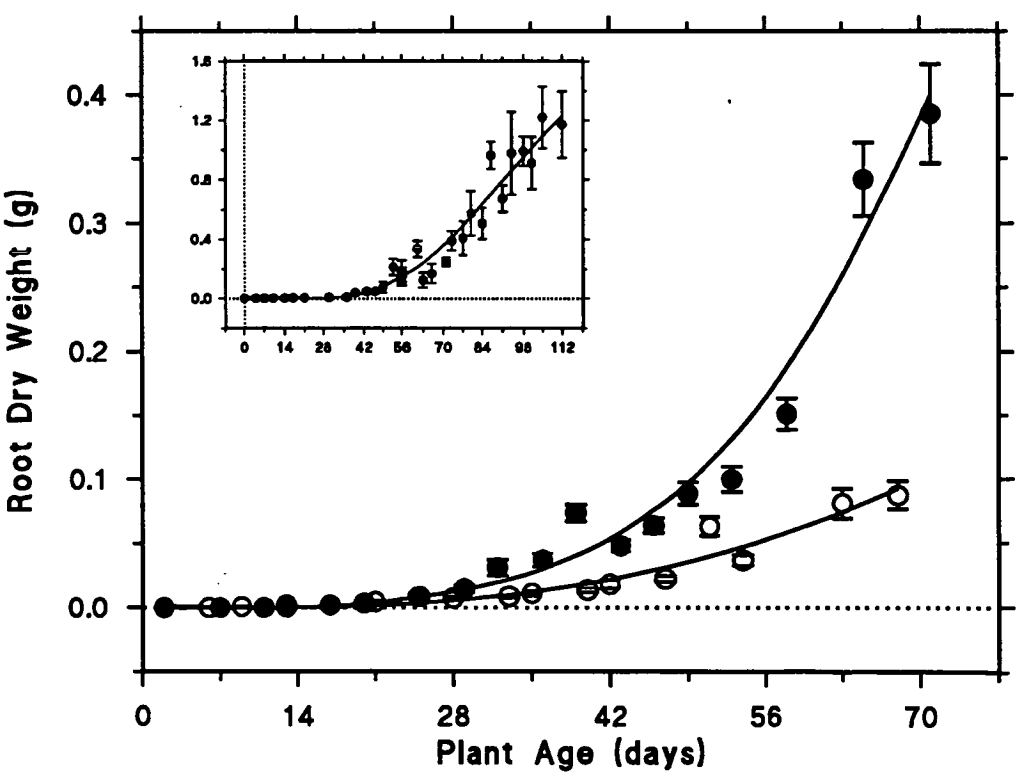


Figure 3.10 Changes in root dry weight with age for *K. coriacea* seedlings grown under controlled (●; *C.C.*2) and field (○; *F.C.*) conditions: each point is the mean of 7 and 10 replicates respectively; error bars represent standard errors of the mean. The inset shows the *C.C.*1 data. Free-hand curves describe the *C.C.*1, *C.C.*2 and *F.C.* data.

In contrast, for *F.C.* seedlings root growth occurred at a much slower rate, with dry weights of only 0.02 g and 0.09 g by day 42 and day 68, respectively.

When comparing cotyledon dry weight for seedlings grown under controlled (*C.C.*2) and field conditions (*F.C.*) two quite distinct patterns were seen (Figure 3.11). Controlled environment grown seedlings (*C.C.*2) increased in dry weight from day 28 to a value of about 0.2 g at day 42 and maintained this more or less constant value to the end of the study period on day 70. In the longer term *C.C.*1 experiment (inset, Figure 3.11) cotyledon dry weight began a slow decline from its peak value around day 56, to about 0.17 g at day 100. In contrast, under field conditions cotyledon dry weight showed only a slight change over the study period. Up to day 35 cotyledon dry weight remained more or less constant, thereafter increasing slowly. This latter gradual increase in dry weight resulted in a dry weight value of only 0.15 g by day 68. Cotyledon areas at full expansion were not significantly different under controlled and field conditions and together with differences in cotyledon dry weight resulted in specific leaf areas for *F.C.* seedlings approximately 35% greater than for *C.C.* seedlings.

Patterns of foliar leaf dry weight increase for controlled environment (*C.C.*2) and field grown (*F.C.*) seedlings were quite distinct (Figure 3.12). For *C.C.*2 seedlings leaf dry weight increased from day 30 at an exponential rate to the end of the study period, reaching 0.16 g at day 56 and 0.27 g at day 68. This rapid rate of increase continued until day 84 after which point it slowed, to produce a dry weight of 0.8 g by day 112 (*C.C.*1; inset, Figure 3.12). In contrast, for *F.C.* seedlings the increase in foliar leaf dry weight began much later, around day 54, and foliar leaf dry weight reached only 0.05 g by day 68.

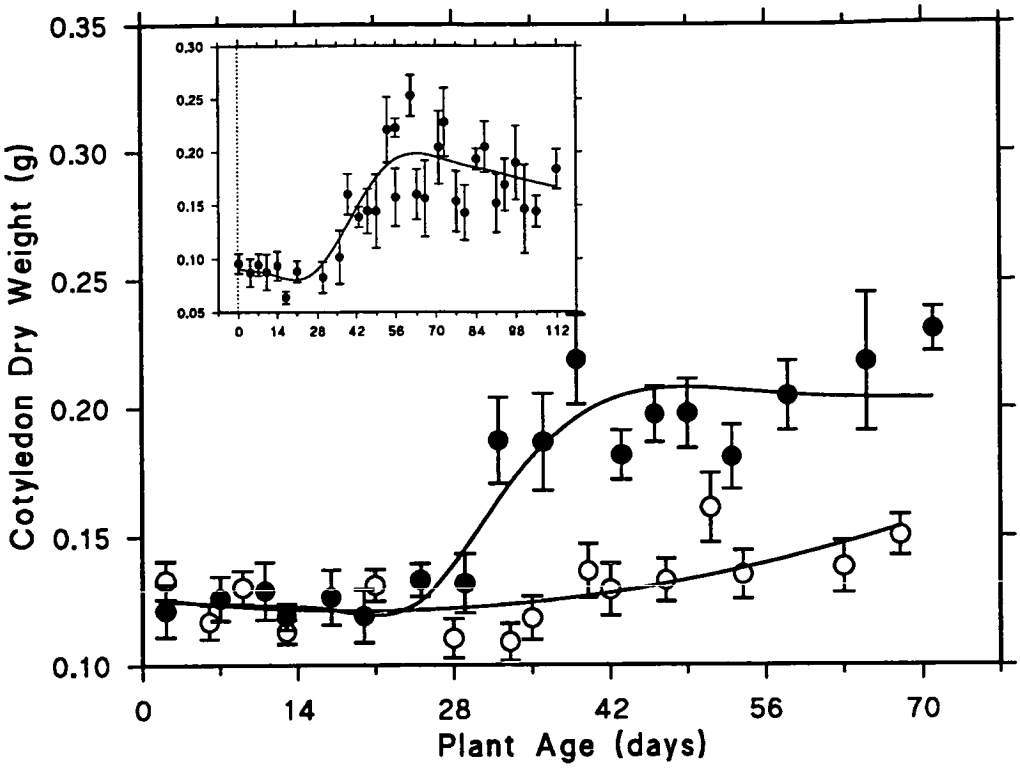


Figure 3.11 Changes in cotyledon dry weight with age for *K. coriacea* seedlings grown under controlled (●; *C.C.*2) and field (○; *F.C.*) conditions: each point is the mean of 7 and 10 replicates respectively; error bars represent standard errors of the mean. The inset shows the *C.C.*1 data. Free-hand curves describe the *C.C.*1, *C.C.*2 and *F.C.* data.

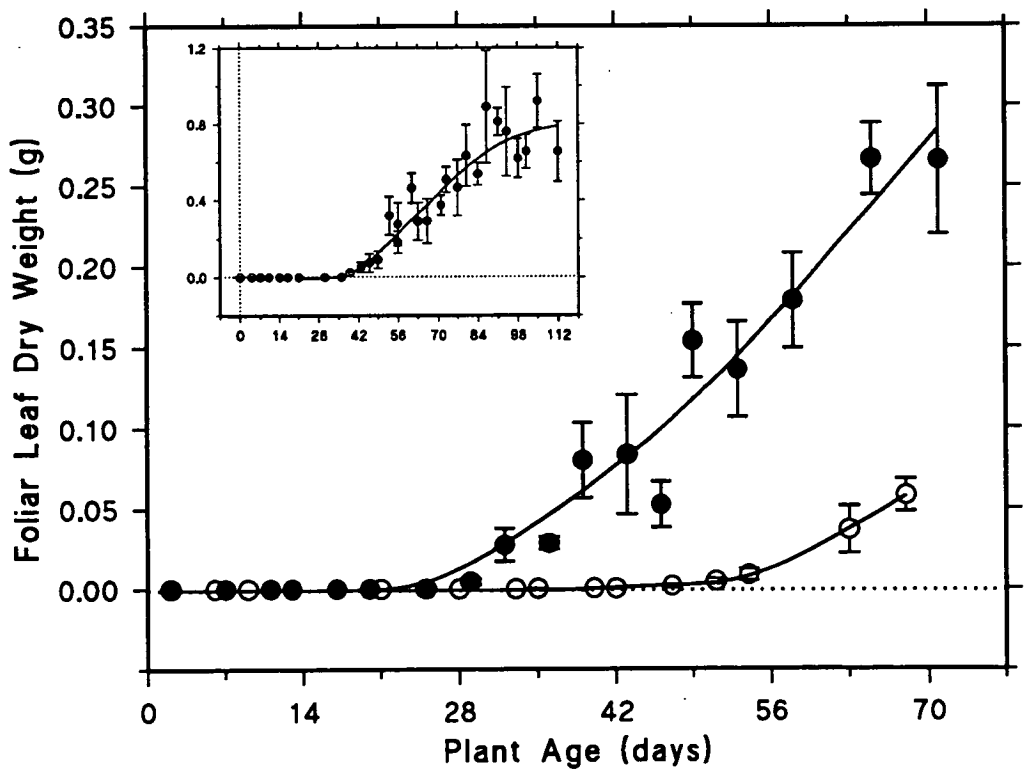


Figure 3.12 Changes in foliar leaf dry weight with age for *K. coriacea* seedlings grown under controlled (●; *C.C.*2) and field (○; *F.C.*) conditions: each point is the mean of 7 and 10 replicates respectively; error bars represent standard errors of the mean. The inset shows the *C.C.*1 data. Free-hand curves describe the *C.C.*1, *C.C.*2 and *F.C.* data.

3.4 Biomass Partitioning

3.4.1 Introduction

In view of the substantial degree of root development in *K. coriacea* under both controlled and field conditions, the level and pattern of biomass partitioning was considered as a possible limitation to plant growth.

Growth of plant organs is frequently related in a logarithmic linear fashion, which can be described by:

$$\ln (Y) = a + K \cdot \ln (X)$$

where X and Y are measures of growth of the organs in question, K is referred to as the allometric coefficient, and a is a constant.

A K value of 1 indicates a proportional allocation to X and Y, and values greater than 1 indicate a greater allocation to Y than X. Ontogenic shifts may be seen as changes in the allometric relationship.

3.4.2 Dry Matter Partitioning between Root and Shoot

In the seed, which consists predominately of cotyledon, the root to shoot dry weight ratio (r:s) approaches zero (Figure 3.13). From germination, dry matter partitioning to the roots was substantial, resulting in r:s values of 0.2 and 0.4 by day 40 and day 54, and 1.4 by day 112 (inset, Figure 3.13). This partitioning, in favour of the roots, is reflected in the allometric coefficient for *C.C.* seedlings of 1.88 (Y=root, X=shoot; Figure 3.14). *F.C.* seedlings partitioned an even greater proportion of dry matter to their root system with an allometric coefficient of 2.76 (Figure 3.14), although showing slightly lower r:s values for a comparable age (Figure 3.13).

3.4.3 Dry Matter Partitioning within Root, to Main and Lateral Roots

Having established the substantial allocation of biomass to the root system, partitioning to main root and therefore, to xylopodium development, was considered.

From day 21, lateral root growth accounted for an increasing proportion of the root dry weight, reaching about 40% by day 50 (Figure 3.15).

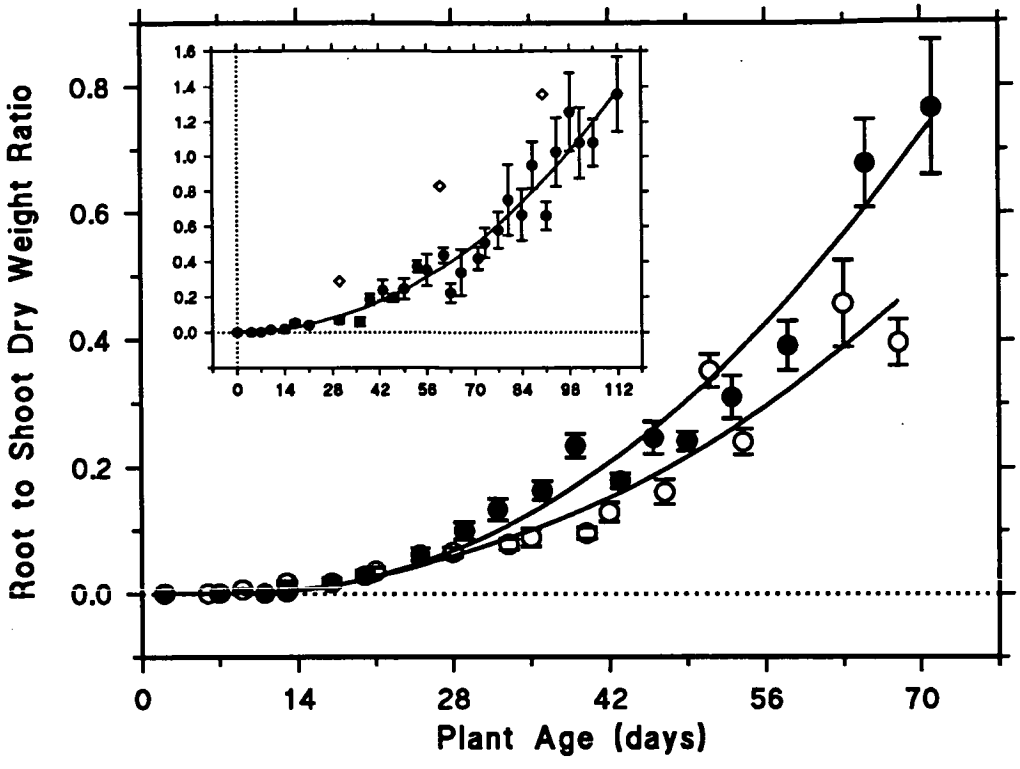


Figure 3.13 Changes in root to shoot dry weight ratio with plant age for *K. coriacea* seedlings grown under controlled (●; *C.C.*2) and field (○; *F.C*) conditions. The inset shows the *C.C.*1 data, with field data from Arasaki (1988) shown as open diamonds. Free-hand curves describe the *C.C.*1, *C.C.*2 and *F.C* data.

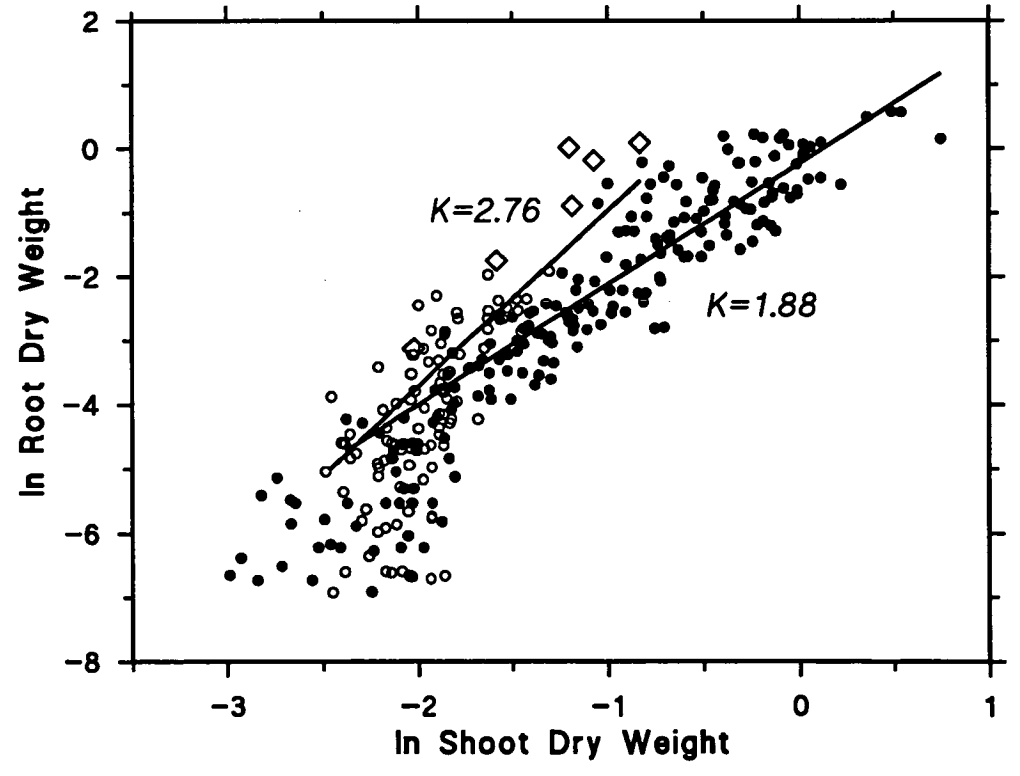


Figure 3.14 Relationships between ln (root dry weight) and ln (shoot dry weight) for *K. coriacea* seedlings grown under controlled (●; *C.C.*1 and *C.C.*2) and field (○; *F.C*) conditions. Field data from Arasaki (1988) is shown as open diamonds. Lines are linear regressions ($y=a+K \cdot x$) of the *C.C.*1 and *C.C.*2 (a=-0.231; K=1.88; r^2=0.84), and *F.C* and Arasaki (a=1.79; K=2.76; r^2=0.63) data.

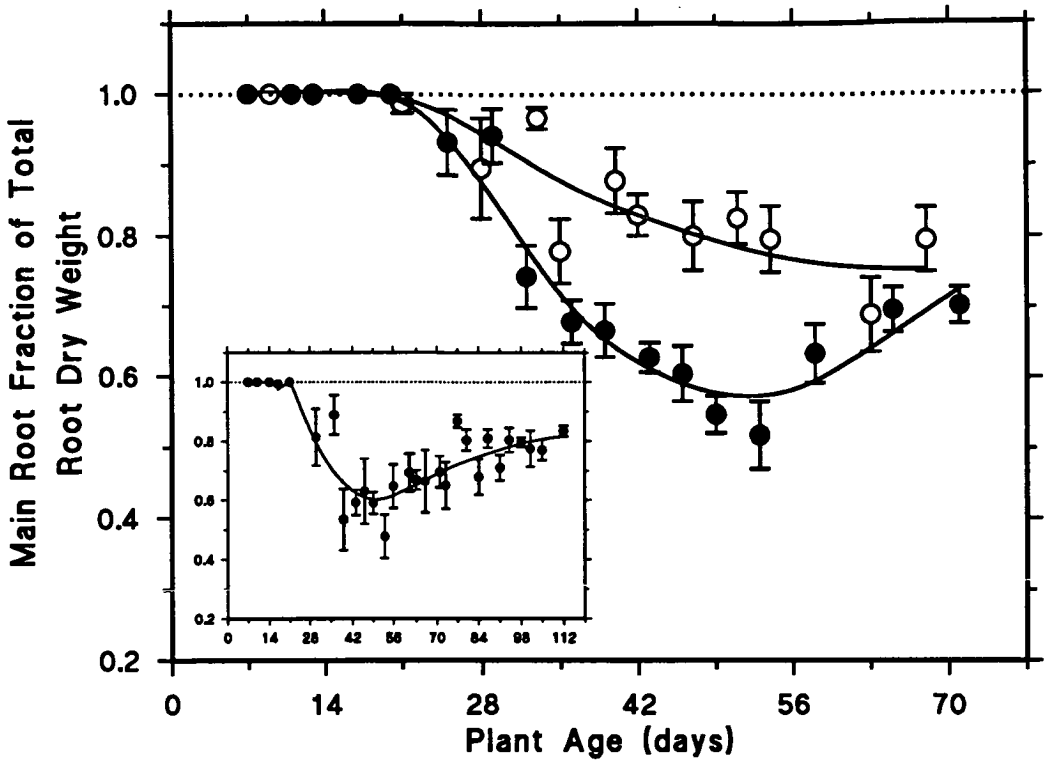


Figure 3.15 Changes in main root fraction (of total root dry weight) with plant age for *K. coriacea* seedlings grown under controlled (●; *C.C.*2) and field (○; *F.C.*) conditions. The inset shows the *C.C.*1 data. Free-hand curves describe the *C.C.*1, *C.C.*2, and *F.C.* data.

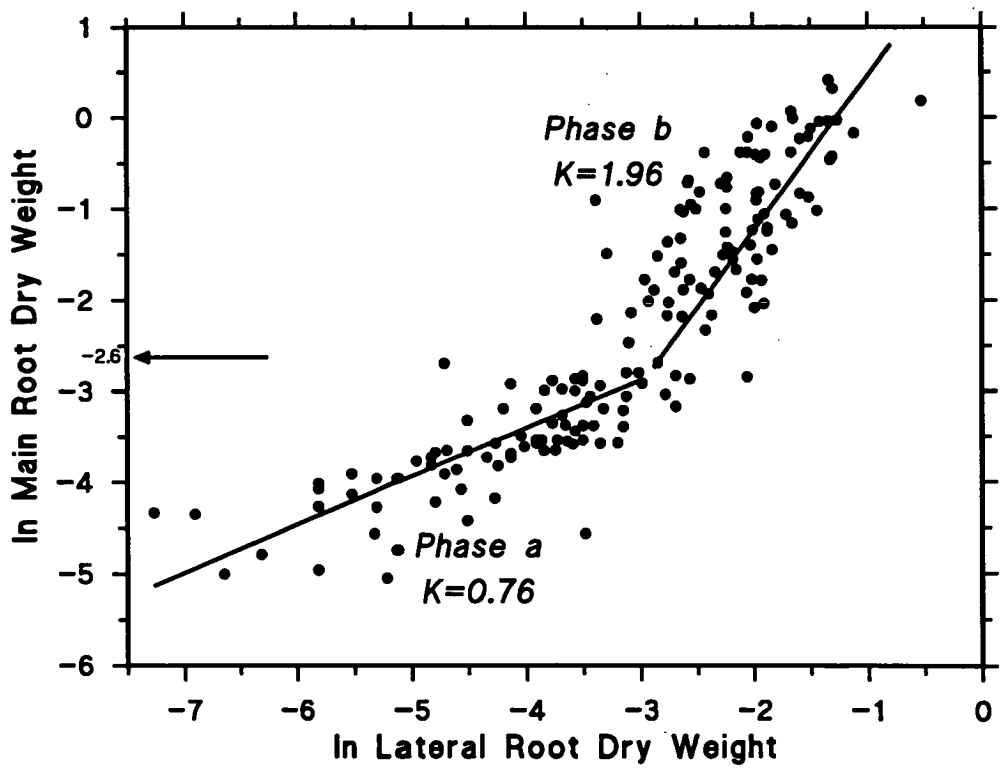


Figure 3.16 Relationship between ln (lateral root dry weight) and ln (main root dry weight) for *K. coriacea* seedlings grown under controlled (●; *C.C.1* and *C.C.*2) and field (○; *F.C.*) conditions. Linear regressions ($y=a+K \cdot x$) for phase *a* (a=-1.3; K=0.76; r^2=0.5) and phase *b* (a=1.27; K=1.96; r^2=0.43) are separated at ln (main root dry weight) of -2.6, marked by the arrow.

Thereafter, main root: root total dry weight ratio (r_m:r_t) values increased, and approached a plateau value of 0.85 (85%) by day 112 (inset, Figure 3.15). The allometric relationship between main and lateral roots (Y=main root, X=lateral root; Figure 3.16), shows an initial 'phase *a*' of lateral root favoured growth with K=0.76, followed by a 'phase *b*' of predominantly main root (*i.e.* xylopodium) growth with K=1.96. The transition between 'phase *a*' and 'phase *b*' occurred at a ln (main root dry weight) of -2.6, that is around day 54. *F.C.* seedlings partitioned less dry weight to the lateral roots (Figure 3.15), with a single allocation coefficient of 1.16.

3.4.4 Dry Matter Partitioning within Shoot, to Cotyledons and Foliar Leaves

The allometric relationship between cotyledons and shoot dry weight consisted of two phases (Figure 3.17): before and after respectively, a ln (shoot dry weight) of -1.0, equating to a plant age of 54 days. Dry weight partitioning to the cotyledons during early growth with an allometric coefficient of 0.53 ('phase *a*'; Y=cotyledons, X=shoot), was followed by a phase where dry weight did not appear to change.

The allometric relationship between foliar leaf and shoot dry weight was again two phased (Figure 3.18), also with a transition point at a ln (shoot dry weight) of -1.0 (370 mg, 54 days). The initial 'phase *a*', consisted of a substantial dry weight partitioning to the leaves (K=2.66; Y=foliar leaves, X=shoot) as Leaf 1 and Leaf 2 developed, followed by a 'phase *b*' of lower partitioning (K=1.38), as the 3rd and subsequent leaves developed. The combined leaf (cotyledon and foliar leaf) and shoot dry weight allometric relationship (inset, Figure 3.18) shows K to be constant at 1.0 (r^2=0.998) despite the two phased nature of the allometric relationship between shoot, and cotyledons and foliar leaves.

Thus, although the allometric relationships show partitioning between root and shoot remain constant, growth within these organs can be separated into two distinct phases: the first 'phase *a*', up to day 54, consists of high allocation to the lateral roots and cotyledons, and very high allocation to foliar leaves; the second 'phase *b*', after day 54, consists of reduced partitioning to foliar leaves, and a switch of substantial allocation from lateral to main root. 'Phase *a*' maybe considered as the initial establishment of the seedling, in terms of the development of assimilatory area (cotyledons, and Leaf 1 and Leaf 2) and fine root structure (lateral roots) for resource capture, whereas 'phase *b*' consists of the development of the perennating xylopodium from the subsequently accumulated dry matter.

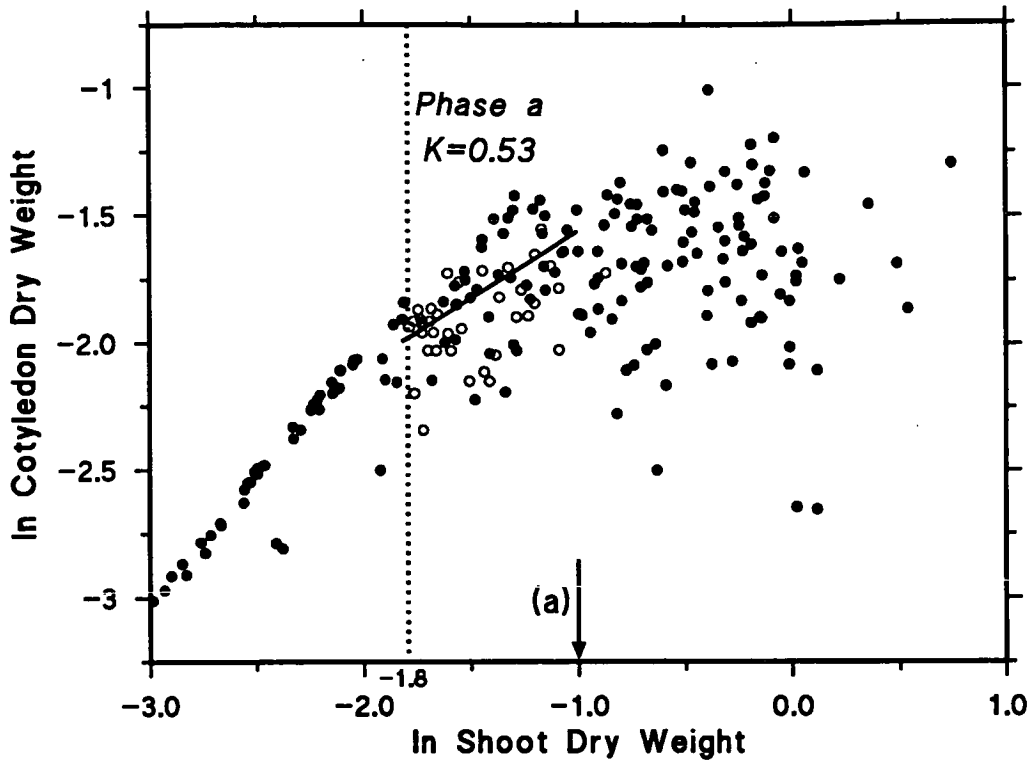


Figure 3.17 Relationship between ln (cotyledon dry weight) and ln (shoot dry weight) for *K. coriacea* seedlings grown under controlled (●; *C.C.*1 and *C.C.*2) and field (○; *F.C*) conditions. A linear regression ($y=a+K \cdot x$) for phase *a* (a=-1.03; K=0.53; r^2=0.26) ends at a ln (plant dry weight) of -1.0, marked by arrow (a).

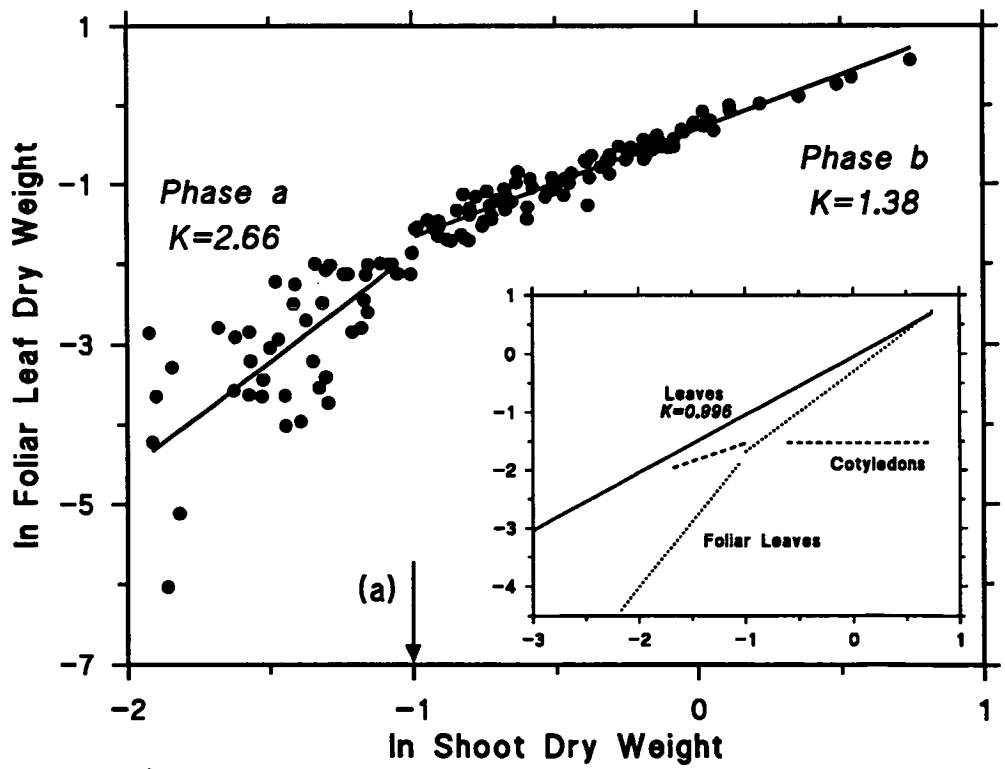


Figure 3.18 Relationship between ln (foliar leaf dry weight) and ln (shoot dry weight) for *K. coriacea* seedlings grown under controlled (●; *C.C.*1 and *C.C.*2) conditions. Linear regressions ($y=a+K \cdot x$) for phase *a* (a=0.755; K=2.66; r^2=0.51) and phase *b* (a=-0.302; K=1.38; r^2=0.94) are separated at a ln (shoot dry weight) of -1.0, marked by the arrow. The inset shows ln (leaf), ln (shoot) relationship (a=-0.05; K=0.996; r^2=0.999).

3.5 Discussion

As is common with unselected and especially woody material, genotypic variation appears to be high in *Kielmeyera coriacea* Mart.. This is clearly seen as the wide range of rates of leaf-area and particularly dry matter production, under what are uniform and constant (day-time) controlled environment conditions.

It is generally acknowledged that woody species exhibit low maximal specific growth rates relative to herbaceous species (Jarvis and Jarvis, 1964; Loach, 1970; Grime and Hunt, 1975), and this has been attributed to the expenditure of photosynthate on the production of woody tissue, a process paralleled with a slow rate of leaf-area expansion. It is for this reason that this discussion will restrict itself, where relevant, to comparisons only with other woody species.

The patterns of change of specific growth rate under field and controlled conditions are similar, with the rapid attainment of a maximum plateau value and a gradual decline thereafter, a pattern reported to be almost universal (Hunt and Lloyd, 1987). The maximum specific growth rate observed for *K. coriacea* under field conditions (0.026 d^{-1} on day 56) is slightly below the narrow range (0.031-0.050 d^{-1}) known for other Cerrado woody species in the field (Table 3.1), and slightly higher than that previously recorded for the species by Self (1989), and Arasaki and Felippe (1990).

Table 3.1 Table of maximum specific growth rates (**R**) for a selection of Cerrado woody species grown under field (*F.C.*), and favourable controlled conditions (*C.C.*).

Species	Growing Conditions	**R** (d^{-1})
K. coriacea	*F.C.*	0.026
Dimorphandra mollis Benth.[a]	*F.C.*	0.031
Qualea grandiflora Mart.[b]	*F.C.*	0.031
Qualea cordata (Spreng.)[c]	*F.C.*	0.035
Dalbergia miscolobium Benth.[d]	*F.C.*	0.035
Stryphenodendron adstringens (Mart.) Coville[e]	*F.C.*	0.043
Sweetia pseudelegans Mohlenbr.[e]	*F.C.*	0.050
Q. grandiflora[f]	*C.C.*	0.036
K. coriacea	*C.C.*	0.054

[a] calculated† from Poggiani (1973)
[b] Paulilo (1991)
[c] calculated† from Godoy (1991)
[d] calculated† from Sassaki (1991)
[e] calculated† from Poggiani (1971)
[f] Felippe and Dale (1990)
† See Appendix 3.2 for full table and details of **R** calculation

This small range of maximum specific growth rates is interesting in view of the diverse morphologies (*Qualea cordata* Spreng. has paired entire leaves whereas *Dalbergia miscolobium* Benth. has pinnate leaves), and ecologies (*Da. miscolobium, Dimorphandra mollis* Benth., *Stryphenodendron adstringens* (Mart.) Coville, and *Sweetia pseudelegans* Mohlenbr. are all members of the Leguminosae, whereas the others are not) of the species considered. However, all these species are epigeal germinators with photosynthetically active cotyledons, which would be responsible for a large proportion of the dry weight gain at the time of maximum specific growth rate.

Maximum growth rate for *K. coriacea* under nutritionally-favourable, controlled conditions is slightly more than double that found under nutritionally-poor, field conditions, with a maximum specific growth rate of only 0.054 d^{-1}. This limited response to substantially more fertile conditions has previously been noted for species of stressed environments (Bradshaw *et al.*, 1960[a]; Bradshaw *et al.*, 1960[b]; Bradshaw *et al.*, 1964; Rorison, 1968), and similarly Grime (1974), and Grime and Hunt (1975) have drawn associations between soil fertility and species' maximum specific growth rate for vegetation associations.

The maximum specific growth rate under favourable conditions, that is the 'maximum potential specific growth rate' (*sensu* Grime and Hunt, 1975; Evans, 1972), is low in *K. coriacea* seedlings ($\mathbf{R}_{max}$ on day 48 = 0.054 d^{-1}), but within the range seen for other woody species (Table 3.2). Although $\mathbf{R}_{max}$ for *K. coriacea* is well below that for recognised 'fast-growing species' such as willows and birches, it is comparable with those found for late successional species, such as oak and sycamore. Similarly, with respect to subtropical and tropical species, the value is comparable with those for slower growing mahogany species such as *Khaya senegalensis*, but clearly below that found for commercial plantation species (*Terminalia* and *Trema* sp.). Thus, at least in the juvenile stage *K. coriacea* grows no more slowly than other woody species.

Table 3.2 Table of maximum specific growth rates ($\mathbf{R}_{max}$) for *K. coriacea* (*C.C.*), and a selection of temperate, subtropical, and tropical woody species.

Species	$\mathbf{R}_{max}$ (d^{-1})
Temperate Conifers:	
Picea sitchensis (Bong.) Carr.[a]	0.031
Picea nigra ssp. *laricio*[a]	0.047
Pinus sylvestris L.[a]	0.051
Picea abies (L.) Karsten[a]	0.060
Temperate Deciduous Species:	
Acer pseudoplatanus L.[a]	0.049
Quercus rubra L.[b]	0.050*
Betula pubescens Ehrh.[a]	0.114
Fraxinus excelsior L.[a]	0.129
Salix cinerea ssp. *atrocinerea* L.[a]	0.151
Subtropical/Tropical Species:	
Khaya senegalensis (Desv.) A. Juss.[c]	0.026*
Eucalyptus deglupta[d]	0.050*
Ceiba pentandra (L.) Gaertn.[e]	0.080*
Terminalia ivorensis A. Chev[e]	0.097*
Trema guineensis[f]	0.118*
Cerrado Species:	
K. coriacea (*C.C.*)	0.054

* Although determined under favourable conditions, values are not from controlled and well-defined environment conditions, and therefore may be sub-maximal.

[a] Grime and Hunt (1975)
[b] Farmer (1980)
[c] Okali and Dodoo (1973)
[d] Wadsworth and Lawton (1968)
[e] Okali (1971)
[f] Coombe and Hadfield (1962)

Under field conditions specific growth rate (**R**) is lower than under controlled conditions as a consequence of differences in unit leaf rate (**E**) and leaf area ratio (**F**). Leaf area ratios under field conditions are similar to those under controlled conditions up to day 60, when the delayed phase of leaf growth begins in *F.C.* seedlings. However, under controlled conditions seedlings rapidly attain and maintain high **E** values (maximum of 5 g m^{-2} d^{-1}), whereas *F.C.* seedlings more slowly reach a maximum of only half this value (2.7 g m^{-2} d^{-1}).

The causes for differences in growth rate under field conditions, may be illustrated by the relative contributions of **E** and **F** to **R**, at the points of maximum specific growth rate (Table 3.3).

Table 3.3 Table of specific growth rates (**R**), and unit leaf rates (**E**), leaf area ratios (**F**), specific leaf areas (SLA) and leaf weight ratios (LWR) at that **R** value, for *K. coriacea* and *Qualea grandiflora* seedlings grown under controlled (*C.C.*) and field conditions (*F.C.*). Bracketed percentages (*i.e.* *(-85%)*) indicate proportional contributions to changes in **R**, as compared with *C.C.* seedlings on day 48 (shown in **BOLD**).

Species seedling age	**R** (d^{-1})	**E** ($g\ m^{-2}\ d^{-1}$)	**F** ($m^2\ g^{-1}$)	SLA ($m^2\ g^{-1}$)	LWR
K. coriacea (*F.C.*) d56	0.026	2.69*(-85%)*	0.0098*(-15%)*	0.0135*(-6%)*	0.730*(-9%)*
***K. coriacea* (*C.C.*) d48**	**0.054**	**4.98**	**0.0109**	**0.0140**	**0.778**
K. coriacea (*C.C.*) d100	0.010	1.30*(-76%)*	0.0075*(-24%)*	0.0160*(+8%)*	0.450*(-32%)*
Q. grandiflora (*C.C.*) d45[a]	0.036	5.78	0.0062	0.0107	0.582
Q. grandiflora (*F.C.*) d63[b]	0.031	3.11	0.0100	0.0164	0.607

[a] Felippe and Dale (1990) [b] Paulilo (1991)

Data in Table 3.3 show that differences in maximum specific growth rate between *K. coriacea* seedlings grown in controlled and field conditions are predominantly due to differences in unit leaf rate (85%), with only 15% of the difference due to a lower leaf area ratio. Of this small proportion, 6% is due to a lower specific leaf area and 9% is due to a lower leaf weight ratio in field grown seedlings.

The decline in specific growth rate after $\mathbf{R}_{max}$ for *C.C.* seedlings (Table 3.3) is attributable to the decline in unit leaf rate and leaf area ratio. From day 48 to day 100 the decline in **R** is predominantly (76%) due to the decline in unit leaf rate, with the decrease in leaf area ratio accounting for only 24% of the decline. Of this, specific leaf area is responsible for an 8% increase (note positive sign in Table 3.3; SLA actually increases over this period), and leaf weight ratio for a 32% decrease in **R**.

Thus, the post maximal decline in specific growth rate for *C.C.* seedlings is primarily due to the decline in unit leaf rate. However, this does not necessarily equate with a decline in assimilatory capacity of the cotyledons and leaves. Unit leaf rate represents the functional components of carbon exchange, and is determined by photosynthesis, respiration, exudation and mortality (McDonald *et al.*, 1991).

Assuming no carbon loses due to exudation and mortality, which is reasonable for young seedlings, daily carbon balance of the plant can be calculated as:

$$\mathbf{E} = P_n \cdot L_A \cdot T_L \; - \; (R_D \cdot L_W \cdot T_D \; + \; R_D \cdot (W - L_W) \cdot T_L \; + \; R_D \cdot (W - L_W) \cdot T_D)$$

Photoperiod Leaf Assimilation	Darkperiod Leaf Respiration	Photoperiod Nonleaf Respiration	Darkperiod Nonleaf Respiration

where: **E** is unit leaf rate; P_n is net photosynthetic rate on an area basis; L_A is leaf-area; T_L is photoperiod; R_D is specific respiration rate; W is plant dry weight; L_W is leaf dry weight; and T_D is dark-period.

Thus, with a disproportionate partitioning of dry matter to non-leaf-area during development (leading progressively to $W >> L_W$), increases in dark respiratory demand from the latter two 'Nonleaf' equation components could result in a decline in unit leaf rate, despite a constant net photosynthetic rate per unit area (P_n).

A more detailed consideration of net photosynthetic rates for field and controlled environment grown *K. coriacea* seedlings is provided in Chapter 5. Specific leaf area is determined by plant leaf-area and leaf dry weight. The development of leaf-area is considered in more detail in Chapter 4.

Leaf weight ratio is the ratio of leaf to plant dry weight. Developmentally this ratio is determined by the partitioning of biomass to leaf growth. As shown LWR is associated with both leaf area ratio, and unit leaf rate. The substantial decline in leaf weight ratio from a value of 0.778 on day 48, to 0.45 by day 100 is the consequence of the rapidly increasing root to shoot dry weight ratio. Leaf weight ratio is responsible for a 32% decline in **R** between these two points (Table 3.3), as a consequence of reduced weight re-invested in leaf-area. However this change in LWR also represents an increase in non-photosynthetic biomass from 22.2% (d48, LWR=0.778) to 55% (d100, LWR=0.45), a doubling which may at least in part account for some of the decline in unit leaf rate, which in itself accounts for a 76% reduction in **R** over this period. Thus xylopodium development may be a greater carbon burden than immediately apparent.

Grime and Hunt (1975) describe the relationships between $\mathbf{R}_{max}$ and plant morphology, notably the frequency with which many slow growing (in this case herbaceous) species are known to develop very long, often swollen, tap-root systems. Two species considered, *Heracleum sphondylium* and *Anthriscus sylvestris*, were thought to exhibit slow specific growth rates due to translocation of photosynthate into

their swollen root-stock. This translocation begins at a very early stage of seedling development (commencing with the appearance of the first leaf), and provides the capital for growth in the second year. Parallels can be drawn between this behaviour, and that of *K. coriacea*.

Table 3.4 indicates the position of *K. coriacea* (*C.C.*) in relation to a number of other temperate and tropical woody species with respect to specific growth rate and it's components. Reference to the specific growth rate for *Pinus sylvestris* (**R** = 0.019 d^{-1}; Table 3.4), and that provided in Table 3.2 ($\mathbf{R}_{max}$ = 0.051 d^{-1}) indicates that some of these values do not describe **E**, **F**, SLA and LWR at $\mathbf{R}_{max}$, but rather at some time after this point.

Table 3.4 Table of specific growth rates (**R**), unit leaf rates (**E**), leaf area ratios (**F**), specific leaf areas (SLA) and leaf weight ratios (LWR) for *K. coriacea*, *Pinus sylvestris* L., *Khaya senegalensis* (Desv.) A. Juss., *Khaya senegalensis* A. Chev., *Quercus rubra* L., *Betula verrucosa* Ehrh., *Populus tremula* L., and *Terminalia ivorensis* A. Chev. grown under favourable conditions. *n.d.* indicates no data available for comparison.

Species	**R** (d^{-1})	**E** ($g\ m^{-2}\ d^{-1}$)	**F** ($m^2\ g^{-1}$)	SLA ($m^2\ g^{-1}$)	LWR
Pi. sylvestris[a]	0.019	4.61	0.0044	0.0080	0.55
Kh. senegalensis[b]	0.026	3.23	0.0104		
			0.0062	0.0213	0.29
K. coriacea (*F.C.*)	0.026	2.69	0.0098	0.0135	0.73
Kh. ivorensis[b]	0.027	2.13	0.0150		
			0.0090	0.0236	0.38
Q. rubra[c]	0.050	3.86	0.0130	*n.d.*	*n.d.*
K. coriacea (*C.C.*)	0.055	4.98	0.0109	0.0140	0.77
B. verrucosa[a]	0.067	4.54	0.0163	0.0342	0.47
Po. tremula[a]	0.078	3.66	0.0226	0.0428	0.52
T. ivorensis[d]	0.097	5.94	0.0290	0.0510	0.57

[a] Jarvis and Jarvis (1964)
[b] Okali and Dodoo (1973)
[c] Farmer (1980)
[d] Okali (1971)

As can be seen in Table 3.4 there is more than a 5-fold variation in specific growth rate in this selection of species, and yet less than a 2-fold variation in unit leaf rate. Unit leaf rate of *K. coriacea* is high under these controlled conditions, even in relation to the faster growing temperate and tropical species (*Populus* and *Terminalia*). Variation in specific growth rate is largely attributable to the more than 6-fold variation in leaf area ratios. *K. coriaceas* leaf area ratio is low relative to other species of comparable (*Quercus*) and faster growth rate (*Populus* and *Terminalia*). This low **F** value is due to a low specific leaf area, which is the lowest shown with the exception of *Pinus sylvestris* with its distinct leaf morphology. The significance of

this low leaf area ratio, due to low specific leaf area, will be emphasised with development, as SLA approaches a low plateau value of 0.016 $m^2\ g^{-1}$ (Figure 3.6), and LWR continues to decline at 0.006 d^{-1} reaching 0.45 by 100 days (*K. coriacea* (*C.C.*), Table 3.3). Interestingly *Kh. senegalensis*, a West African savanna species, shows similar **R**, **E** and **F** values to *K. coriacea* under field conditions, but even here the specific leaf area of *K. coriacea* is notably low.

The decline in leaf weight ratio is due in large part to the rapid rate of root growth, there being little stem development in this initially rosette species. The rapid increase in root to shoot dry weight ratios (r:s) is a consequence of the high partitioning of biomass to the root system (Table 3.6).

Table 3.6 Table of root to shoot dry weight ratios at day 50, 100 and 180 ($r{:}s_{d50}$, $r{:}s_{d100}$, and $r{:}s_{d180}$, respectively), and allometric coefficients (*K*; where $\ln(Y) = a + K \cdot \ln(X)$) between root and shoot (Y=root dry weight, X=shoot dry weight) for a selection of Cerrado woody species grown under field conditions. Species referred to are: *Dalbergia miscolobium* Benth.; *Dimorphandra mollis* Benth.; *Kielmeyera coriacea* Mart.; *Qualea cordata* (Spreng.); *Qualea grandiflora* Mart.; *Stryphenodendron adstringens* (Mart.) Coville; *Sweetia pseudelegans* Mohlenbr.. *n.d.* indicates no data available for comparison.

Species	$r{:}s_{d50}$	$r{:}s_{d100}$	$r{:}s_{d180}$	*K*
St. adstringens[a]	0.27	*n.d.*	*n.d.*	1.0
Q. cordata[b]	0.31	*n.d.*	*n.d.*	1.3
Di. mollis	0.27[c]	0.81[d]	2.02[d]	1.4[c]/1.5[d]
Da. miscolobium	0.41[e]	1.19[f]	*n.d.*	1.5[f]
Sw. pseudelegans[a]	0.49	*n.d.*	*n.d.*	2.1
Q. grandiflora[g]	0.24	0.82	2.51	2.6
K. coriacea	0.21	1.74[h]/2.54[i]	3.41[h]/6.55[i]	2.7

[a] calculated from Poggiani (1971)
[b] calculated from Godoy (1991)
[c] calculated from Poggiani (1973)
[d] calculated from Mendes (1991)
[e] calculated from Sassaki (1991)
[f] calculated from Arasaki unpublished
[g] Paulilo (1991)
[h] calculated from Arasaki (1988)
[i] Moreira (1990)

The apparently low initial root to shoot ratios of these Cerrado species is a consequence of the dominance of shoot weight during early development by the relatively large cotyledons. Allometric coefficients (*K*) range from 1.0 for *Stryphenodendron adstringens*, to a maximum for *K. coriacea* of 2.7, this latter value resulting in the very rapid increase in r:s values seen. This increase in root to shoot dry weight ratio for *K. coriacea* continues to at least 210 days, when a r:s of 8.6 has been recorded (Moreira, 1990). *Dimorphandra mollis* with its mid-range allometric coefficient (*K*=1.4/1.5) has been recorded with leaf weight ratios of 0.40, 0.25, and 0.19 at day 90, day 180, and day 270, respectively (Mendes, 1991). This continuing

decline in LWR will directly reduce leaf area ratio, and indirectly reduce unit leaf rate through increasing respiratory load. *K. coriaceas* specific growth rate, because of the species' high allometric coefficient (K=2.7), will decline more rapidly than that for a species with a more modest rate of root development, such as *D. mollis*.

This extensive root development could be justified as necessary in what is a naturally nutrient-stressed soil environment. However there is only a short-lived initial phase (up to day 54 under controlled conditions) of partitioning, which favours the lateral roots (K=0.76; Y=main root, X=lateral root), before a transition to a phase of predominantly main root (K=1.96), that is xylopodium, favoured development.

Table 3.7 indicates the position of *K. coriacea* r:s in relation to a number of temperate and tropical woody species. As was seen in Table 3.6 Cerrado species under field conditions have $r:s_{d100}$ greater than 0.8 (when known), and all had allometric coefficients greater or equal to 1.3 (bar *St. adstringens*). This places them, and particularly *K. coriacea* with higher r:s values than many other temperate and tropical species, with the exception of another African savanna species, *Kh. senegalensis*. Indeed the relatively high root/shoot biomass ratios of savanna trees has previously been recognised (Sarmiento *et al.*, 1985).

Table 3.7 Table of root to shoot dry weight ratios at day 100 ($r:s_{d100}$), for *K. coriacea* and a selection of temperate and tropical woody species grown under favourable conditions.

Species	$r:s_{d100}$*
Q. rubra[a]	0.22
T. ivorensis[b]	0.36[d112]
Acer rubrum L.[c]	0.39[d70]
Fagus grandiflora Ehrh.[c]	0.57[d122]
Kh. ivorensis[d]	0.58[d121]
Kh. senegalensis[d]	0.84[d121]
K. coriacea	1.10

* Bracketed superscript values indicate actual age at harvest, if not day 100 (d100).
[a] Farmer (1980)
[b] Okali (1971)
[c] Loach (1970)
[d] Okali and Dodoo (1973)

Within the shoot, biomass partitioning to the foliar leaves is strongly favoured up to day 54 with an allometric coefficient of 2.66 (Y=foliar leaves; X=shoot). This leads to the rapid development of Leaf 1 and Leaf 2, as is described in Chapter 4. Thereafter partitioning is lower (K=1.38) and leads to the slower growth of the 3rd and subsequent leaves.

Growth of *Kielmeyera coriacea* under field conditions is slow, but is comparable to that of other Cerrado woody species. The maximum growth rate potential of *K. coriacea* is low, but within the range seen for temperate and tropical woody species, and comparable with that of other late successional trees. Growth rate plasticity for *K. coriacea* is low, as is characteristic of species from nutrient-stressed environments. Lower growth rates under field conditions are primarily due to lower unit leaf rates. Growth rates under controlled conditions decline towards day 100, predominantly due to declining unit leaf rates, but also declining leaf area ratios (this phenomenon is considered further in Chapter 4). Declining leaf weight ratio is associated with the decline in leaf area ratio and indirectly responsible for part of the decline in unit leaf rate. *K. coriacea* has low leaf area ratios because of this pattern of declining LWR, and an inherently low specific leaf area. Leaf weight ratio declines, and is predicted to continue to decline because of the rapid and continued root development in *K. coriacea*, a consequence of the high partitioning of biomass to the root system. During an initial phase, up to day 54, partitioning within the shoot favours foliar leaf development, and within the root favours lateral root development. Thereafter root development is dominated by xylopodium formation. These patterns are consistent with those known for other Cerrado species, although *K. coriacea* does appear to represent an extreme example.

Chapter 4

Leaf Development of *Kielmeyera coriacea* Mart. Seedlings

4.1 Introduction

This chapter describes the results of leaf development analyses of *Kielmeyera coriacea* Mart. seedlings grown under controlled, and field conditions. This follows the analysis of changes in dry weight and biomass partitioning for leaf development described in the previous chapter. The aim of these studies was to investigate leaf development under 'natural', and very favourable conditions, and thereby determine environmental and inherent limitations to leaf development. Objectives were: (1) to determine, under controlled conditions, patterns of leaf-area increase, and its components, leaf emergence, leaf primordia formation, individual leaf expansion, and individual leaf areas at full expansion; (2) to relate the differences seen in leaf-area increase under field conditions to differences in these components. Despite having determined the changes in plant leaf-area (L_A) in Chapter 3 (see section 3.3.2), it was considered necessary to measure L_A increase non-destructively, and thereby avoid the random sampling error inherent in destructive harvesting.

Leaf development under controlled conditions was examined in two separate experiments both involving non-destructive measurements of small *K. coriacea* population samples. The first (*LGA*1) considered leaf development from day 0 to day 154 with a relatively large interval between measurements (14 days). The second (*LGA*2) considered leaf development at 3-4 day intervals from day 0 to day 70. Developmental increase in leaf primordium number for seedlings grown under controlled (*PNA*1) and field (*PNA*2) conditions, was determined by regular destructive harvesting of shoot apices up to day 70. Full expanded leaf areas were determined for *K. coriacea* trees by destructive harvesting of 6 growing tips in February 1991. Phyllotaxis was determined at day 100 for eight *K. coriacea* seedlings grown under controlled conditions.

4.2 Leaf-Area Development

4.2.1 Leaf-Area Growth

Changes in leaf-area for *K. coriacea* seedlings grown under controlled conditions (*LGA*1) are shown in Figure 4.1. Initially increase in area was slow, with a mean absolute leaf-area growth rate (G_A) of 3.21 $cm^2\ d^{-1}$. However from day 70 a faster rate of leaf-area increase was seen until the end of the study period (G_A=8.23 $cm^2\ d^{-1}$). Rates of area increase for different plants were highly variable, as indicated by the coefficients of variation for mean leaf-area, which increased from 43% on day 28 to 48% on day 154. Mean relative leaf-area growth rate (R_A), calculated between successive measurements, showed abrupt and significantly different changes during the study period (Figure 4.2). Between day 28 and day 42 R_A reached 0.07 d^{-1}, thereafter decreasing significantly ($p<0.05$) to 0.035 d^{-1} at day 56, and 0.042 d^{-1} to day 84. Values then significantly ($p<0.05$) decreased to 0.02 d^{-1} by day 98, and progressively declined to 0.01 d^{-1} by the end of the study period. The initially high R_A values (d28-d42) resulted from expansion of Leaf 1 and Leaf 2, with the second peak in values between day 56 and day 84, a consequence of the expansion of Leaf 3 to Leaf 6-8.

*LGA*1 provided long term data for leaf-area development, but at low resolution and with a lack of detail for the early stages of seedling development. Consequently a second, more detailed leaf growth analysis (*LGA*2) was conducted considering leaf-area development in the first 70 days of growth.

Changes in leaf-area for *K. coriacea* seedlings grown under controlled (*LGA*2) and field (*F.C.*) conditions are shown in Figure 4.3. Under controlled conditions the cotyledons steadily expanded from imbibition, however from day 28 there was a much more rapid increase in leaf-area, as Leaf 1 and Leaf 2 expanded (Figure 4.3). G_A values declined as these leaves reached full expansion (towards d56), before increasing again as Leaf 3 and subsequent leaves began to emerge and expand. Figure 4.4 shows that under controlled conditions R_A for cotyledon expansion was constant at 0.04-0.05 d^{-1}. These values contrast with the rapid expansion of Leaf 1 and Leaf 2 (L1 and L2 respectively) from day 28, when values reached a maximum of 0.17 d^{-1} around day 35, before falling to low values at day 56. Under field conditions foliar leaf development was both later, and slower (Figure 4.3).

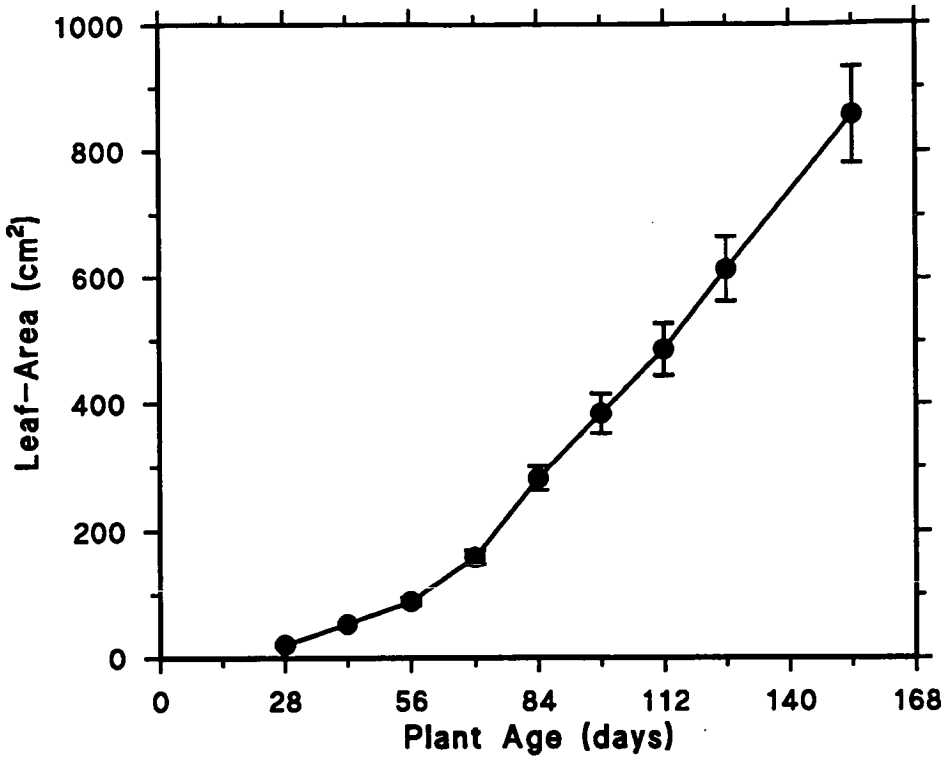


Figure 4.1 Changes in plant leaf-area (●) with age, for *K. coriacea* seedlings grown under controlled conditions (*LGA*1). Each point is the mean of a population sample of 30 individuals, with bars representing standard errors of the mean.

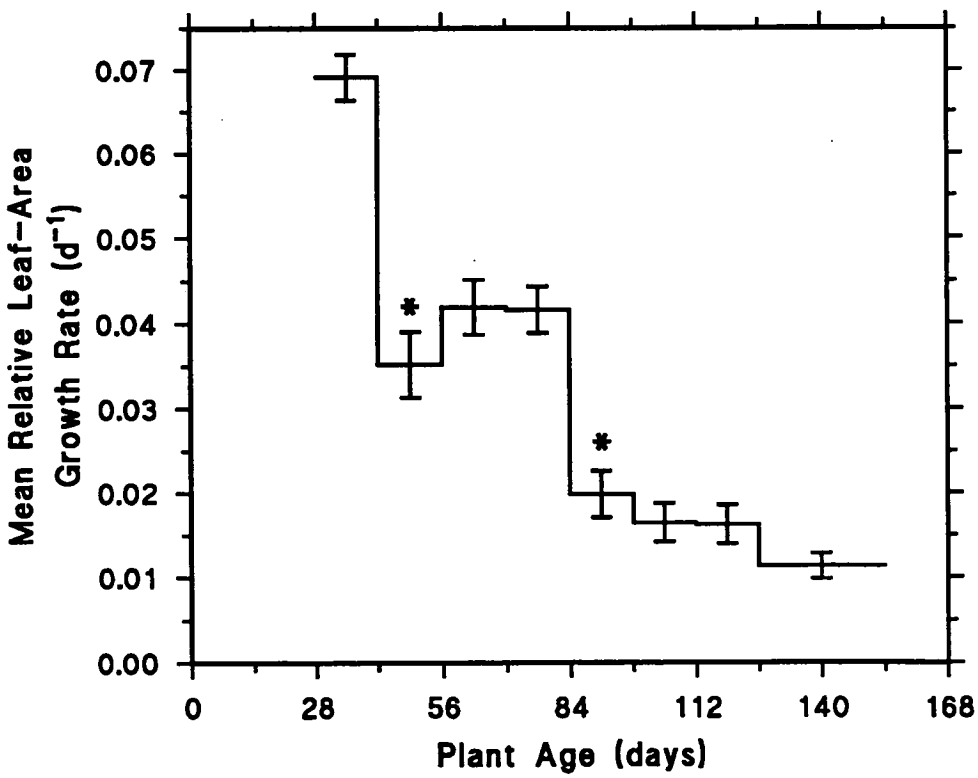


Figure 4.2 Changes in mean relative leaf-area growth rate (R_A) with plant age, for a small population sample (n=30) of *K. coriacea* seedlings grown under controlled conditions (*LGA*1). R_A values were calculated between successive measurements, with bars representing standard errors of the mean. * indicates an R_A value significantly ($p<0.05$) different from the preceeding R_A value.

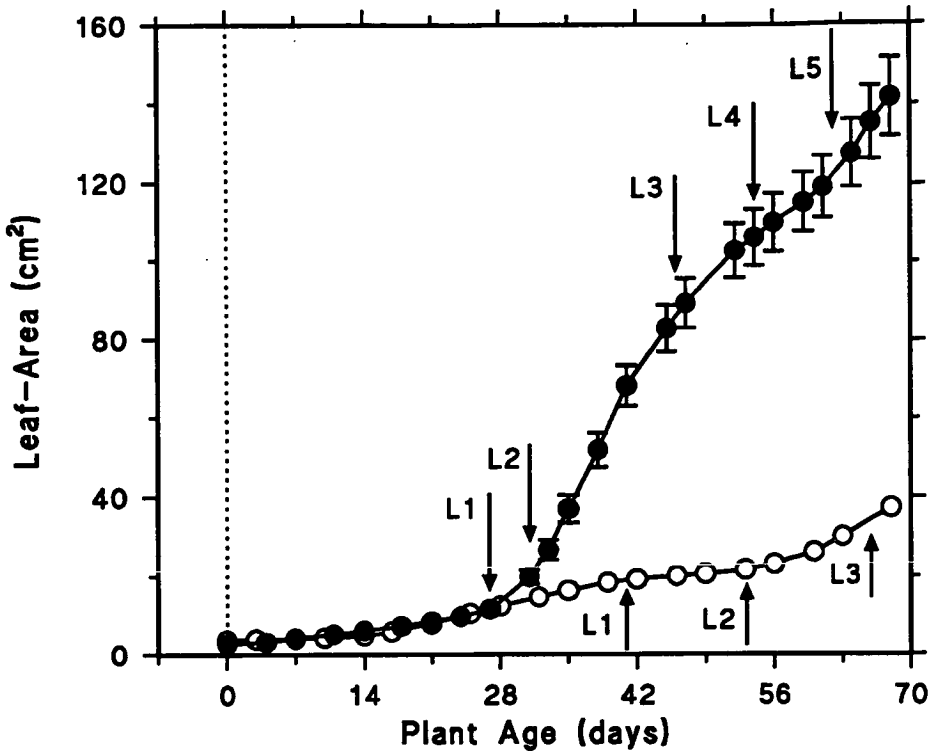


Figure 4.3 Changes in leaf-area with age, for *K. coriacea* seedlings grown under controlled (●; *LGA*2) and field (○; *F.C.*) conditions. For the *LGA*2 data each point is the mean of 14 replicates, with bars representing standard errors of the mean. Field data was provided by the 10 replicate destructive harvests of the *F.C.* data set. Arrows indicate points of emergence for Leaf 1 (L1), Leaf 2 (L2), *etc.* for *LGA*2 and *F.C.*.

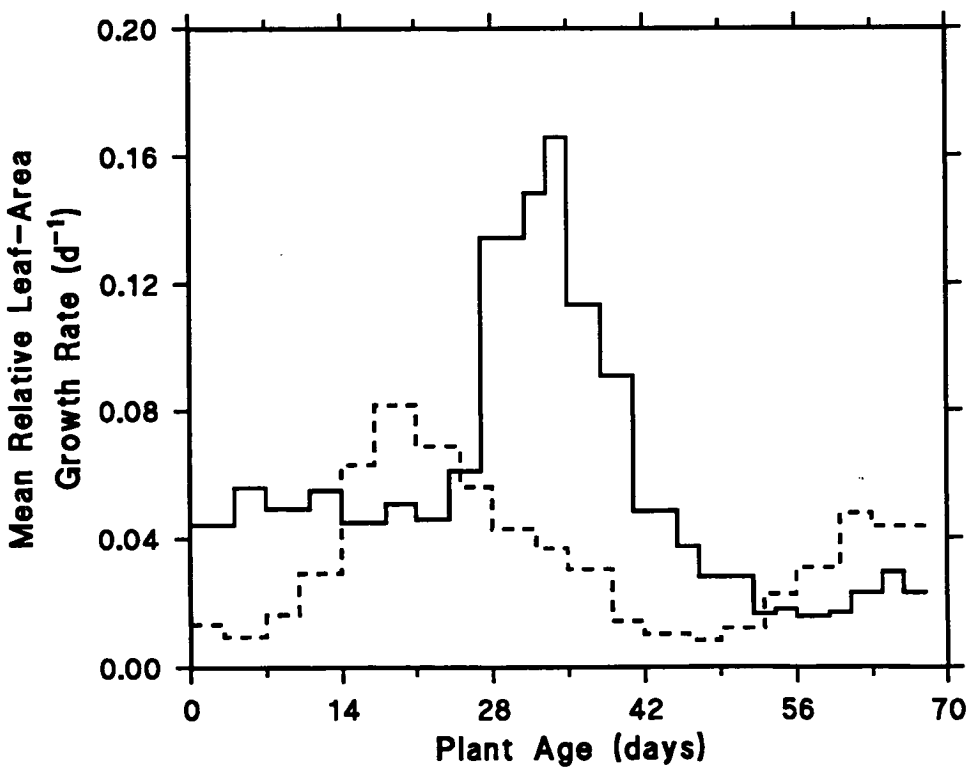


Figure 4.4 Changes in mean relative leaf-area growth rate (R_A) with plant age, for *K. coriacea* seedlings grown under controlled (——; *LGA*2) and field (- - -; *F.C.*) conditions. R_A values were calculated between successive measurements.

Cotyledon expansion paralleled that seen for *LGA2*, however emergence of L1, L2, and L3 was later than that seen for these leaves under controlled conditions, and the expansion of these leaves was relatively much slower. Although L1 emerged before d42, plant leaf-area increase due to the expansion of L1 was not seen until after d56. This results in the differing pattern of mean relative leaf-area increase seen in Figure 4.4.

4.3 Leaf Number Growth

4.3.1 Introduction

Plant leaf-area is determined by mean individual leaf area, and leaf number,

$$L_A = A_i \cdot N_L \quad (4.1)$$

where L_A is plant leaf-area; A_i is mean individual leaf area; and N_L is leaf number.

Leaf-area growth rate is determined by, the rate of expansion of individual leaves, the interval between the emergence of successive leaves (phyllochron), and, the duration of expansion of individual leaves,

$$G_A = G_i \cdot (d/p) \quad (4.2)$$

where G_A is absolute plant leaf-area growth rate; G_i is individual leaf area growth rate; p is phyllochron; and d is the duration of individual leaf expansion.

As the duration of individual leaf expansion (d) is determined by the mean individual leaf area at full expansion (A_i) and the individual leaf area growth rate (G_i), where $d=A_i/G_i$, then,

$$G_A = A_i/p \quad (4.3)$$

Thus the rate of leaf-area increase will be determined by leaf emergence rate ($1/p$) and mean leaf area at full expansion (A_i). Consequently investigations focused on, leaf formation and emergence rates, and leaf areas at full expansion. The phyllochron may be extended by slow leaf primordium production at the shoot apex. The interval between the formation of successive leaf primordia is known as the plastochron.

4.3.2 Leaf Emergence Rate

Changes in emerged leaf number with plant age for seedlings grown under controlled (*LGA*1 and *LGA*2) and field (*F.C.*) conditions are shown in Figure 4.5 and Figure 4.6. Leaf emergence under controlled conditions was initially rapid with Leaf 1 and Leaf 2 emerging in rapid succession after day 21, with a mean phyllochron of 4.2 d ('*phase 1a*'; Figure 4.5). This was followed by a short phase of little apparent leaf development up to day 45 ('*phase 1b*'; Figure 4.5). Thereafter rapid leaf emergence resumed with a mean phyllochron of 8.1 d^{-1}, and continued to at least day 154 ('*phase 2*'; Figure 4.5 and Figure 4.6). Leaf emergence under field conditions (Figure 4.5) started later and continued at a slower rate than under controlled conditions: Leaf 1 was not emerged until day 41, and L3 only by day 65.

4.3.3 Leaf Flushing

The mean sample data (*LGA*1 and *LGA*2) shows that absolute rates of leaf-area increase (Figure 4.1) and foliar leaf emergence (Figure 4.5 and Figure 4.6) were essentially constant after the rapid emergence and expansion of Leaf 1 and Leaf 2. However, individual plants continued this characteristic flushing phenology, which is masked beyond L1 and L2 emergence (flush 1: F1) by averaging values of this highly variable population sample. Many faster growing individuals showed 3, or even 4 periods of rapid leaf number increase, and so area increase, punctuated by periods of relatively little leaf development.

Figure 4.7 shows the development of foliar leaf number and mean relative leaf-area increase ($\mathbf{R_A}$) for KCS1 a representative *LGA*2 seedling. Leaf 1 and Leaf 2 rapidly emerged (d24 and d27 respectively), and expanded between day 28 and day 50. From day 45 to day 65 there was a flush of leaf emergence (F2) as Leaf 3 to Leaf 7 appeared. No new leaf emergence occurred thereafter up to the end of the study period on day 84. The expansion of L1 and L2 resulted in a synchronous peak in $\mathbf{R_A}$, whereas the expansion and so area increase, of the subsequent foliar leaves (L3-L7) was delayed and peak values were only seen once leaf emergence has ceased (after d65). The reasons for this delay are discussed in section 4.5. Figure 4.8 shows this leaf flushing over a longer period for KCS2, a fast growing *K. coriacea* seedling (*LGA*1).

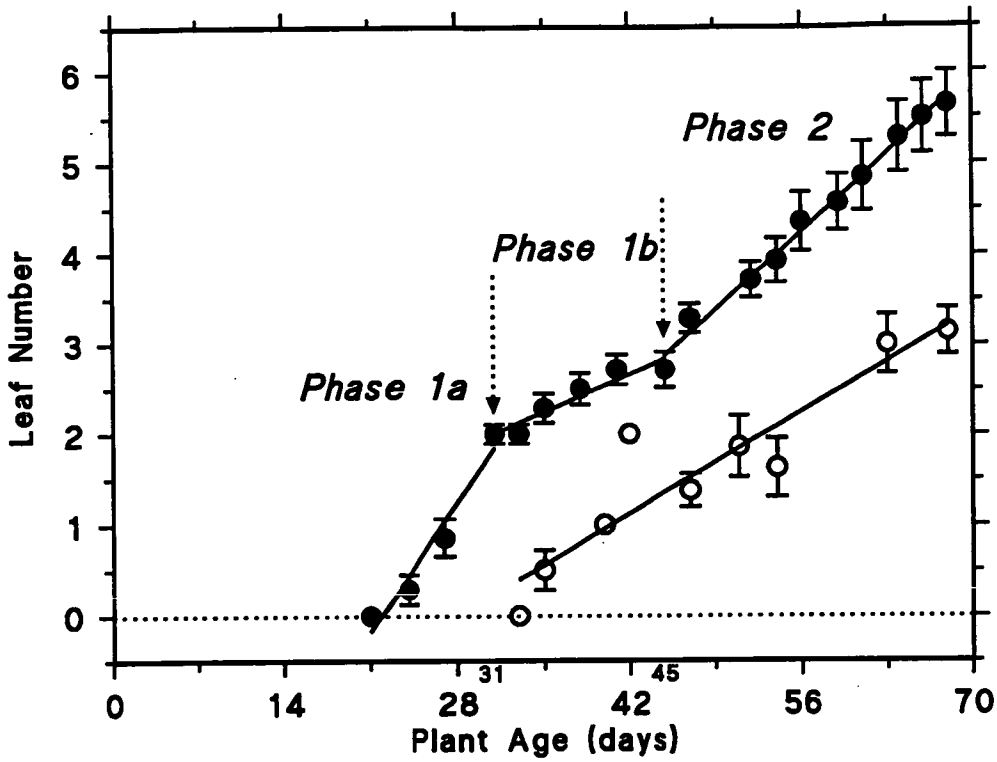


Figure 4.5 Changes in leaf number with age, for *K. coriacea* seedlings grown under controlled (●; *LGA*2) and field (○; *F.C.*) conditions. Each point is the mean of 14 and 10 replicates respectively, with bars representing standard errors of the mean. The arrows delimit suggested transition points between distinct phases of leaf number increase for the *LGA*2 data.

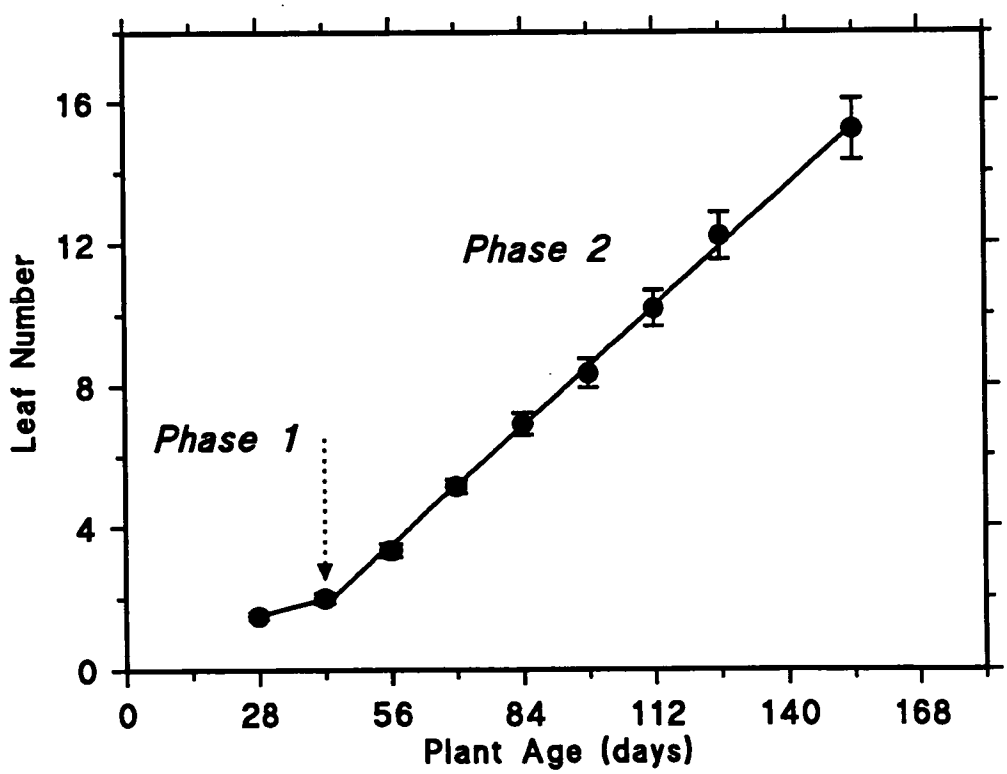


Figure 4.6 Changes in leaf number with age, for *K. coriacea* seedlings grown under controlled conditions (●; *LGA*1). Each point is the mean of 30 replicates, with bars representing standard errors of the mean. The arrow delimits the suggested transition point between two distinct phases of leaf number increase.

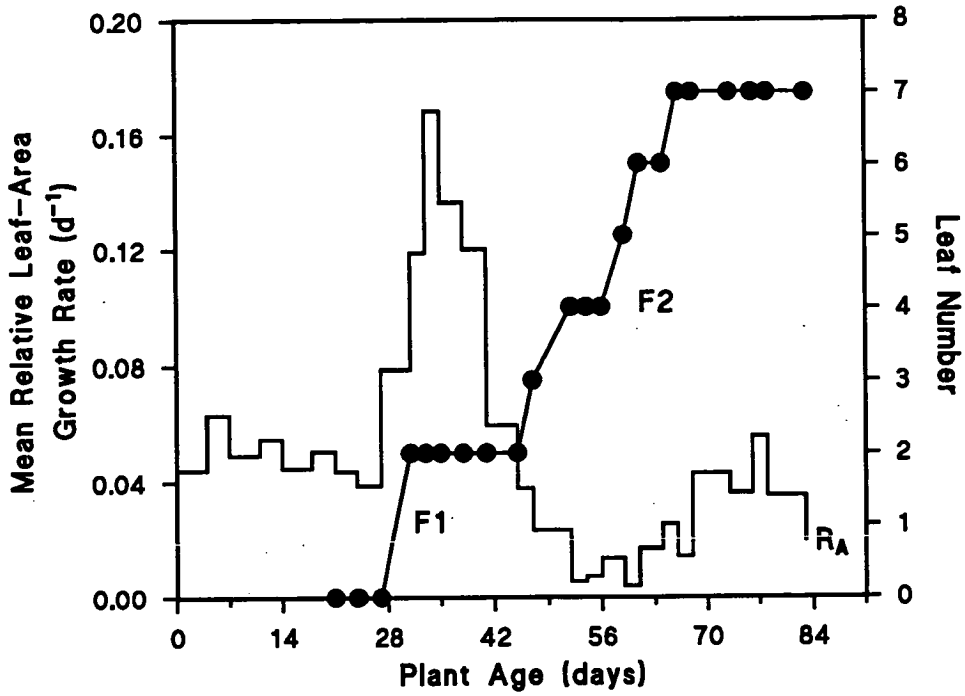


Figure 4.7 Changes in mean relative leaf-area growth rate (R_A) and leaf number (●) with plant age, for KCS1 a representative *K. coriacea* seedling grown under controlled conditions (*LGA*2). F1 and F2 indicate periods of rapid leaf emergence, or leaf flushing.

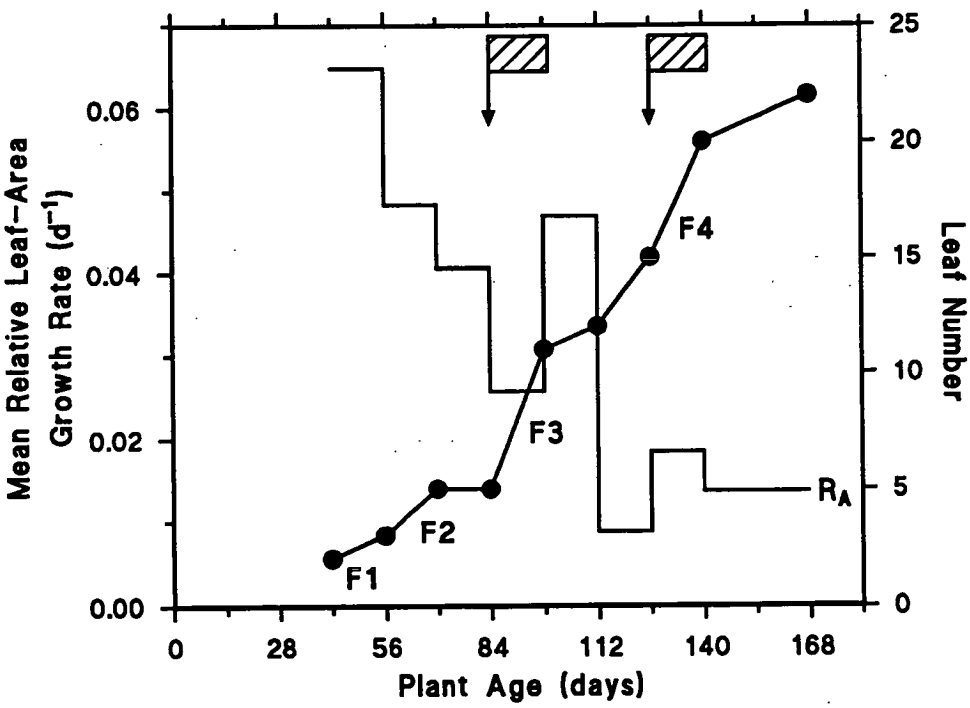


Figure 4.8 Changes in mean relative leaf-area growth rate (R_A) and leaf number (●) with plant age, for KCS2 a fast growing *K. coriacea* seedling under controlled conditions (*LGA*1). F1, F2, F3 and F4 indicate successive periods of rapid leaf emergence, or leaf flushing. Arrows and hatched boxes indicated ages at which stem elongation was initially seen and continued to, respectively.

In this 4 separate flushes of leaf growth were seen, the latter two accompanied by periods of stem elongation. Lag phases between flushes of leaf growth were seen at 5, 11 and 20 emerged foliar leaves. The expansion of L1 and L2 (F1) is merged with that of the second flush (F2, L3-L5) resulting in a block of high $\mathbf{R_A}$ values to day 84. The third flush (F3) between day 84 and day 98, produced Leaf 6 to Leaf 11, however the resultant peak in $\mathbf{R_A}$ values was not seen until the subsequent measurement interval (d98-d112). The reason for this lack of synchrony is explained in section 4.4.3. The fourth flush (F4) between day 112 and day 140 was accompanied by only 30 mm of stem elongation, as compared with the 80 mm seen for the third flush.

Although leaf emergence was irregular, flushing was generally associated with the emergence of specific leaves as shown in Table 4.1.

Table 4.1 Initial and final leaf positions for successive leaf flushes seen in *K. coriacea* seedlings grown under controlled conditions (*LGA*1 and *LGA*2). L1, L2, L3 are Leaf 1, Leaf 2, and Leaf 3 respectively, and so on. **Bold** values are modal leaf positions of the ranges indicated.

Flush Number	Initial Leaf Position	Final Leaf Position
F1	**L1**	**L2**
F2	**L3**	(L6- **L7** -L8)
F3	(L7- **L8** -L9)	(L12- **L13** -L14)
F4	(L13- **L14** -L15)	(L21- **L22** -L23)

This flushing habit of leaf growth poses the question, at what stage is this flushing determined, at primordium formation or leaf emergence.

4.3.4 Primordium Number Growth

Comparison of mean leaf primordium numbers for *K. coriacea* seedlings grown under controlled (*PNA*1) and field (*PNA*2) conditions are shown in Figure 4.9. Primordium numbers in the seed were one (Plate 4.1), occasionally two. From germination on day 6-7 primordium numbers began to increase at an almost constant rate. The rate of increase for *C.C.* seedlings (plastochron=7.2 d) was double that seen for *F.C.* seedlings (plastochron=16.4 d), and resulted in 3 primordia by day 22, and 7 primordia by day 48.

However, as for leaf-area and leaf number development, averaging this population sample data obscures the real behaviour of individual plants. Considering the development of individual plants is not possible because of the destructive nature of primordium number determination.

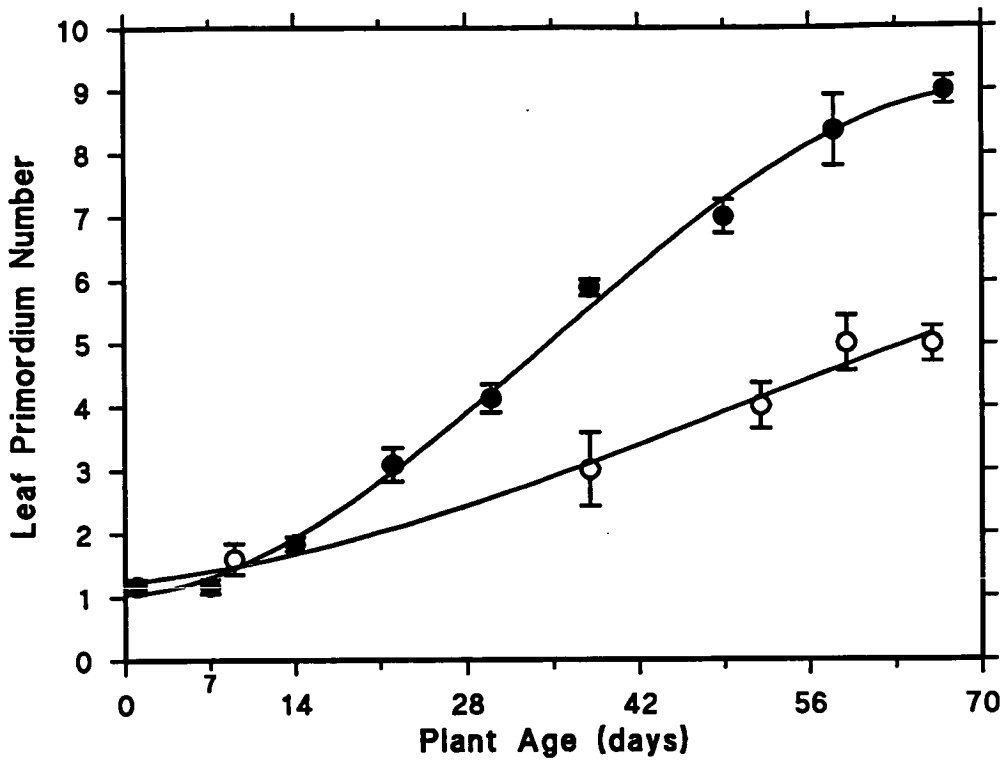


Figure 4.9 Changes in leaf primordium number with plant age, for *K. coriacea* seedlings grown under controlled (●; *PNA*1) and field (○; *PNA*2) conditions. Each point is the mean of 8 and 5 replicates respectively, with bars representing standard errors of the mean. Lines are free-hand curves of the *PNA*1 and *PNA*2 data.

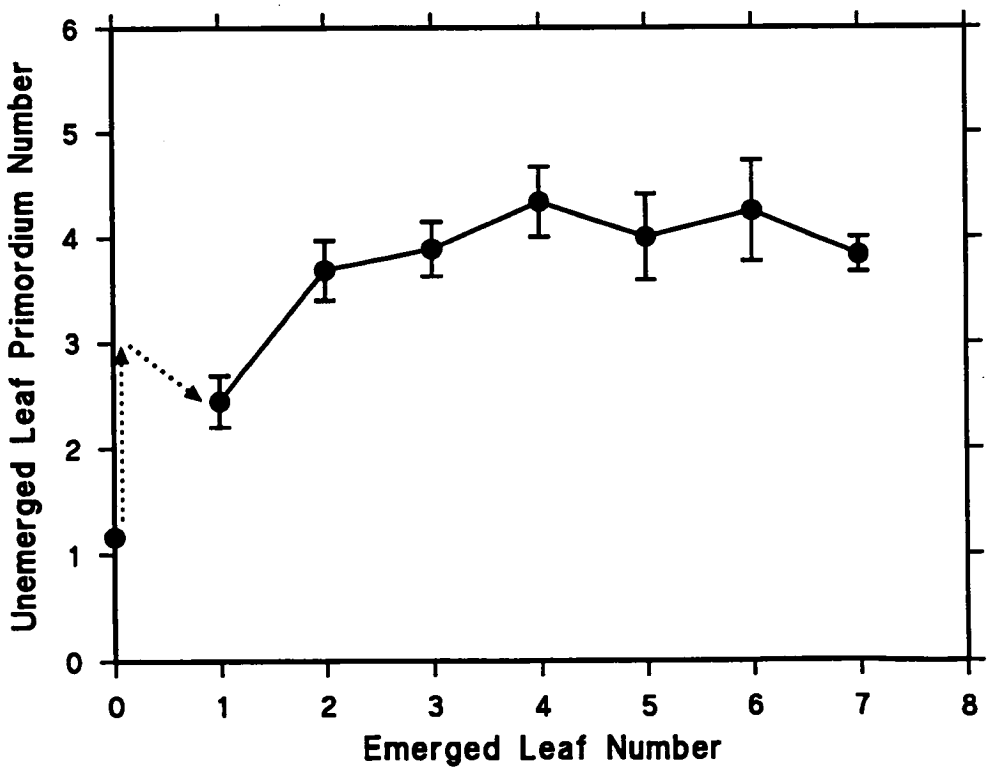


Figure 4.10 Relationship between unemerged leaf primordium number (U_N) and emerged leaf number, for *K. coriacea* seedlings grown under controlled conditions (●; *PNA*1). Each point is a mean of 8 replicates, with bars representing standard errors of the mean. Arrows indicate path of U_N up to L1 emergence.

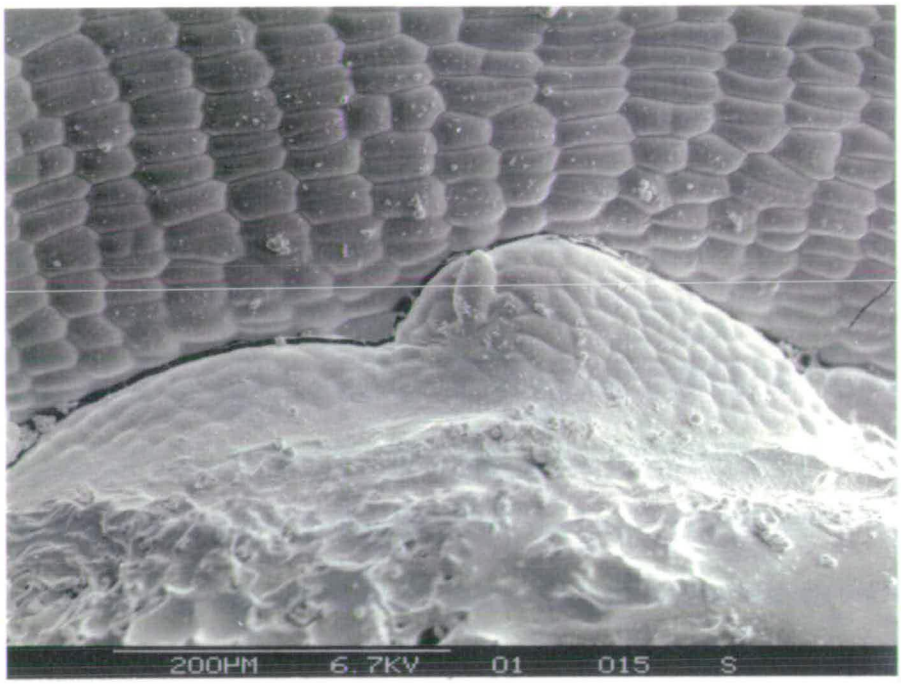


Plate 4.1 First leaf primordium on the embryo apical tip present in the seed (d0). Plate is an electron micrograph obtained using low temperature scanning electron-microscopy. Scale-bar indicates magnification.

Primordia production may be constant with time (type A), as suggested by the mean primordia number data (Figure 4.9), in which case leaf flushing (F1, L1 and L2; F2, L3-L7; *etc.*) would be independent of primordium production (which is constant up to L9). Alternatively primordia production may be associated with leaf flushing, itself occurring in flushes (type B), averaging the sample data serving only to obscure this detail. The increase in emerged leaf and primordium number for these two possibilities (A and B) are shown in Figure 4.11 (A1 and B1, respectively). Figures are drawn with a plastochron of 7.2 d (the sample mean value), and the leaf emergence pattern of KCS1 (phyllochron of 8.7 d, the sample mean value). Figure 4.11 A2 and B2 show the consequent relationships between unemerged leaf number (U_N) and emerged leaf number (N_L) for A and B, respectively. For A, the more rapid emergence of L1 and L2 ('*phase 1a*' phyllochron of 4.0 d) over plastochron (7.2 d), means that the transition from N_L 0 to N_L 2 must be accompanied by a decrease in U_N. Consequently leaf flushing results in an irregular stepped pattern of changing U_N with N_L (Figure 4.11 A2). For type B, primordium production is flushing (Figure 4.11 B1), and U_N is constant with N_L, by definition.

Figure 4.10 shows the relationship between unemerged leaf primordium number and emerged leaf number for individual *K. coriacea* seedlings grown under controlled conditions (*PNA*1). Unemerged leaf number is essentially constant from 2 emerged leaves onwards. Thus leaf primordium production itself occurs in flushes and leaves emerge maintaining an approximately constant number of unemerged primordia at the shoot apex. The pattern seen from zero to 2 emerged leaves indicates relatively slow primordia production up to U_N 3, followed by rapid production to produce U_N 4, L_N 2.

4.4 Individual Leaf Areas

4.4.1 Introduction

Despite the constant and uniform controlled environment growing conditions (*LGA*1 and *LGA*2), substantial variation was seen in the morphology and area of foliar leaves produced by *K. coriacea* seedlings. Although the majority of leaves were typically more than 25 cm^2 in area, many leaves were small, with areas of less than 1 cm^2. Without exception all *LGA*1 and *LGA*2 plants produced at least one such 'miniature' leaf. Miniature leaf production was also seen under field conditions.

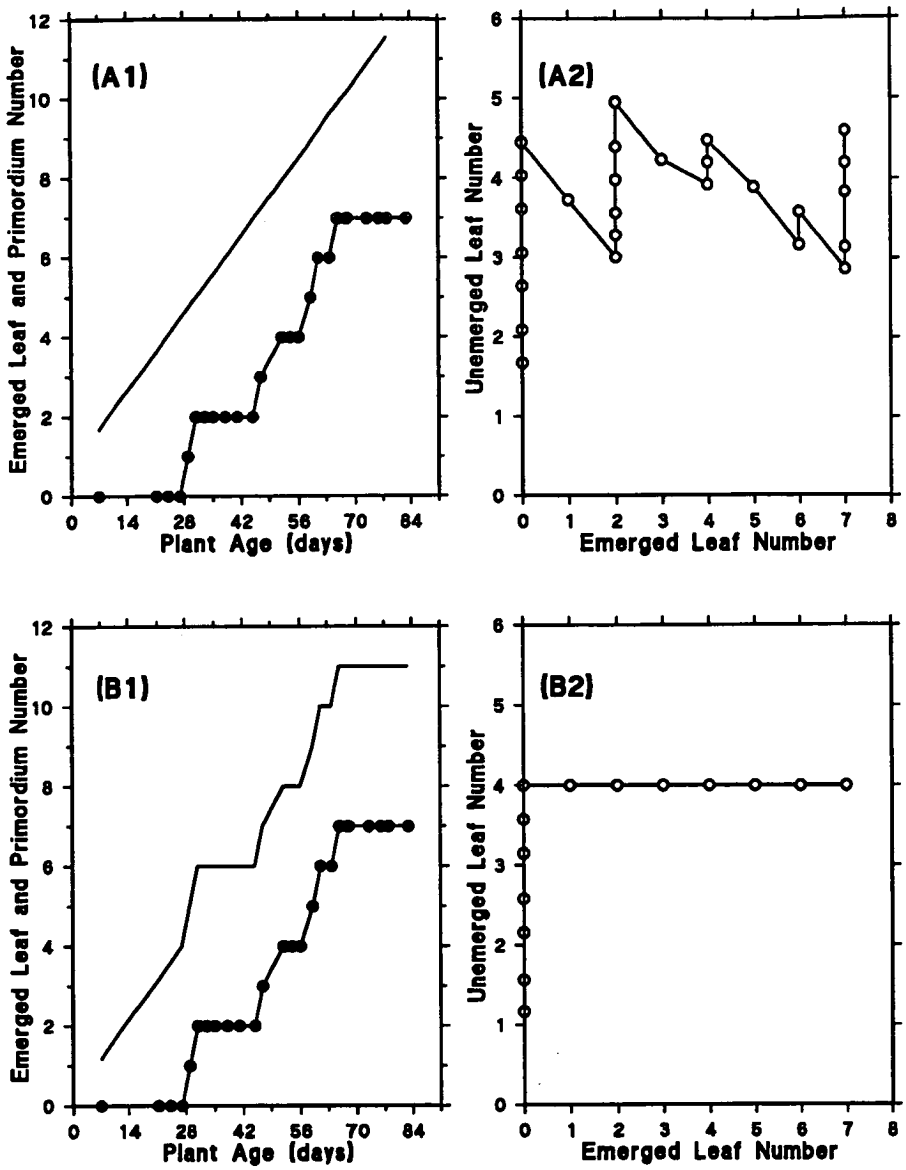


Figure 4.11 Two theoretical patterns of primordia production: (A) constant production; and (B) primordia production paralleled by leaf emergence.
A1 and B1 show, constant primordia production (●, A1) and primordia production paralleled by leaf emergence (●, B1) and plant age, for a typical flushing leaf emergence pattern (as for KCS1). Phyllochrons are equal to the mean of the population sample (8.8 d), and plastochrons are equal to the mean of the population sample (7.2 d).
A2 and B2 show the consequent relationships between the number of unemerged leaf primordia at the shoot apex (U_N) and emerged leaf number (N_L) for constant primordia production (A2), and primordia production paralleled by leaf emergence (B2).

4.4.2 Miniature Leaf Production

Miniature leaves were small and poorly developed, typically 5-10 mm in length, with a vascular mid-rib and peripheral achlorophyllous parenchyma as for 'normal' leaves, but with a poorly developed lamina. They correspond to and include cataphylls, and intermediate forms between these and 'normal' foliar leaves. Often 2, 3 or more miniature leaves were produced in succession and would mark the end or beginning of a leaf flush. They maintained the phyllotaxis, and often senesced prematurely leaving minute leaf scars on the stem.

Although miniature leaves were recorded for every leaf position, the frequency with which they were produced varied with position (Figure 4.12). Leaf 1 to Leaf 5 were infrequently miniature, however high frequencies (up to 0.55: 55%) of miniature leaves were seen at position L6, L7, L8; L12, L13, L14; and L21, L22, L23, L24. Where substantial stem elongation occurred during development, this began immediately after the production of a number of miniature leaves.

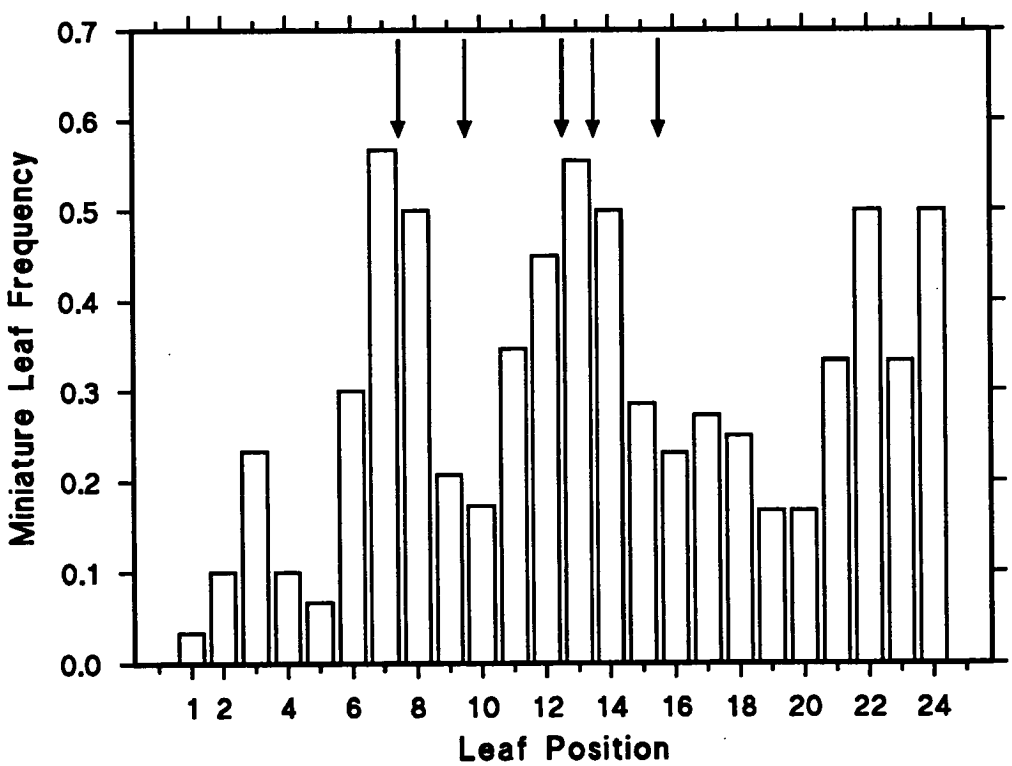


Figure 4.12 Miniature leaf frequency (open bars) at each leaf position, for a small (n=30) *K. coriacea* population sample grown under controlled conditions (*LGA*1). Arrows indicate points at which stem elongation was seen to begin. Data was provided by measurement on day 154.

4.4.3 Individual Leaf Areas

Thus leaf growth typically consisted of an initial rapid emergence of Leaf 1 and Leaf 2, followed by a flush (F2) of leaf production producing Leaf 3 to L6-L8, the latter often miniature. This was followed by a third flush (F3) of leaf growth producing leaves L7-L9 to L11-L13, possibly accompanied by stem elongation, and so on. This can be most easily seen by referring to a particularly fast growing individual (again KCS2, see also Figure 4.8), which showed 4 flushes of leaf growth during the 154 day *LGA*1 study period (Figure 4.13). KCS2 showed a pattern of increase in leaf area with leaf position typical of other *LGA*1 seedlings. Flushed leaves showed progressively larger leaf areas, a progression abruptly curtailed by the production of one or more miniature leaves, in this instance 1 (L6), 3 (L12, L13, L14) and 2 (L21, L22). The production of miniature leaves at position L6 and L7 is expressed as the delayed increase in relative leaf-area growth rate after F3 seen in Figure 4.8. F3 and F4 were accompanied by substantial elongation of the stem.

Table 4.2 describes mean individual leaf areas for *K. coriacea* seedlings grown under field and controlled conditions. Areas and accompanying coefficients of variation indicate the progressive increase in leaf areas with leaf position, mediated by the increased frequency of miniature leaves at certain leaf positions notably L6, L7, and L8. At least for Leaf 1 and Leaf 2 foliar leaf areas under field conditions were substantially reduced, and as is indicated by the high coefficients of variation were often miniature.

Table 4.2 Mean individual leaf areas for cotyledons and foliar leaves at full expansion, for *K. coriacea* seedlings grown under field (*F.C.*) and controlled conditions (*LGA*1). Each value is the mean of 17 and 30 leaves, respectively. *n.d.* indicates no data available.

Leaf	Mean Individual Leaf Area in cm^2 (coefficient of variation)			
	Field Conditions		Controlled Conditions	
C1	9.6	(24%)	7.6	(25%)
C2	9.7	(24%)	7.7	(24%)
L1	4.5	(131%)	32.1	(42%)
L2	4.9	(126%)	34.3	(46%)
L3	*n.d.*		41.2	(71%)
L4	*n.d.*		58.9	(53%)
L5	*n.d.*		74.2	(41%)
L6	*n.d.*		53.7	(96%)
L7	*n.d.*		35.4	(122%)
L8	*n.d.*		43.3	(115%)

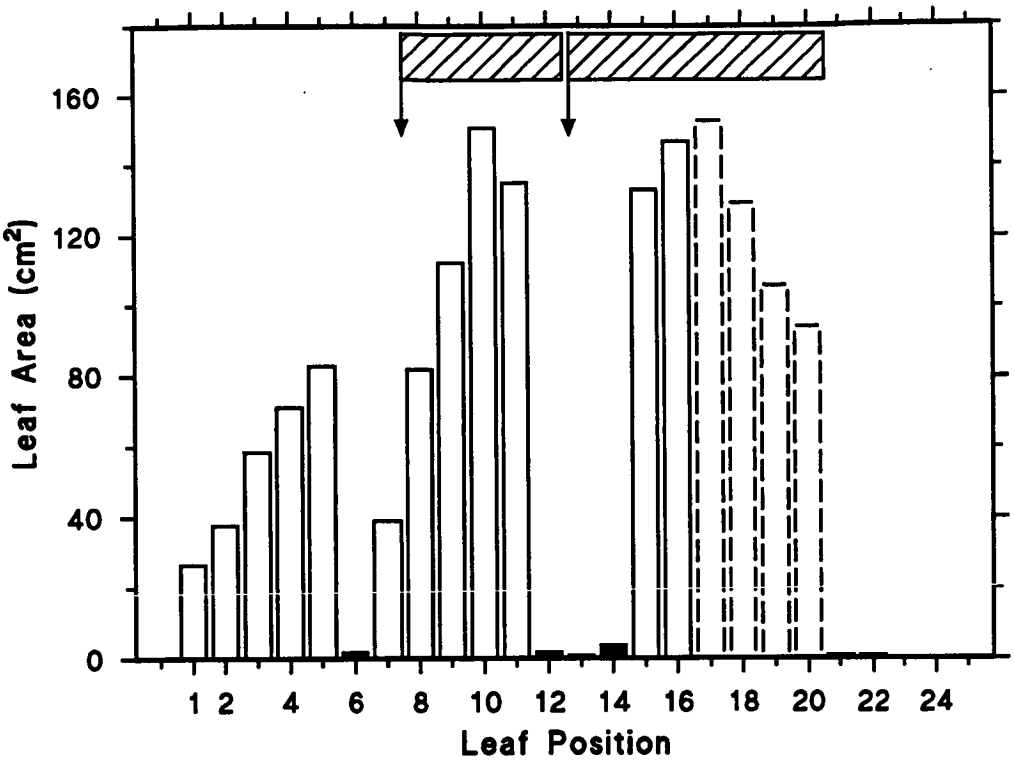


Figure 4.13 Leaf areas for successive leaf positions for KCS2, a fast growing *K. coriacea* seedling under controlled conditions (*LGA*1). Bars show fully expanded (open, solid), expanding (open, dashed) and miniature (solid filled) leaves. Arrows and hatched boxes indicate positions over which stem elongation occurred.

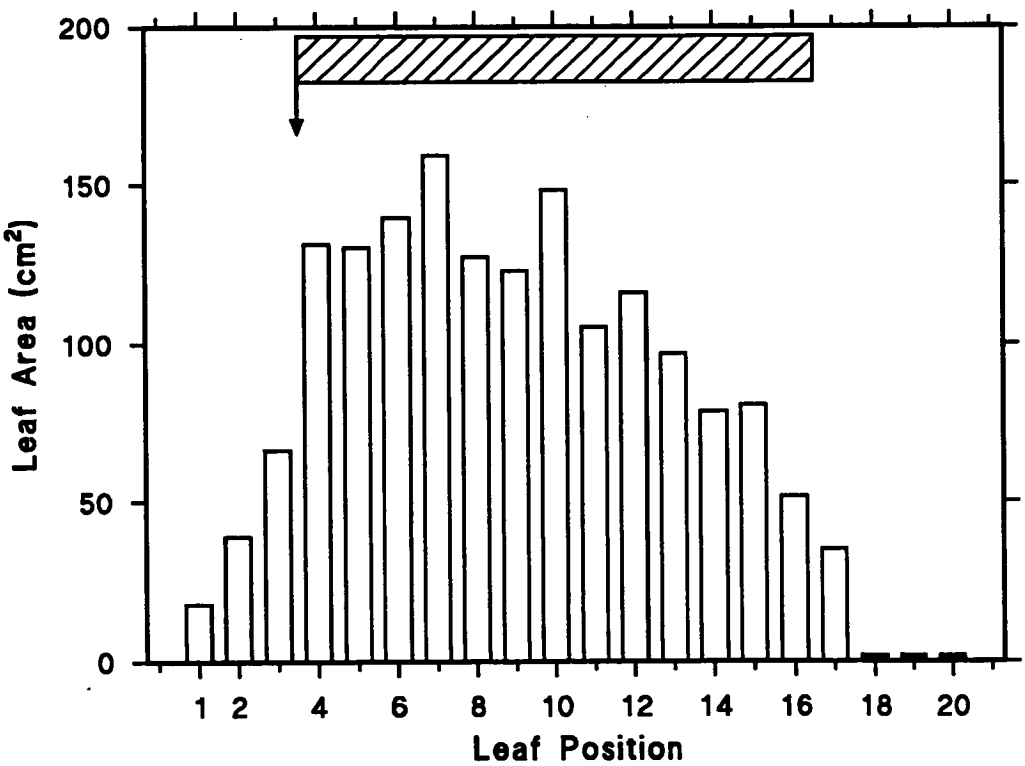


Figure 4.14 Leaf areas at successive leaf positions for KCT1, a growing tip from a *K. coriacea* tree collected in the field (17/10/91). All leaves are fully expanded, and miniature leaves are indicated as solid filled bars. Arrow and hatched box indicates positions over which stem elongation occurred.

This pattern of leaf flushing and the individual leaf areas produced shows many similarities to the seasonal growth shown by tree branch tips in the field. Figure 4.14 shows the pattern of leaf areas for KCT1 a medium sized branch tip with all leaves fully expanded. The first 3 leaves were small, however from the point of stem elongation leaf areas are large, and progressively decreased to the shoot apex. As stem elongation ceased leaves became particularly small and the tip was surrounded by a cluster of cataphylls (miniature leaves). All measured tips produced approximately 20 leaves.

4.5 Expansion of Individual Leaves

Thus, the real pattern of leaf development is a combination of flushing leaf emergence with an associated pattern of variable leaf areas at full expansion. This may be illustrated by reference to the leaf development of KCS1. Figure 4.15 shows the emergence and expansion of individual leaves, and consequent patterns of leaf number increase and mean relative leaf-area growth rate (inset, Figure 4.15) for KCS1. Cotyledon expansion began at imbibition and continued steadily to day 42. L1 and L2 emerged and began to expand from day 24 and day 27, respectively. The expansion of L1 and L2, combined with the continuing expansion of the cotyledons resulted in the maximal peak in $\mathbf{R_A}$ values from d27 to d45. A lag in leaf emergence was seen until day 45, when L3 appeared. From this point steady leaf emergence was seen, resulting in seven leaves visible by the end of the study period on day 84. In this instance Leaf 3 is miniature, and expanded to less than 0.5 cm^2. The failure of L3 to expand fully resulted in the increased depth and duration of the inter-F1/F2 trough seen in $\mathbf{R_A}$ (d45-d56). Leaf areas at full expansion increased from 27 cm^2 for L1, through L2 and L4, to 62 cm^2 for L5. The second flush of leaf growth is ended by the production of two miniature leaves, L6 and L7.

4.6 Phyllotaxis and Leaf Orientation

Concurrent with these patterns of leaf production and leaf expansion, is a change in phyllotaxis and ontogenic changes in leaf orientation. From opposite decussate positioning for the cotyledons, and Leaf 1 and Leaf 2 there is a progressive change to a spiral (3:5) phyllotaxis with increasing leaf position.

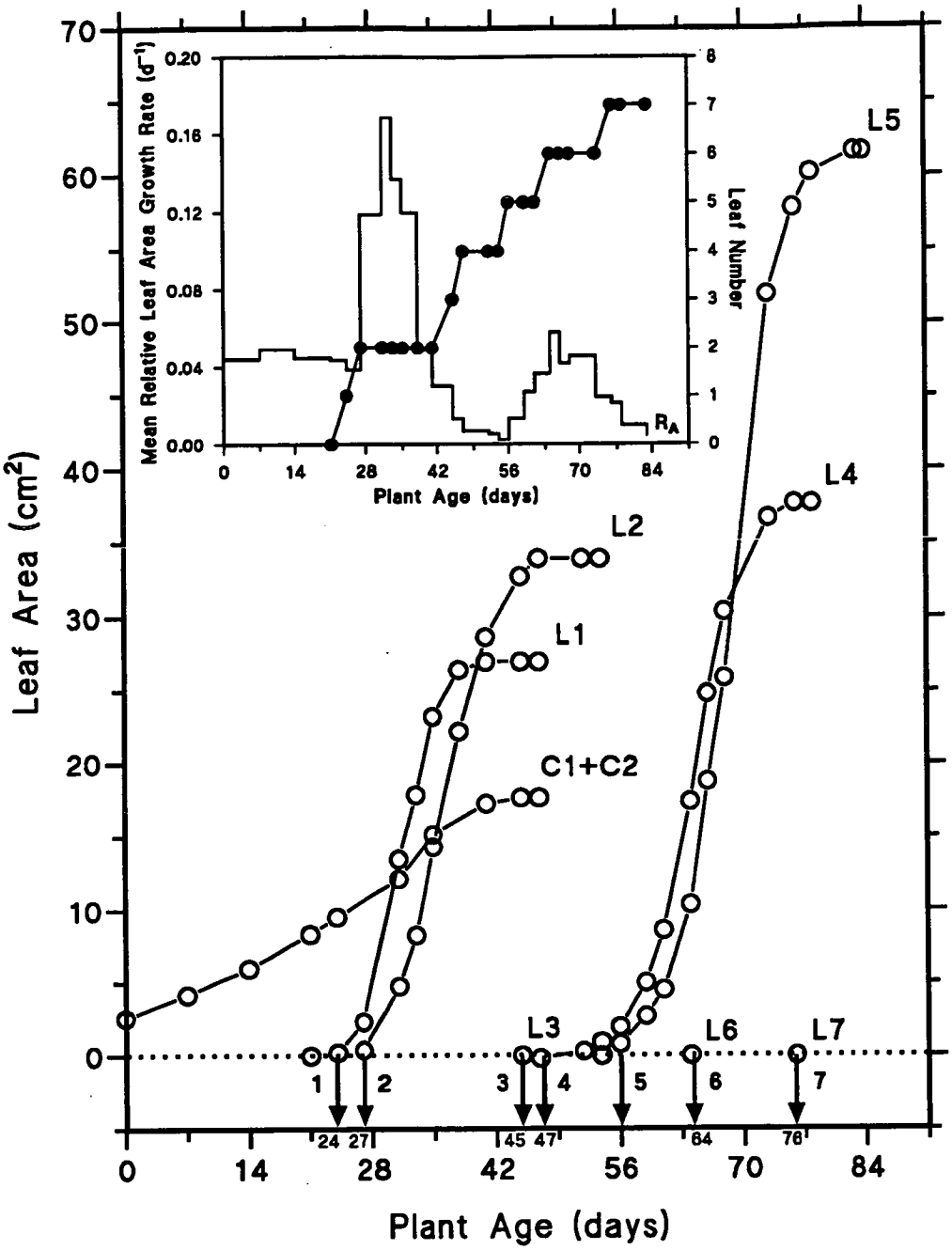


Figure 4.15 Area increase with plant age, for the cotyledons (○; C1+C2) and Leaf 1 to Leaf 7 (○; L1 to L7) of KCS1, a *K. coriacea* seedling grown under controlled conditions (*LGA*2). Arrows mark points of leaf emergence, and leaf area patterns terminate at full expansion. Leaf 3, Leaf 6, and Leaf 7 were miniature and are not displayed beyond their points of emergence.
The inset shows changes in mean relative leaf area growth rate ($\mathbf{R}_A$) and leaf number (●) with plant age for the same *LGA*2 plant.

Branch tips of *K. coriacea* trees had a regular spiral (3:5) phyllotaxis. Figure 4.16 shows the angular displacements between successive leaves for seedlings grown under controlled conditions. Angular displacement between C1 and C2, and C2 and L1 is clearly opposite decussate. Angular displacements between L2 and L3, L3 and L4, and so on, progressively approach that of a spiral phyllotaxis, 137.15°. Residual angles between C1 and C2, and C2 and L1 are not significantly ($p<0.05$) different from that of opposite decussate phyllotaxis. Residuals between L2-L3, L3-L4 and so on, and a spiral phyllotaxis, progressively decrease.

Figure 4.18 shows schematic plan and side view diagrams describing phyllotaxis and leaf orientations at successive developmental stages for *K. coriacea* seedlings grown under controlled conditions. With increasing age all leaves assume elevations progressively closer to the horizontal. This allows the physical accumulation of numerous leaves without stem elongation, and reduces self-shading. Thus by the end of F2, with L6/L7 emerged, leaves effectively occupy a hemisphere about the shoot apex (Figure 4.18 (d)).

4.7 Effect of Nutrient Feeding

Figure 4.17 shows the effects of nutrient feeding on leaf development for *K. coriacea* seedlings grown under field conditions. Nutrient applications were at the rate of 25 cm^3 full-strength Hoaglands solution per week from the beginning of Leaf 1 emergence on day 42. Feeding significantly ($p<0.05$) increased leaf-area within 21 days, as a result of both a significant ($p<0.05$) increase in leaf number, and mean individual leaf area (calculated as Leaf-Area/Leaf Number).

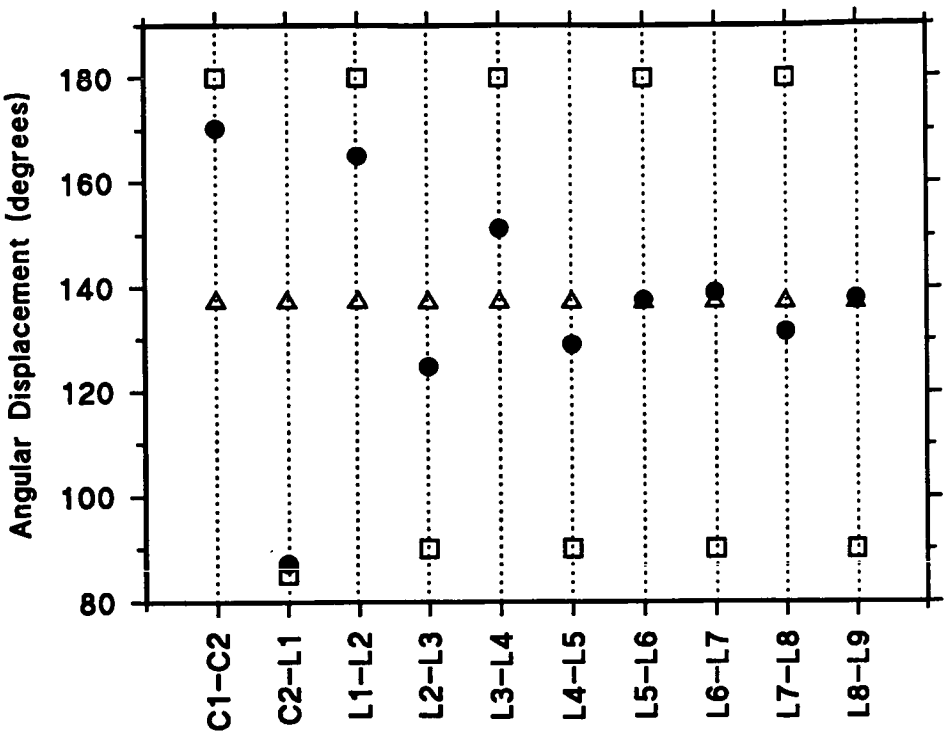


Figure 4.16 Angular displacement between successive leaves for *K. coriacea* seedlings grown under controlled conditions (●; *LGA2*), each point is the mean of 8 replicates. Cotyledons (C1 and C2), and Leaf 1 to Leaf 9 (L1-L9). Open squares and triangles mark the values for theoretical opposite decussate and spiral (3:5) phyllotaxis, respectively.

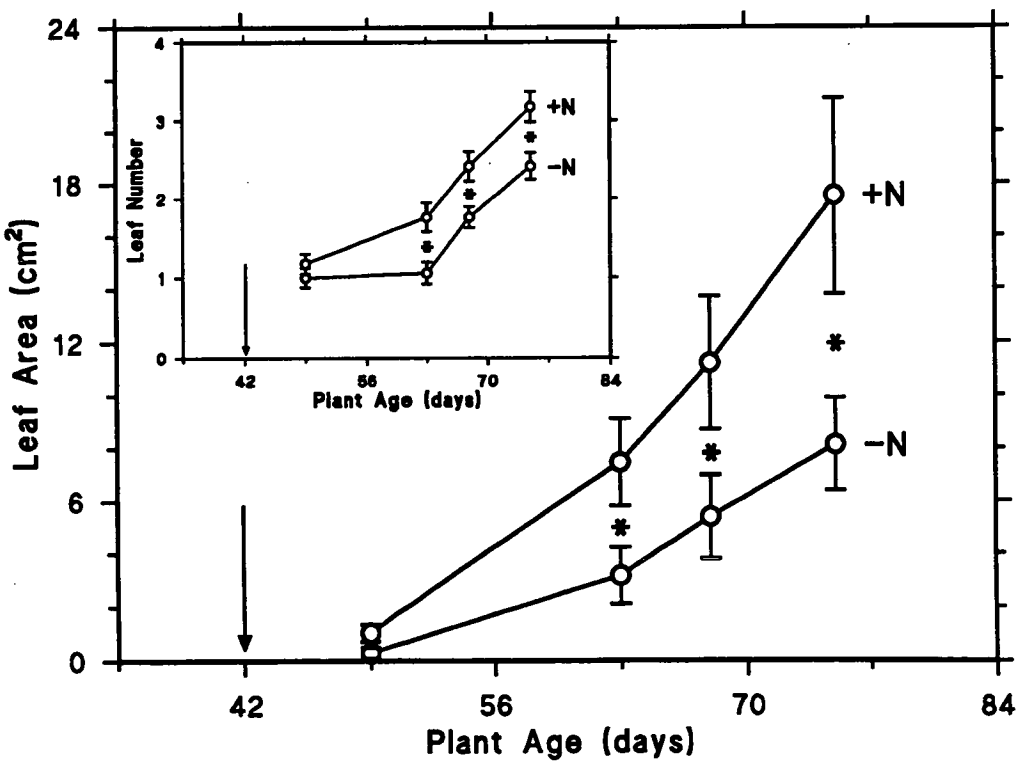


Figure 4.17 Effect of nutrient feeding (+N) to increase in leaf-area and leaf number (inset) for *K. coriacea* seedlings grown under field conditions. * indicates significant ($p<0.05$) difference between control (-N) and treatment (+N). Arrow indicates starting point of weekly nutrient feeding (25 cm^3 full strength Hoaglands solution per week).

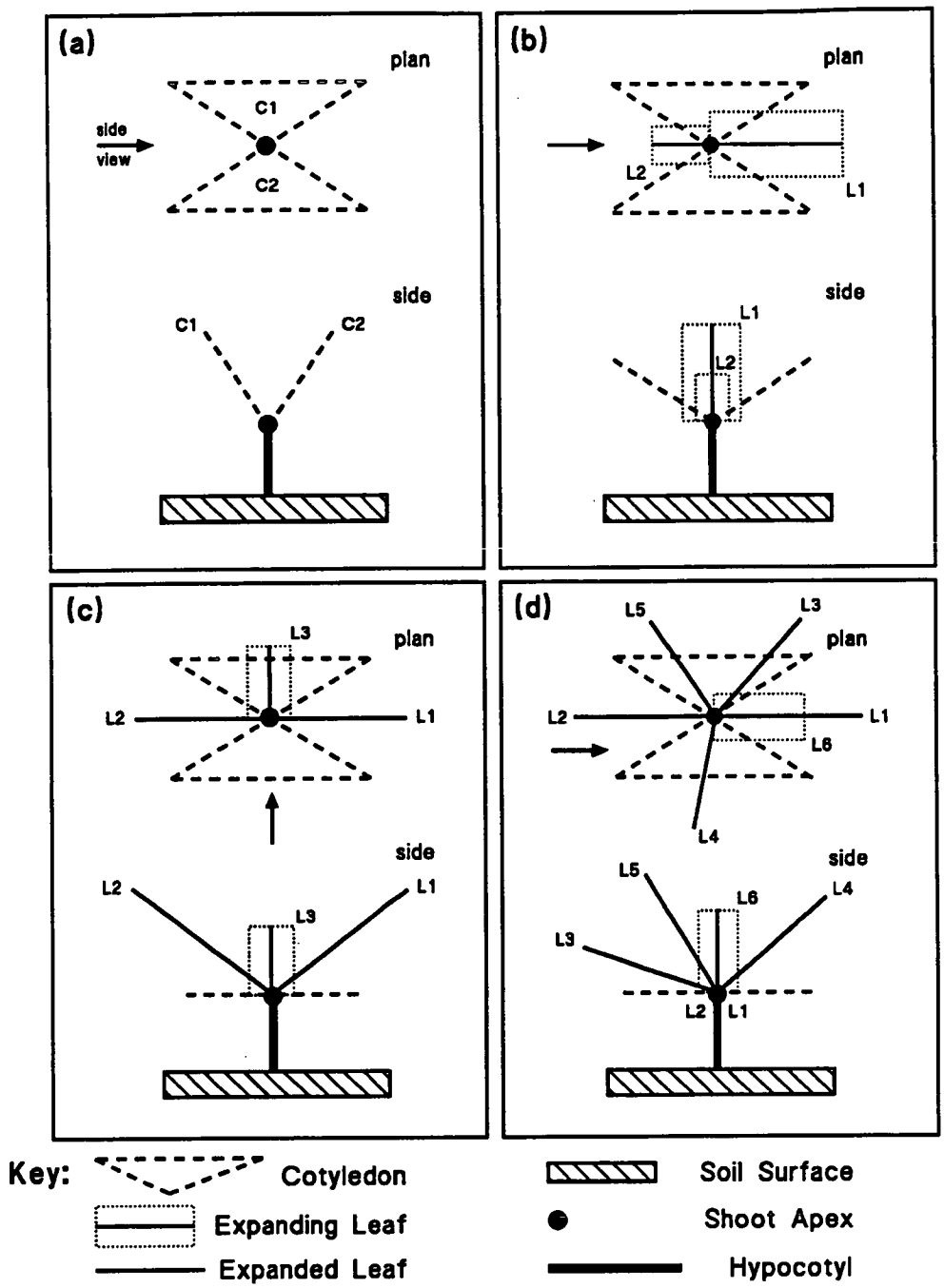


Figure 4.18 Schematic plan and side view diagrams showing phyllotaxis and leaf orientation at succesive developmental stages, for *K. coriacea* seedlings grown under controlled conditions (*LGA2*). Plan and side views show approximate phyllotaxis and leaf orientations (elevations), respectively. Arrows on plan views indicate side view perspectives.

(a) Day 21, expanding cotyledons opposite decussate, raised, and separate, although at an acute angle.

(b) Day 35, angle of separation between cotyledons increases as Leaf 1 and Leaf 2 expand near vertically, in an opposite decussate phyllotaxis.

(c) Day 50, cotyledons horizontal, Leaf 1 and Leaf 2 fully expanded and inclined at approximately 45° to horizontal; Leaf 3 expanding near vertically as first leaf in spiral phyllotaxis.

(d) Day 84, Leaf 1 and Leaf 2 horizontal; Leaf 3-Leaf 5 fully expanded in spiral phyllotaxis; Leaf 6 expanding near vertically. Leaves inclined at steeper angles with increasing leaf position.

4.8 Discussion

Leaf-area development under controlled conditions is irregular. Averaging the population sample data for leaf-area and its components obscures this irregularity beyond the emergence Leaf 1 and Leaf 2. This irregularity is a consequence of an irregular leaf emergence rate (Figure 4.7 and Figure 4.8), and variable individual leaf areas at full expansion (Table 4.2). Leaf emergence occurs in distinct flushes typically involving the emergence of L1-L2 (F1), L3-L7 (F2), L8-L11 (F3), and L12-L21 (F4) (Table 4.1). Periods of stem elongation are occasionally associated with the latter two leaf flushes (Figure 4.8). Leaf emergence is associated with a flushing pattern of primordia production. The areas of expanded leaves broadly increase with increasing leaf position, but decline at the end of leaf flushes, with the production of miniature leaves (Figure 4.13). Leaf areas during a flush show a pattern similar to that seen for the growing tips of trees in the Cerrado (Figure 4.14). Multiple leaf flushing has similarly been recorded for tree growing tips in the field (Arasaki pers. com., 1992).

Under field conditions leaf-area development, after cotyledon expansion, is very slow (Figure 4.3). This is because of a later commencement of slower leaf emergence (Figure 4.5), and smaller individual leaf areas at full expansion (Table 4.2). Slow leaf emergence is associated with slow leaf primordium formation at the shoot apex (Figure 4.9).

Table 4.3 Mean individual leaf areas for L1-L5 ($A_{iL1\text{-}5}$), leaf emergence rates ($1/p$), and calculated absolute leaf-area growth rates (G_A) for *K. coriacea* seedlings, grown under controlled and field conditions. $A_{iL1\text{-}5}$ for field conditions is estimated assuming a proportional increase in individual leaf area after L1 and L2 as for controlled conditions. Bracketed percentages (*i.e.* *(-82%)*) indicate proportional contributions to changes in G_A as compared with controlled conditions.

Conditions	$A_{iL1\text{-}5}$ (cm^2)	$1/p$ (d^{-1})	G_A ($cm^2\ d^{-1}$)
Controlled Conditions	48.1	0.1136	5.46
Field Conditions	6.8 *(-82%)*	0.0806 *(-18%)*	0.55

Table 4.3 shows mean individual leaf areas ($A_{iL1\text{-}5}$) for Leaf 1 to Leaf 5 and leaf emergence rates ($1/p$) for the period of L1 to L5 emergence, and calculated mean absolute leaf-area growth rates (G_A) for seedlings grown under controlled and field conditions. $A_{iL1\text{-}5}$ under field conditions is an estimation based upon L1 and L2 areas at full expansion and a proportional increase in area as for controlled conditions (Table 4.2). The calculated G_A value for controlled conditions (5.46 $cm^2\ d^{-1}$)

compares well with the value found for *LGA*1 of 5.25 $cm^2 d^{-1}$. The substantially reduced individual leaf areas under field conditions are the prime cause of reduced leaf-area development, accounting for 82% of the difference in G_A as compared with only 18% due to a slower leaf emergence rate.

Nutrient feeding under field conditions confirms that the reduction in leaf-area development under field conditions is, at least in part, nutritionally determined. Proportional contributions to the differences seen in leaf-area show (Table 4.4), that individual leaf area is predominantly (64%) responsible for the reduction in leaf-area development, slower leaf emergence responsible for only 36% of the variation.

Table 4.4 Plant leaf-areas (L_A), leaf numbers (N_L) and mean individual leaf areas (A_i) for *K. coriacea* seedlings provided with (+N) and without (-N) nutrient feeding under field conditions. Data for 75 day old seedlings. Bracketed percentages (*i.e.* *(-36%)*) indicate proportional contributions to differences in leaf-area as compared with treated (+N) seedlings.

Treatment	L_A (cm^2)	N_L	A_i (cm^2)
Field Conditions +N	17.53	3.18	5.52
Field Conditions -N	8.15	2.41 *(-36%)*	3.38 *(-64%)*

The rapid emergence and expansion of Leaf 1 and Leaf 2 up to full expansion towards day 56 (see section 4.2.1), is associated with the high allocation of biomass to foliar leaf development up to day 54 (phase *a*; see section 3.4.4, and Figure 3.18). The transition to the phase of lower biomass partitioning for foliar development (phase *b*), is coincident with the lag phase between the first and second flushes of leaf emergence (F1 and F2, respectively), and a change in phyllotaxis.

Although proportionally more dry weight is partitioned to root than shoot development (see section 3.4.2), leaf-area production is maximised through minimal accompanying stem development (see section 3.2), leading to high leaf-area to shoot dry weight ratios (L_A:W_S). However, this developmental pattern may only proceed and remain efficient, to the point at which the benefits of high L_A:W_S out-weigh the limitations of increasing self shading and super-optimal leaf area index. The potential effects of increasing self shading in *K. coriacea* are reduced by a change in phyllotaxis, and leaf orientation with increasing developmental stage (Figure 4.16 and Figure 4.18). This transition from opposite decussate (C1-C2, L1-L2) to spiral (L3+) phyllotaxis is common to most dicotyledenous species (Schwabe, 1984), and may be achieved through a slight delay in the timing of leaf primordium production (Chapman and Perry, 1987; Chapman, 1988). The cruciform positioning of C1-C2, L1-L2

produces little if any self-shading, however a continuation thereafter would lead to substantial self-shading of alternate leaf pairs (L3-L4 to C1-C2, L5-L6 to L1-L2, and so on). This effect is reduced by a transition to a spiral phyllotaxis, and effective use of the hemisphere above the shoot apex by increasing leaf elevation (to the horizontal) with increasing leaf position. With this combination of phyllotaxis, L6 is the first leaf to lie directly above another (L1). It may be significant that from this point, the end of F2, that subsequent leaf flushes (F3, F4) are known to be accompanied by stem elongation. In addition, in the field *K. coriacea* seedlings typically form up to six leaves during the first growing season (Oliveira, 1986; Arasaki, pers. com., 1992).

Table 4.5 Mean plastochrons and phyllochrons for *K. coriacea* seedlings grown under controlled and field conditions. Data for controlled condition grown seedlings was taken from two leaf growth analyses (*LGA*1 and *LGA*2), and a primordium number analysis (*PNA*1). See section 4.3.2, and Figure 4.5 and Figure 4.6 for an explanation of the *phases* of leaf emergence. Data for field condition grown seedlings was taken from a functional growth analysis (*F.C.*), and a primordium number analysis (*PNA*2). *n.d.* indicates no data available.

Conditions and Experiment	Plastochron (d)	Phyllochron (d)
Controlled Conditions		
*PNA*1	7.2	*n.d.*
*LGA*1 (study period mean)	*n.d.*	8.7
Phase 1b	*n.d.*	15.3
Phase 2	*n.d.*	8.2
*LGA*2 (study period mean)	*n.d.*	8.8
Phase 1a	*n.d.*	4.0
Phase 1b	*n.d.*	16.8
Phase 2	*n.d.*	8.1
Field Conditions		
*PNA*2	16.4	*n.d.*
F.C.	*n.d.*	12.4

Table 4.5 shows mean plastochrons and phyllochrons for *K. coriacea* seedlings grown under controlled and field conditions. Mean phyllochrons under controlled conditions were 8.7 d and 8.8 d (*LGA*1 and *LGA*2, respectively), similar to the mean leaf plastochron from germination of 7.2 d. This, taking into account the Leaf 1 primordium present in the seed (Plate 4.1) and the earlier commencement of primordia formation, suggests an approximately constant number of unemerged leaf primordia at the shoot apex, of just over 3. As was shown by the leaf primordium number analysis (*PNA*1; see section 4.3.4, and Figure 4.10), seedlings maintain an approximately constant number of 4 unemerged leaf primordia at the shoot apex from the point of two emerged leaves. The phyllochron lag phase, '*Phase 1b*', may be due to the primordium production delay required to achieve the change in phyllotaxis at this stage, the L2 to L3 transition (Chapman, 1988). Indeed the unexplained pattern of

*PNA*1 data up to L2 emergence (Figure 4.10), may be accounted for by the slow formation of the L3 primordium.

Under field conditions leaf plastochron slightly exceeds phyllochron but because of the Leaf 1 primordium present within the seed and the particularly late commencement of leaf emergence under field conditions (*ca.* d41), there is only a very slow decrease in unemerged leaf primordium number at the shoot apex, 2 still present at day 70.

Periodic (or episodic) rather than continuous growth is almost universal among trees (Zimmermann and Brown, 1971), and flushing growth has been reported for seedlings of temperate (*Quercus* and *Pinus*), and tropical species (*Hevea* and *Theobroma*) (Hallé and Martin, 1968; Greathouse *et al.*, 1971; Borchert, 1975; Vogel, 1975; Drew and Ledig, 1980; Reich *et al.*, 1980; Hanson *et al.*, 1986). The pattern of rhythmic growth seen in *K. coriacea* under constant environmental conditions indicates an endogenous growth periodicity. The pattern of developmental changes occurring in *K. coriacea* is also seen in *Hevea brasiliensis*, and most temperate and tropical trees (Hallé and Martin, 1968). The alternation between periods of rest and growth of the apical meristem, and also the reversible transition between fully developed foliar leaves and reduced leaf organs, such as the miniature leaves, is unique to this *Hevea*-type of development (Borchert, 1991). The flushing of leaf primordium formation is essentially synchronous with leaf emergence, resulting in the approximately constant number of unemerged leaf primordia at the shoot apex (Figure 4.10). Thus, unlike the initiation of leaf primordia in tea (*Camellia thea*), which is reported to be constant despite leaf flushing (Bond, 1945), and in *Callestemon viminalis*, which is reported to be periodic but out of phase with leaf flushing (Purohit and Nanda, 1968), the periodic and in phase primordium formation in *K. coriacea* is similar to that reported for *Theobroma cacao* (Greathouse *et al.*, 1971). It has been suggested that internal water deficits resulting from an unbalanced root:shoot ratio are the physiological basis for the arrest of shoot growth during periodic growth, which is therefore not genetically determined (Borchert, 1978; Borchert, 1991).

Table 4.6 shows leaf-areas and leaf-area growth rates for *K. coriacea* and *Qualea grandiflora* Mart. (Vochysiaceae) seedlings grown under controlled and field conditions. Under field conditions leaf-areas for *K. coriacea* and *Qualea grandiflora* are broadly similar, and relatively low. Both show minimal foliar leaf development after cotyledon expansion, and rely heavily on the area contribution of these organs to

at least 100 days. This limited foliar leaf growth is not a result of poor inherent potential, at least in *K. coriacea*, which under favourable controlled conditions shows very substantial leaf-areas by day 100, and even day 63. The apparently low potential of *Q. grandiflora* for improved leaf-area development under these controlled conditions may be the result of specific nutrient-deficiencies or toxicities, under these nutritionally favourable conditions (see section 1.5).

Table 4.6 Leaf-areas at day 63 and day 100 (L_A^{d63} and L_A^{d100}, respectively), absolute leaf-area growth rates (G_A), and relative leaf-area growth rates (R_A) for *K. coriacea* and *Qualea grandiflora* Mart. seedlings grown under controlled (*C.C.*) and field (*F.C.*) conditions.

Species	L_A^{d63} (cm^2)	L_A^{d100} (cm^2)	G_A ($cm^2\ d^{-1}$) d63/d100	R_A (d^{-1}) d63/d100
K. coriacea (*F.C.*)	30	34[c]	1.42/0.0[c]§	0.044/0.0[c]§
Q. grandiflora[a] (*F.C.*)	21.3	40.2	0.55/0.0§	0.022/0.0§
K. coriacea (*C.C.*)	125	400	3.21/8.23	0.042/0.016
Q. grandiflora (*C.C.*)	16.0[a]/18.2[b]	21.0[b]	0.24[b]/0.09[b]	0.015[b]/0.004[b]

§ data of Arasaki and Paulilo indicate a decrease in leaf-area, which in view of the large degree of variation in the data is assumed to approximate to zero.
[a] Paulilo (1991)
[b] Felippe and Dale (1990)
[c] Arasaki (1988)

Table 4.7 indicates specific growth rates (**R**), leaf-areas, absolute leaf-area growth rates, relative leaf-area growth rates (R_A), and **R**:R_A ratios, for a selection of temperate and subtropical/tropical woody species. As was noted in section 3.5, variation in specific growth rate for this same selection of species is attributable to a more than 6-fold variation in leaf area ratios. Variation in relative leaf-area growth rate is of a similar magnitude. Considering three species with similar leaf-areas at the beginning of the harvest interval, *Pinus sylvestris*, *K. coriacea* and *Populus tremula*, specific growth rate positively correlates with absolute leaf-area growth rate. This correlation is associated with a similar pattern of increasing leaf area ratios for these species, 0.0044 $m^2\ g^{-1}$, 0.0109 $m^2\ g^{-1}$, and 0.0226 $m^2\ g^{-1}$, respectively (Table 3.4). Thus, the high leaf area ratios, which are associated with high specific growth rates, are maintained by high rates of leaf-area growth.

Table 4.7 Specific growth rates (**R**), leaf-areas at beginning of harvest interval (L_A), absolute leaf-area growth rates (G_A), and relative leaf-area growth rates (R_A) for *K. coriacea* and *Picea abies* (L.) Karsten, *Pinus sylvestris* L., *Khaya senegalensis* (Desv.) A. Juss., *Khaya ivorensis* A. Chev., *Quercus rubra* L., *Betula verrucosa* Ehrh., *Populus tremula* L., *Ceiba pentandra*, *Terminalia ivorensis* seedlings grown under favourable conditions.

Species	**R** (d^{-1})	L_A (cm^2)	G_A (cm^2d^{-1})	R_A (d^{-1})	**R**:R_A
Pic. abies[a]	0.005	17.4	0.02	0.0011	4.5
Pin. sylvestris[a]	0.019	62	0.6	0.0081	2.3
Kh.senegalensis[b]	0.026	123	1.9	0.0109	2.4
Kh. ivorensis[b]	0.027	86	1.7	0.0131	2.1
Q. rubra[c]	0.050	200	8.0	0.0343	1.5
K. coriacea	0.054	71	2.5	0.0352	1.5
B. verrucosa[a]	0.067	108	5.9	0.0367	1.8
P. tremula[a]	0.078	76	9.1	0.0611	1.3
C. pentandra[d]	0.080	320	37.4	0.0590	1.4
T. ivorensis[d]	0.097	49	7.6	0.0600	1.6

[a] Jarvis and Jarvis (1964)
[b] Okali and Dodoo (1973)
[c] Farmer (1980)
[d] Okali (1971)

As would be expected for the cyclical nature of specific growth rate and relative leaf-area growth rate, **R** and R_A closely correlate for this selection of woody species (Table 4.7). In all cases **R** exceeds R_A. Assuming a constant specific leaf area, if leaf weight ratio remains constant, **R** will equal R_A. Assuming specific leaf area remains constant is not unreasonable under constant environmental conditions, particularly with respective to light intensity and nitrogen availability to which SLA is most sensitive (Dijkstra, 1990). Therefore **R**:R_A values greater than 1 reflect the ontogenic decline in leaf weight ratio. In this context *K. coriacea* has a **R**:R_A ratio comparable to species with similar (*Quercus*) and higher (*Betula* and *Terminalia* sp.) specific growth rates. It is note worthy that those coniferous and *Khaya* species, which have low specific growth rates, have distinctly high **R**:R_A ratios.

Chapter 5

Photosynthesis of *Kielmeyera coriacea* Mart. Seedlings

5.1 Introduction

This chapter describes the results of photosynthetic analyses conducted on *Kielmeyera coriacea* Mart. seedlings grown under controlled and field conditions. The aim of these analyses was to investigate photosynthesis under 'natural', and very favourable conditions, and thereby consider environmental and inherent limitations to carbon-assimilation. This follows on from the discussion of ontogenic changes in unit leaf rate in section 3.5. Objectives were: (1) to determine the changes in net photosynthetic rate (P_n) with time for individual leaf organs under controlled and field conditions §; (2) to determine the changes in carbon assimilatory capacity of individual plants, and to relate these to unit leaf rates; and (3) to determine the limitations of photosynthetic sub-processes to net photosynthetic rate. (§ As every leaf of a plant may contribute fixed carbon for growth, assessments of the contribution of each leaf to the total plant carbon-assimilation are required to estimate accurately the total CO_2 exchange capacity of the whole plant (Chartier and Catsky, 1975). As established by Hodáňová (1981), ontogenic patterns of individual leaves cannot be correctly inferred from simultaneous measurements of many leaves at different stages of development.)

The delicate nature of the young leaves of *K. coriacea* seedlings, and particularly the cotyledons, prevented continuous non-destructive measurement of photosynthetic performance (net photosynthetic rate, stomatal conductance (g_s), and intercellular CO_2 concentration (c_i)). Consequently, photosynthetic performance for seedlings grown under controlled conditions was determined in the growth room on material destined for harvesting for growth analysis (*C.C.*1 and *C.C.*2). This allowed direct comparison between growth analysis and photosynthetic performance data. Photosynthetic performance for field grown seedlings was not determined on growth analysis material (*F.C.*), but on material from a separate experiment (*F.C.*2). However, *F.C.*2 material harvested immediately after photosynthetic measurement, was not significantly different ($p<0.05$), for total dry weight and plant leaf-area, from the respective material of the field growth analysis experiment (*F.C.*). Consequently growth analysis and photosynthetic data under field conditions have also been directly compared.

5.2 Assimilatory Organ Net Photosynthetic Rates

5.2.1 Introduction

All photosynthetic measurements were made using a portable ADC LCA-2 Infra-Red Gas Analyser, except for a small number of light response curves, *i.e.* changes in net photosynthetic rate with incident photosynthetic photon flux density ($PPFD_i$), and P_n/c_i curves, *i.e.* changes in net photosynthetic rate with intercellular CO_2 concentration. The latter were made using a M10 URAS Infra-Red Gas Analyser System, located in the Institute of Ecology and Resource Managment University of Edinburgh, under defined growth room conditions (air temperature 30°C; relative humidity 70%; ambient CO_2 concentration 350 μmol m^{-2} s^{-1} (or variable); incident photosynthetic photon flux 350 μmol m^{-2} s^{-1} (or variable)).

In the field, net photosynthetic rates were measured under a range of environmental conditions, particularly with respect to incident photosynthetic photon flux. Selected data sets (air temperatures 24-32°C, and ambient CO_2 concentrations 340-400 μmol m^{-2} s^{-1}) were used to determine the response of net photosynthetic rate to incident photosynthetic photon flux for different leaves. Scatter diagrams of these data sets (Figure 5.5, Figure 5.6, and Figure 5.7) have been used to determine light saturating net photosynthetic rates under what are favourable conditions, *i.e.* values approximating to photosynthetic capacities. Photosynthetic capacity (P_c) is defined as the net rate of CO_2 exchange (on an area basis) measured under near-optimal conditions (*i.e.* saturating light intensity, near-optimum temperature and low vapour pressure deficit), except with CO_2 and O_2 concentrations at normal atmospheric levels (Larcher, 1961; Ceulemans and Saugier, 1991).

5.2.2 Photosynthesis under Controlled Conditions

5.2.2.1 Net Photosynthetic Rates under Controlled Conditions

Soon after emergence cotyledons were sufficiently separated and expanded to allow photosynthetic measurement. Figure 5.1 shows changes in net photosynthetic rate with plant age for the cotyledons of *K. coriacea* seedlings grown under controlled conditions.

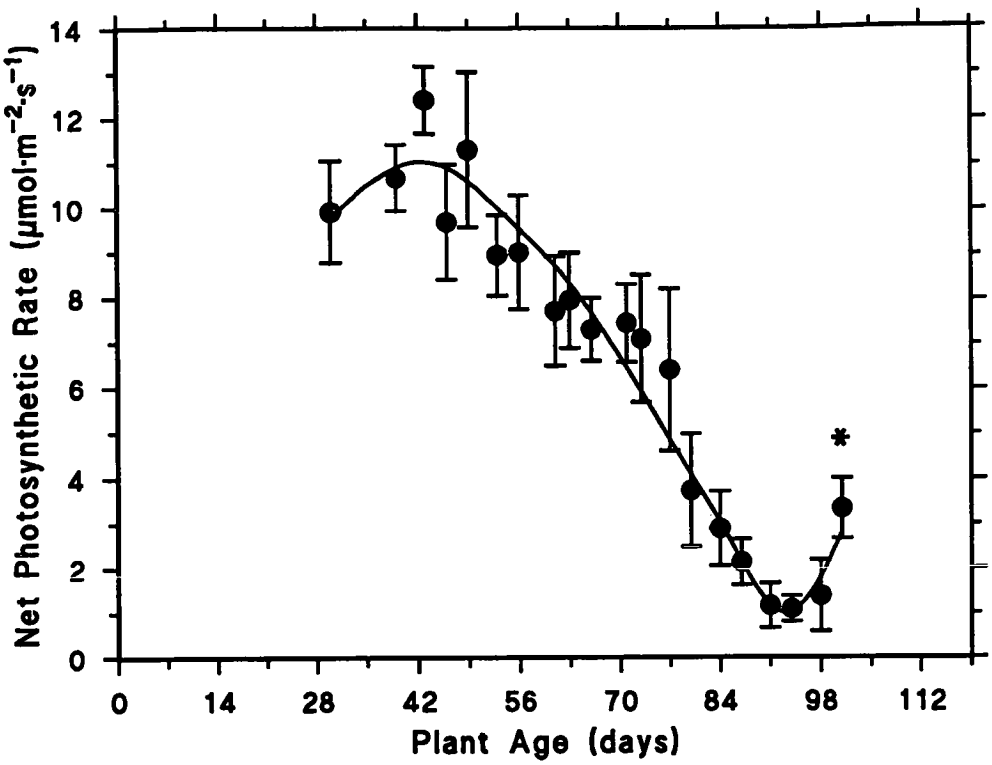


Figure 5.1 Relationship between net photosynthetic rate and plant age for the cotyledons of *K. coriacea* seedlings grown under controlled conditions (*C.C.*1). Points are means of 8 replicates, with bars indicating standard errors of the mean. A free-hand curve describes the *C.C.*1 data. * indicates a value significantly ($p<0.05$) different from previous two values.

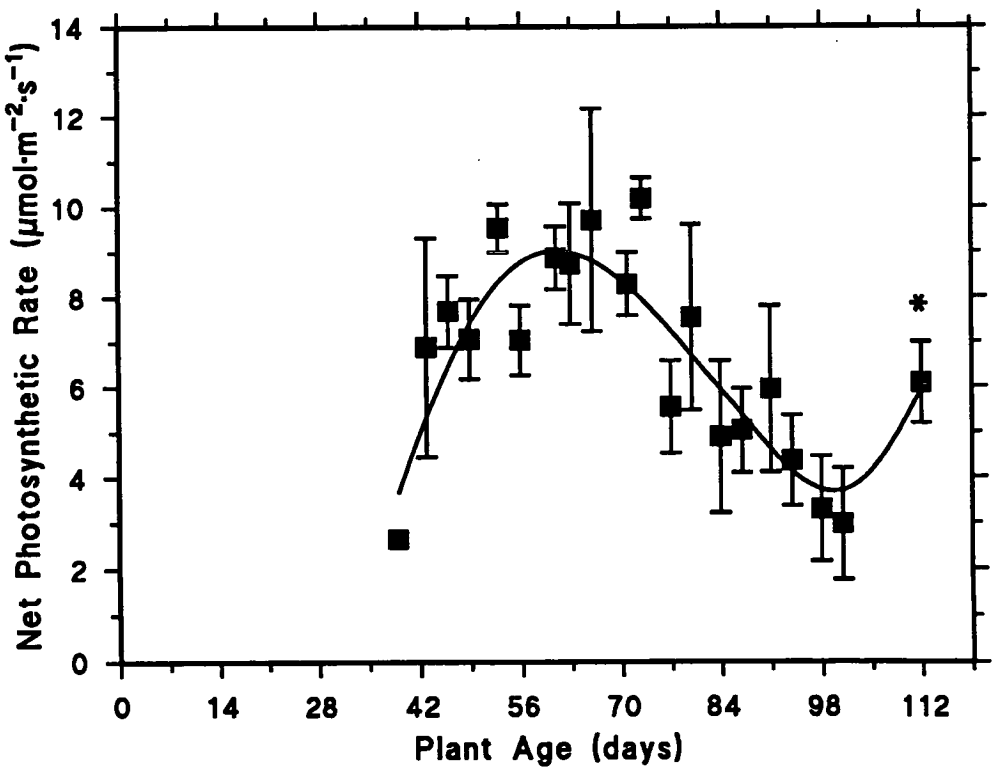


Figure 5.2 Relationship between net photosynthetic rate and age for Leaf 1 of *K. coriacea* seedlings grown under controlled conditions (*C.C.*1). Points are means of 4 replicates, bars indicate standard errors of the mean. A free-hand curve describes the *C.C.*1 data. * indicates a value significantly ($p<0.05$) different from previous two.

The large fleshy cotyledons were the first photosynthetically active leaf organs, and maintained positive net photosynthetic rates to the end of the study period on day 112. Initial net photosynthetic rates (d30) were high at 10.0 μmol m^{-2} s^{-1}, and increased to a peak value of 11.0 μmol m^{-2} s^{-1} between day 42 and day 49, thereafter steadily declining to 1.0 μmol m^{-2} s^{-1} by 95 days. Both cotyledons showed similar photosynthetic performances, in terms of P_n, stomatal conductance, and intercellular CO_2 concentration, unless substantially different in area or shape.

Figure 5.2 shows changes in net photosynthetic rate with plant age for Leaf 1 of *K. coriacea* seedlings grown under controlled conditions. Net photosynthetic rates increased rapidly during expansion, reaching a peak value of 8.9 μmol m^{-2} s^{-1} around full leaf expansion on day 60. Thereafter values steadily declined to 4.0 μmol m^{-2} s^{-1} by day 98.

This asymmetrical pattern of P_n was also seen for Leaf 2 and Leaf 3. Peaks for these successive leaves were sequential and declined in magnitude with progressive leaf position, that is, Leaf 1 peaked earlier and higher than Leaf 2, which peaked earlier and higher than Leaf 3 (Table 5.1). The peak in photosynthetic rate for the cotyledons was higher and well in advance of those of the foliar leaves (L1, L2, and L3), which followed in a rapid overlapping succession. There appeared to be a common decline in P_n towards day 100 for the cotyledons, L1, L2, and L3. All these leaves showed increases in P_n after d100, to P_n levels previously seen around day 84. These increases were significant ($p<0.05$) for the cotyledons and Leaf 1 (Figure 5.1 and Figure 5.2).

Table 5.1 Magnitude and timing of peaks in net photosynthetic rate (P_n) for assimilatory organs of *Kielmeyera coriacea* seedlings grown under controlled conditions (*C.C.*1). Area data taken from Table 4.2.

Assimilatory Organ	Peak P_n Value (μmol m^{-2} s^{-1})	Area (cm^2)	Plant Age (d)
Cotyledons	11.0	15.3	42
Leaf 1	8.9	32.1	60
Leaf 2	7.2	34.3	68
Leaf 3	7.0	41.2	80

5.2.2.2 Light Response and P_n/c_i curves under Controlled Conditions

Light response and P_n/c_i curves were determined for several foliar leaves at around full expansion, and therefore around the point of maximum net photosynthetic rate, for seedlings grown under controlled conditions (Figure 5.3 and Figure 5.4).

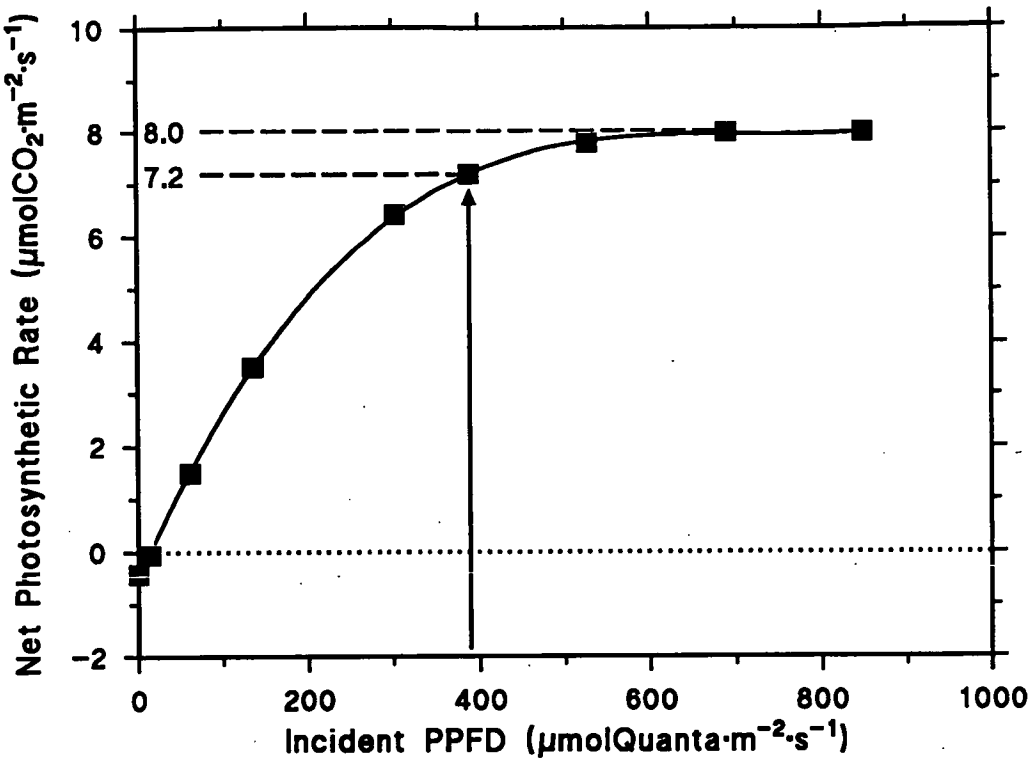


Figure 5.3 Relationship between net photosynthetic rate (P_n) and incident photosynthetic photon flux density ($PPFD_i$), for1Leaf 1 of a day 68 *K. coriacea* seedling grown under controlled conditions (*C.C.*1). The data was measured under defined growth room environmental conditions (section 5.2.1). The arrow indicates growing PPFD, with lines (- - -) marking corresponding, and light saturating P_n.

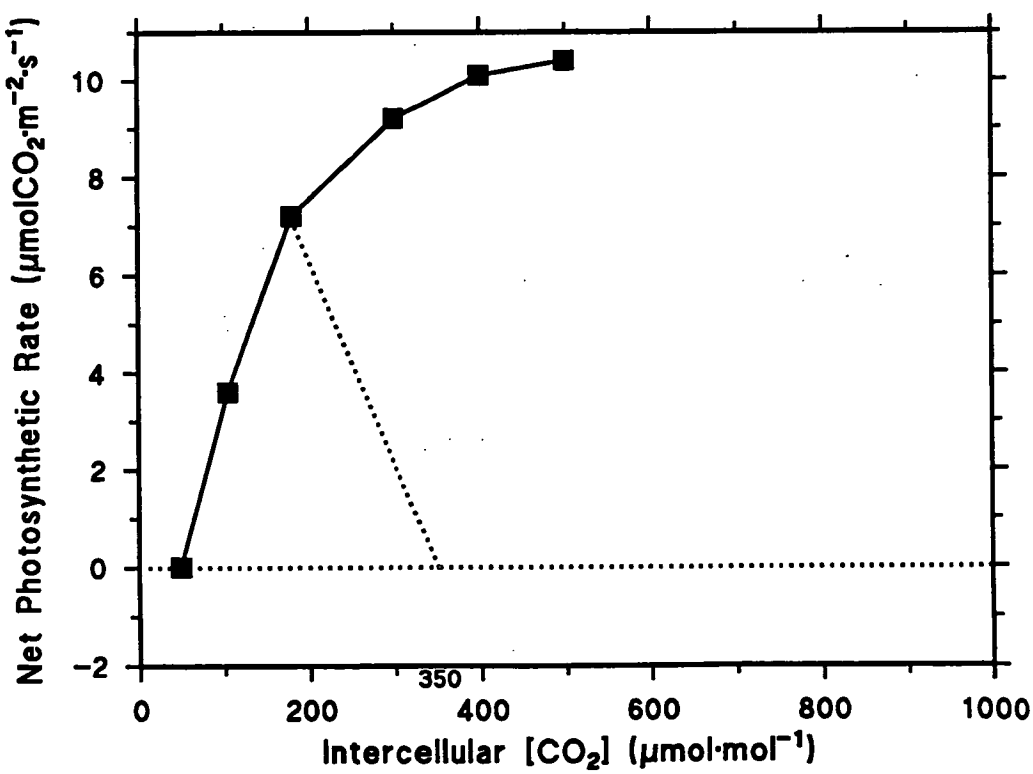


Figure 5.4 Relationship between net photosynthetic rate (P_n) and intercellular CO_2 concentration, for1Leaf 1 of a day 68 *K. coriacea* seedling grown under controlled conditions (*C.C.*1). The data was measured at light saturation, and under defined growth room conditions for air temperature and relative humidity (section 5.2.1).

These indicated variations in light saturating P_n, apparent quantum yield, and carboxylation efficiency for different leaves, despite similar plant ages. However, the following general points were established: light saturating net photosynthetic rates were greater than those exhibited under growth room light intensities (10-20% greater), and occurred around a $PPFD_i$ of 600-800 $\mu molQuanta\ m^{-2}\ s^{-1}$; apparent quantum yields varied between 0.029-0.042 $molCO_2\ molQuanta^{-1}\ m^{-2}\ s^{-1}$; dark respiration rates were between 0.42-0.51 $\mu molCO_2\ m^{-2}\ s^{-1}$; light compensation points were between 15-20 $\mu molQuanta\ m^{-2}\ s^{-1}$; carboxylation efficiencies were around 0.055 $mol^{-1}\ m^{-2}\ s^{-1}$; CO_2 compensation points were around 50 $\mu molCO_2\ mol^{-1}$; and leaves operated on the initial linear part of the P_n/c_i curve under growth room conditions.

5.2.3 Photosynthesis under Field Conditions

5.2.3.1 Net Photosynthetic Rates under Field Conditions

Maximum daily PPFD for the shaded *F.C.*2 seedlings was approximately 1000 $\mu molQuanta\ m^{-2}\ s^{-1}$ (Figure 2.1). Light intensities above this value, for photosynthetic rate measurement, were obtained by removing the shading covering plants during growth. Net photosynthetic rates for the cotyledons (Figure 5.5) and Leaf 1 (Figure 5.6) were low at low incident photosynthetic photon flux density ($PPFD_i$) and increased as $PPFD_i$ increased, to some plateau value. No plants showed increase in net photosynthetic rate above those values found at 1000 $\mu molQuanta\ m^{-2}\ s^{-1}$, which were thus considered to be light saturating. However, some seedlings did show reduced rates at higher $PPFD_i$, which were associated with low stomatal conductances (Figure 5.7).

P_n values at saturating $PPFD_i$, excluding those that showed declines in P_n associated with stomatal closure at high $PPFD_i$, were used to calculate mean saturating photosynthetic rates at different plant ages (Figure 5.8). Light saturating P_n rates for the cotyledons increased from 3.7 $\mu mol\ m^{-2}\ s^{-1}$ on day 35 to a peak value of 6.5 $\mu mol\ m^{-2}\ s^{-1}$ on day 56, thereafter beginning a slow decline. P_n values for Leaf 1 increased as leaf expansion proceeded, reaching 6.2 $\mu mol\ m^{-2}\ s^{-1}$ by 70 days. Values for day 49 and day 56 appear unusually high because of the non-random selection of Leaf 1 data at these points. At these ages, measurements were only possible on larger and therefore physiologically more mature leaves, which consequently had higher light saturating P_n values. Leaf 2 was too small to measure P_n by day 70.

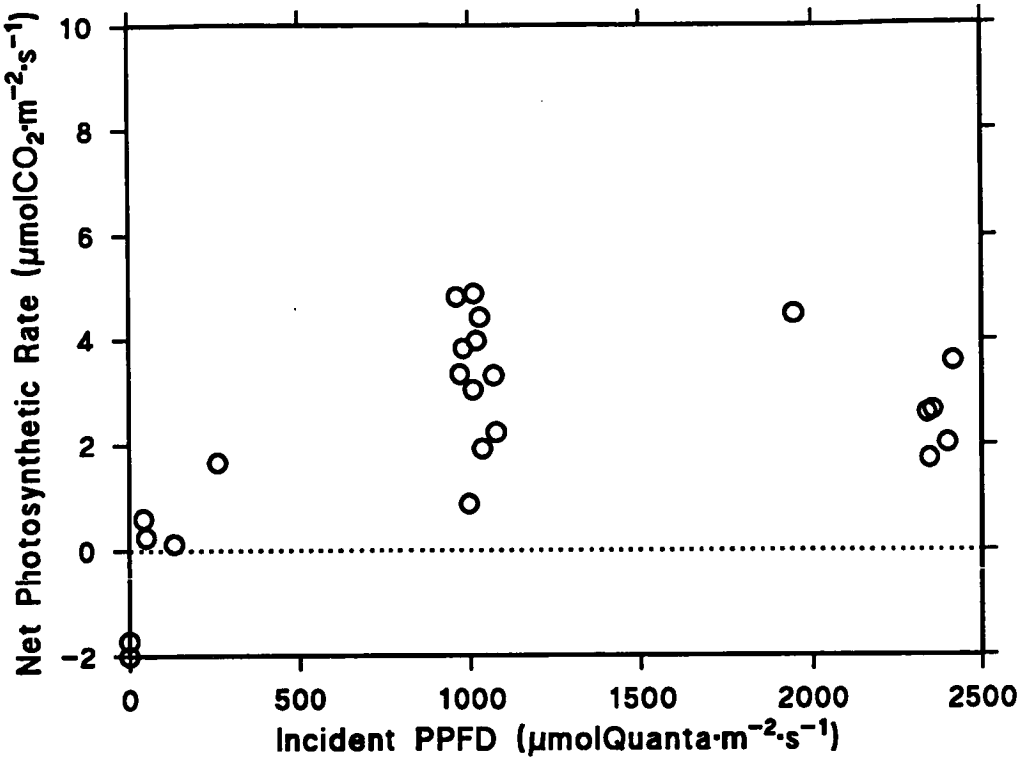


Figure 5.5 Scatter diagram showing relationship between net photosynthetic rate (P_n) and incident photosynthetic photon flux density ($PPFD_i$), for cotyledons of day 35 *K. coriacea* seedlings grown under field conditions (*F.C.*2). Each point is P_n for a single cotyledon.

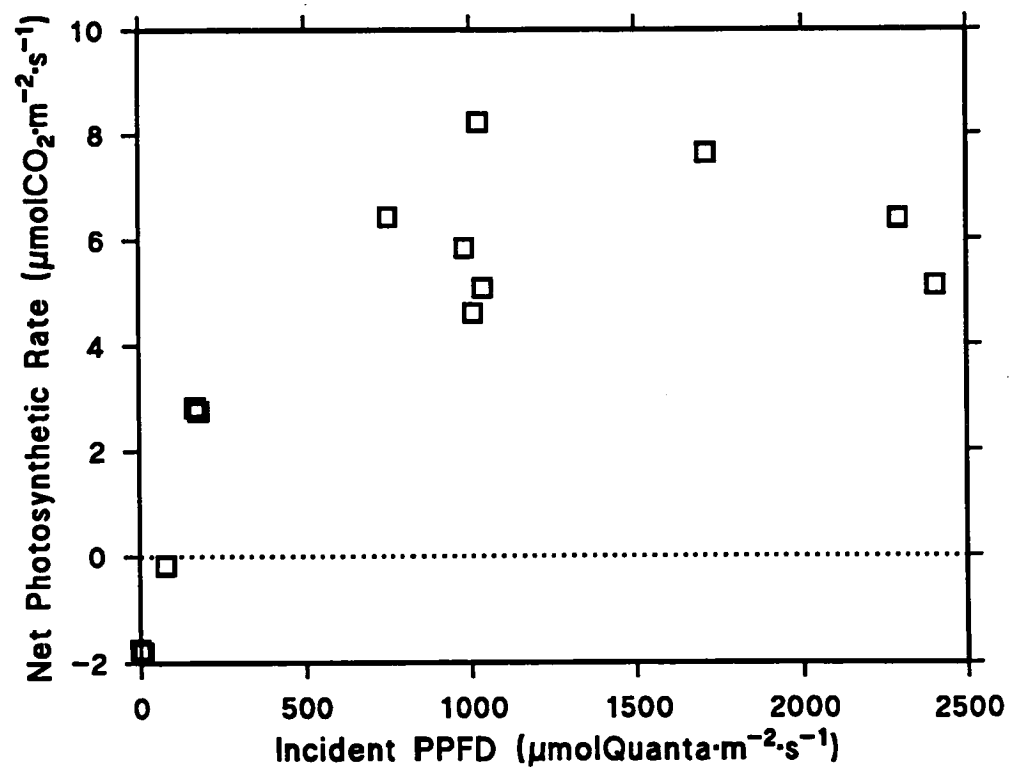


Figure 5.6 Scatter diagram showing relationship between net photosynthetic rate (P_n) and incident photosynthetic photon flux density ($PPFD_i$), for Leaf 1 of day 70 *K. coriacea* seedlings grown under field conditions (*F.C.*2). Each point is P_n for a single leaf.

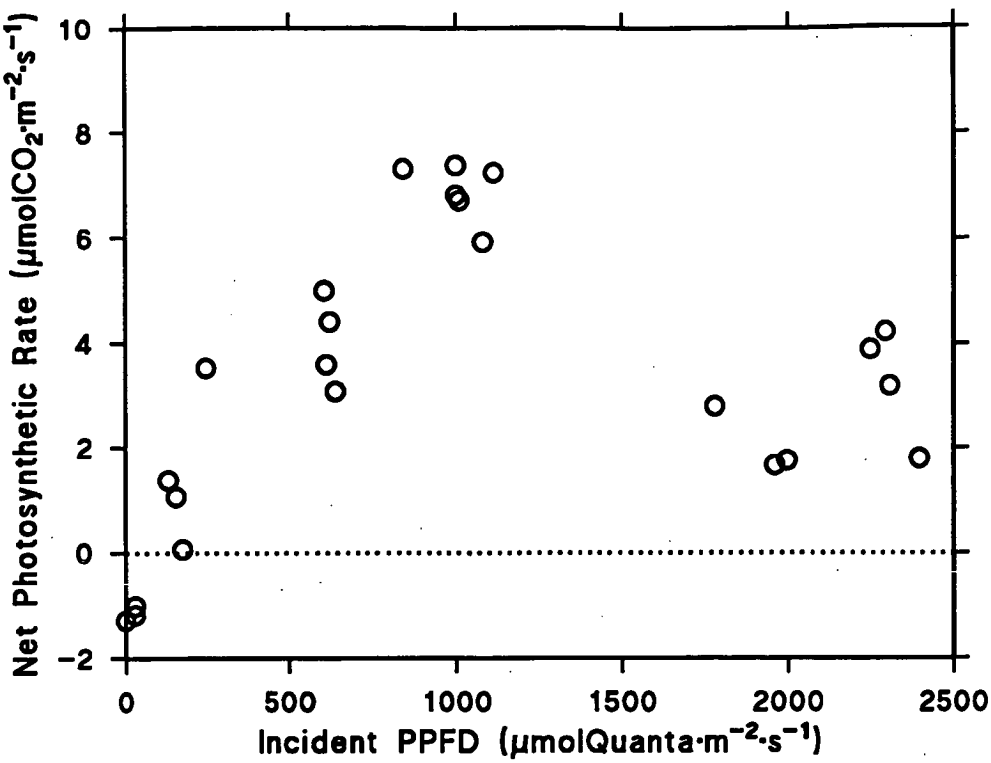


Figure 5.7 Scatter diagram showing relationship between net photosynthetic rate (P_n) and incident photosynthetic photon flux density ($PPFD_i$) for cotyledons of day 56 *Kielmeyera coriacea* seedlings grown under field conditions (*F.C.*2). Each point is P_n for a single cotyledon. Lower P_n values above a $PPFD_i$ of 1500 μmolQuanta m^{-2} s^{-1} are associated with lower stomatal conductances.

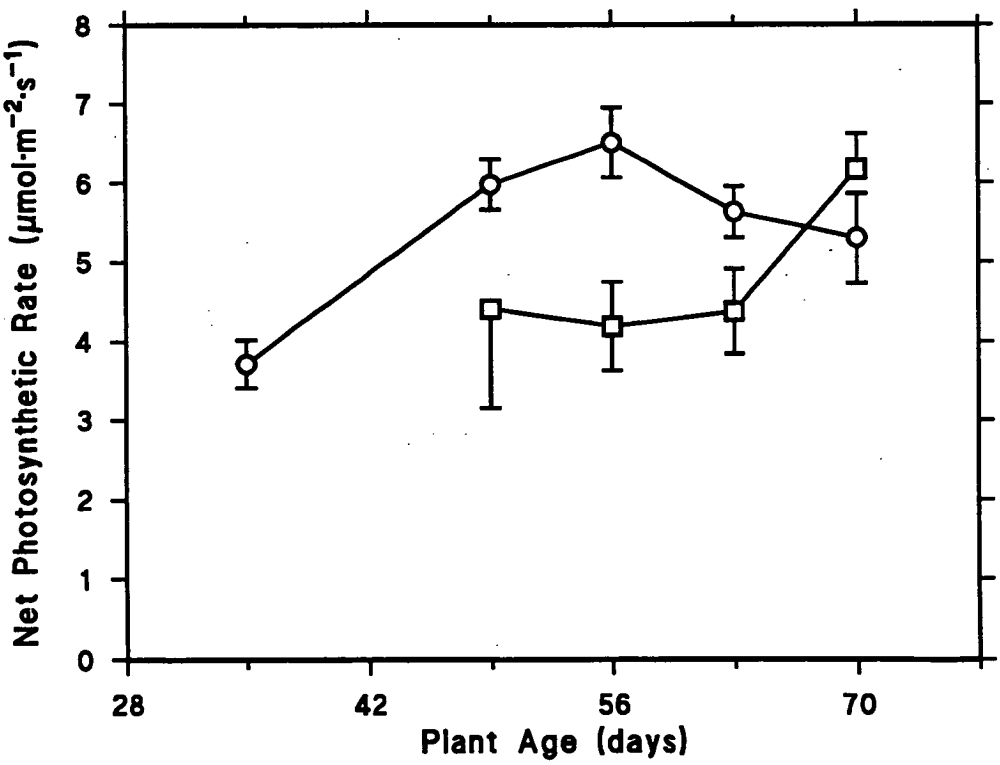


Figure 5.8 Relationships between net photosynthetic rate at saturating light intensity and plant age, for cotyledons (O) and Leaf 1 (□) of *Kielmeyera coriacea* seedlings grown under field conditions (*F.C.*2). Each point is the mean of 12 and 8 replicates respectively, with bars indicating standard errors of the mean.

5.3 Photosynthetic Productivity

5.3.1 Introduction

Plant photosynthetic production (PP) is here defined as the total CO_2 assimilated by all assimilatory organs, per plant, per unit time. PP relates to the productive component of the absolute growth rate, G. Photosynthetic productivities were calculated based on individual leaf areas and net photosynthetic rates,

$$PP = \sum_{1}^{2} CxP_n \cdot CxA + \sum_{1}^{n} LyP_n \cdot LyA$$

where: PP is photosynthetic productivity; CxP_n and CxA are net photosynthetic rate and area of cotyledon number x respectively; and LyP_n and LyA are the net photosynthetic rate and area of foliar leaf number y respectively.

Photosynthetic productivities were considered to be whole plant productivities assuming that, measured net photosynthetic rates are representative of the whole lamina, and the contribution of photosynthetic organs not measured, *i.e.* the hypocotyl, and small emerging leaves, were insignificant.

To permit comparison with unit leaf rate values determined by growth analysis (see section 3.3.3), PP data has also been expressed on a per plant area and per day basis (12 hr photoperiod and 12 hr dark period), and is referred to as unit leaf rate productivity (**EP**),

$$\mathbf{EP} = PP/L_A$$

where: **EP** is unit leaf rate productivity; PP is plant photosynthetic productivity; and L_A is plant leaf-area.

This assumes that measured net photosyntetic rates are mean photoperiod net photosynthetic rates. This is a reasonable assumption, as continuous photosynthetic monitoring for 48 hr indicated that leaves had an essentially constant net photosynthetic rate within 30-40 minutes of 'lights on', and maintained this rate until 'lights off' 12 hr later.

As net photosynthetic rates under controlled conditions increased in the cotyledons, L1, L2 and L3 after day 98 (Figure 5.1 and Figure 5.2), to improve curve-fitting of the data, photosynthetic productivities were only calculated up to this point.

5.3.2 Photosynthetic Productivity under Controlled Conditions

Figure 5.9 shows changes in photosynthetic productivity with plant age for seedlings grown under controlled conditions. As cotyledon and leaf P_n rates increased in parallel with their leaf areas, photosynthetic productivity rapidly increased, from a value of 0.015 $\mu molCO_2\ s^{-1}\ plant^{-1}$ on day 30 to a peak value of 0.065 $\mu molCO_2\ s^{-1}\ plant^{-1}$ around day 77 (inset, Figure 5.9). Thereafter as cotyledon, L1 and L2 photosynthesis decreased, productivity declined, to 0.04 $\mu molCO_2\ s^{-1}\ plant^{-1}$ by day 98.

Unit leaf rate productivity for *C.C.*1 (inset, Figure 5.10), showed a decline from 19 $gCO_2\ m^{-2}\ d^{-1}$ on day 30, to 6 $gCO_2\ m^{-2}\ d^{-1}$ by day 98. *C.C.*2 **EP** (Figure 5.10), although declining from day 42 to day 77, showed the initial decline (from 15 $gCO_2\ m^{-2}\ d^{-1}$ at day 42) due to cotyledonary P_n decrease followed by the increase and peak of Leaf 1 and Leaf 2 photosynthetic maxima (13 $gCO_2\ m^{-2}\ d^{-1}$ at d64-d70).

Figure 5.11 shows the percentage of the total photosynthetic productivity provided by the major assimilatory organs with plant age for seedlings grown under controlled conditions. From separation, the cotyledons provided the majority of photosynthate to beyond 50 days, and continued to provide a substantial proportion of the total PP up to 98 days. Soon after day 42, Leaf 1 began to contribute substantially to plant PP, providing approximately 35% of the total from day 50 to day 98. Similarly from day 60 Leaf 2 began to contribute increasingly to plant productivity, from approximately 25% on day 70 to 45% by day 98. Contributions by the 3rd and successive leaves (L3+) were small but increasing from day 70.

5.3.3 Photosynthetic Productivity under Field Conditions

Photosynthetic productivity values for field grown *K. coriacea* seedlings contrast strongly with those of seedlings grown in controlled environments (Figure 5.9). Values were initially very low at 0.005 $\mu molCO_2\ s^{-1}\ plant^{-1}$ on day 35 and increased slowly (17.1 $\mu molCO_2\ plant^{-1}\ d^{-1}$) to only 0.02 $\mu molCO_2\ s^{-1}\ plant^{-1}$ by day 70. Data from the *C.C.*2 experiment was similar to that of the *C.C.*1 experiment, and is plotted adjacent to indicate the distinct differences in magnitude and rates of change of PP for the *F.C.*2 and *C.C.*2 data.

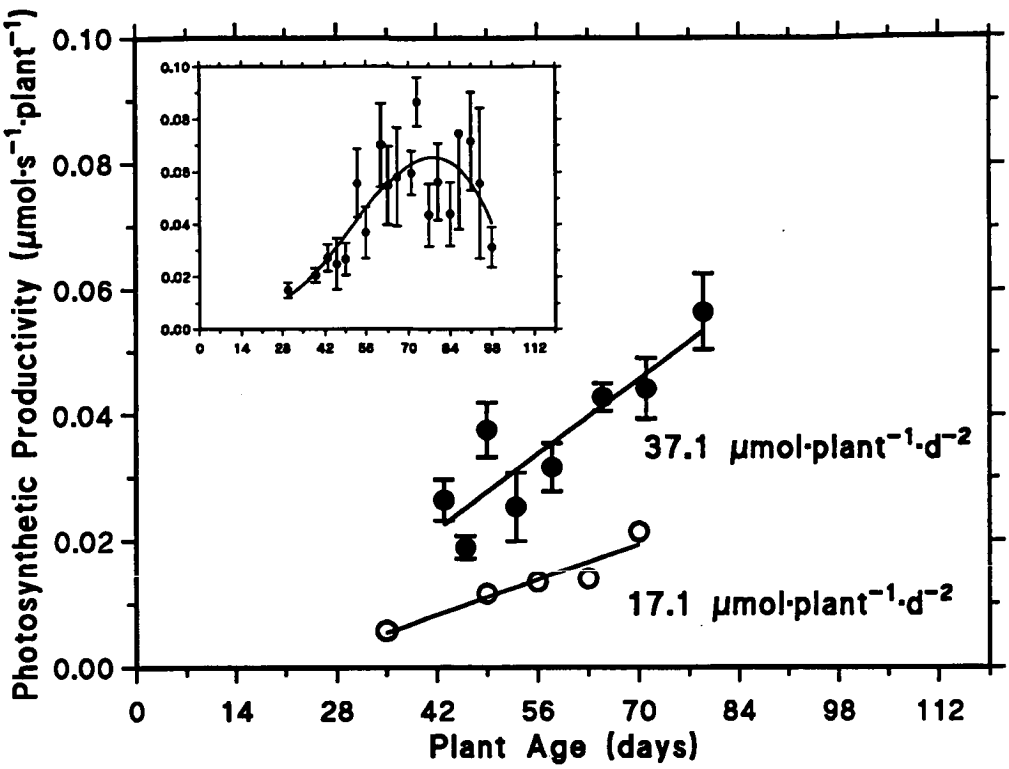


Figure 5.9 Relationship between photosynthetic productivity (PP) and plant age, for *K. coriacea* seedlings grown under field (O; *F.C.*2) and controlled (●; *C.C.*2) conditions. Points are means of 12 and 7 replicates respectively, with bars indicating standard errors of the mean. Lines are best-fit linear regressions of the data, with values indicating rates of change of PP. Inset shows the *C.C.*1 data.

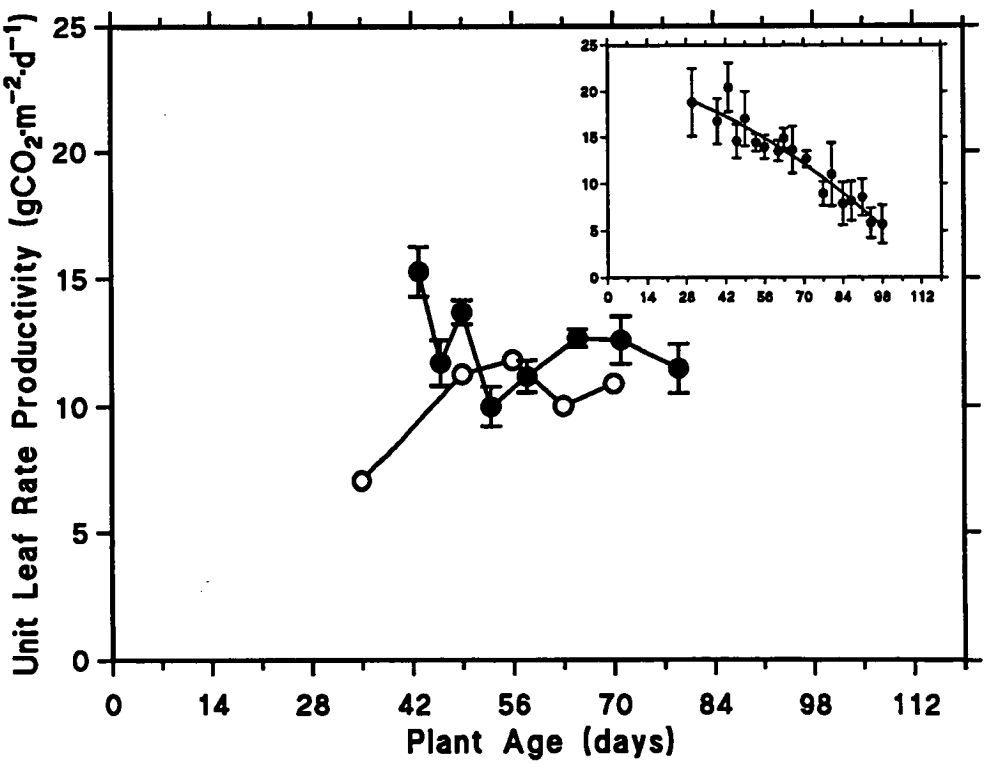


Figure 5.10 Relationship between unit leaf rate productivity and plant age, for *K. coriacea* seedlings grown under field (O; *F.C.*2) and controlled (●; *C.C.*2) conditions. Points are means of 12 and 7 replicates respectively, with bars indicating standard errors. Inset shows the *C.C.*1 data, with a best-fit 2nd-order polynomial regression ($Y=21.87-(0.0664 \cdot X)-(0.0010 \cdot X^2)$; $r^2=0.92$).

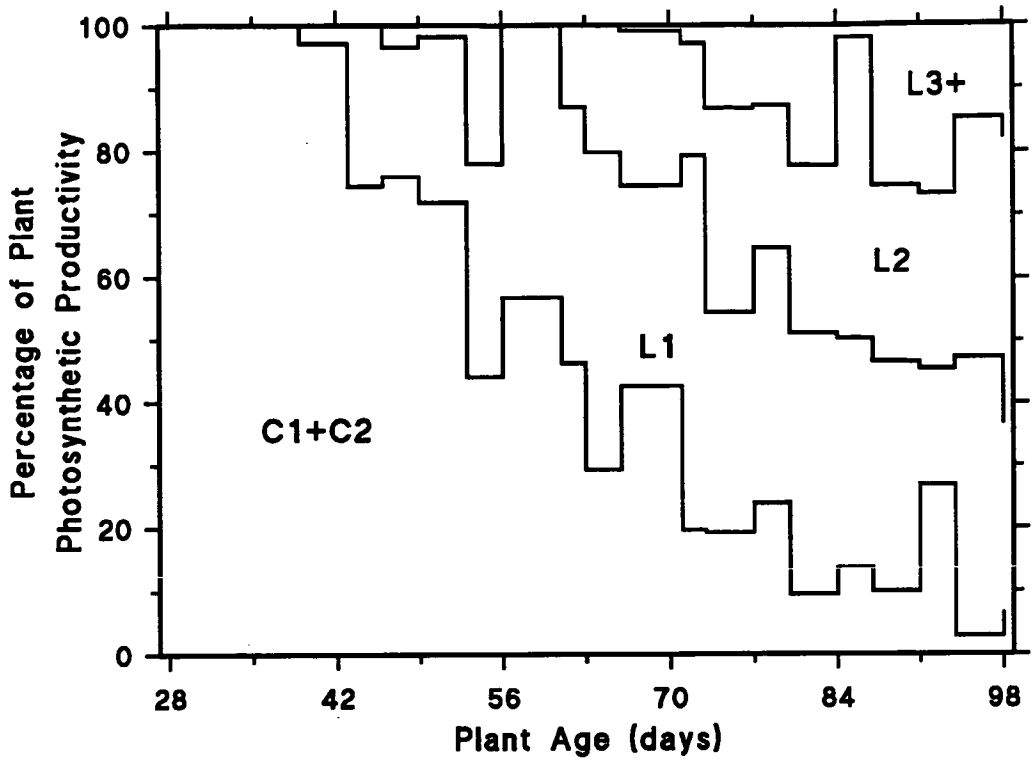


Figure 5.11 Relationships between organ photosynthetic productivity as a percentage of plant total and plant age, for cotyledons (C1+C2) and Leaf 1, Leaf 2 and Leaf 3+ (L1 to L3+ respectively) of *K. coriacea* seedlings grown under controlled conditions (*C.C.*1). Each value is the mean of 4 replicates.

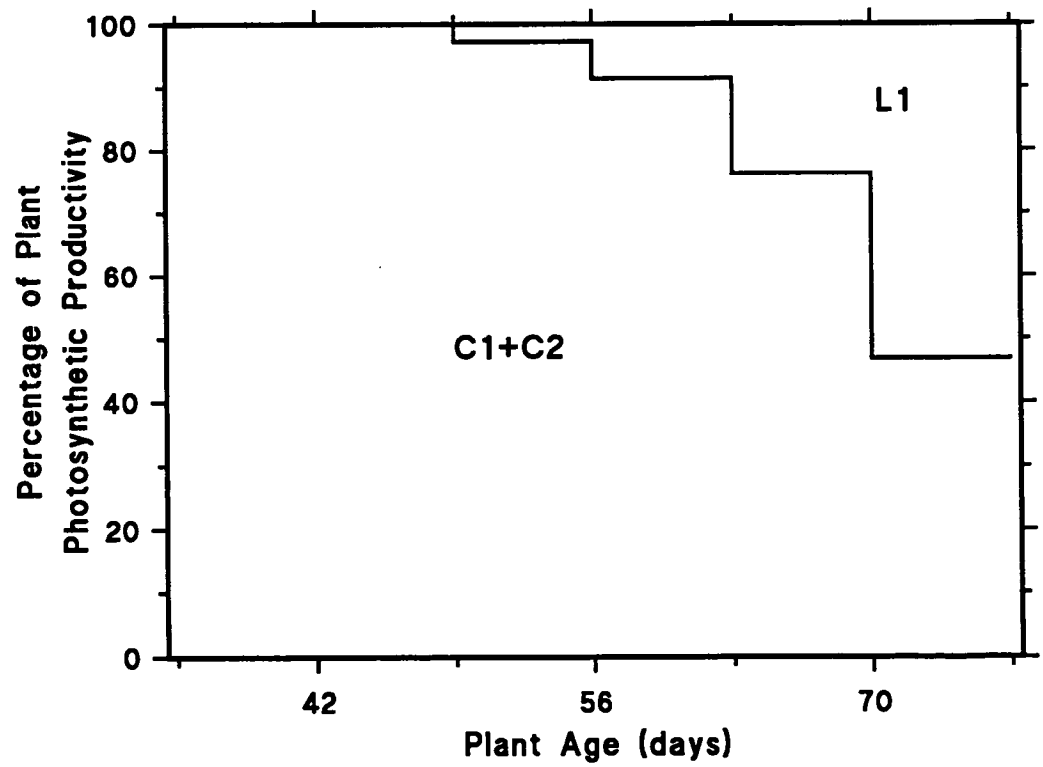


Figure 5.12 Relationships between organ photosynthetic productivity as a percentage of plant total and plant age, for cotyledons (C1+C2) and Leaf 1 (L1) of *K. coriacea* seedlings grown under field conditions (*F.C.*2). Each value is the mean of 12 replicates.

Despite differences in photosynthetic productivity, unit leaf rate productivity was similar for seedlings grown under controlled environment (*C.C.*2) and field (*F.C.*2) conditions (Figure 5.10). Although low at day 35 (6 $gCO_2\ m^{-2}\ d^{-1}$), from day 49 to day 70 values remained between 10 $gCO_2\ m^{-2}\ d^{-1}$ and 12 $gCO_2\ m^{-2}\ d^{-1}$. An initial peak in **EP** (d56) was a result of the peak in cotyledon P_n (Figure 5.1), and the decline around day 63 the transition from cotyledon to L1 dominated photosynthesis. The difference in timing evident from the patterns of unit leaf rate productivity are clearly shown by the percentage contribution of the different photosynthetic organs for the *F.C.*2 data (Figure 5.12). For the *F.C.*2 data the transition from cotyledon to Leaf 1 dominated photosynthesis did not occur until day 70, emphasising the even greater importance of these organs to plant growth under field conditions.

5.4 Associated Photosynthetic Sub-Processes

5.4.1 Introduction

This section describes the results of investigations of photosynthetic sub-processes in *K. coriacea* seedlings grown under controlled and field conditions. The aim was to establish the relative importance of photosynthetic sub-processes to the net photosynthetic rates described in section 5.2. The sub-processes of CO_2 transfer to the intercellular spaces, and the subsequent assimilation of CO_2 were investigated. This involved measurements of stomatal conductance, leaf internal structure, and leaf photosynthetic pigment concentrations. Attempts were made to assay the levels of soluble protein, and the activity of the carboxylating enzyme Ribulose 1,5 Bisphosphate Carboxylase Oxygenase (RuBisCO), however both were unsuccessful. This was thought to be the result of the known high phenolic and latex content of the leaves of this species, which interfered with spectrophotometric protein assays and rapidly reduced RuBisCO activity.

As controlled environment experiments involved frequent (twice weekly) measurements of photosynthetic performance, a functional approach was used to describe the data from these experiments. As for photosynthetic productivity (see section 5.3.1), to improve curve-fitting, only data up to day 98 has been used. Field-based experiments involved harvests at relatively large harvest intervals, and therefore a functional approach was considered inappropriate for the data analysis.

5.4.2 Associated Photosynthetic Sub-Processes under Controlled Conditions

5.4.2.1 Stomatal Conductance and Intercellular CO_2 Concentration under Controlled Conditions

Figure 5.13 and Figure 5.14 show ontogenic changes in net photosynthetic rate (P_n), stomatal conductance (g_s), and intercellular CO_2 concentration (c_i), for the cotyledons and Leaf 1, of seedlings grown under controlled conditions, respectively. Patterns of stomatal conductance for both cotyledons and Leaf 1 were closely associated with patterns of net photosynthetic rate. The peaks in photosynthetic rate seen in the cotyledons and Leaf 1 were associated with peaks in stomatal conductance, although for Leaf 1 the peak in stomatal conductance (d56) slightly proceeded the peak in net photosynthetic rate (d63).

Patterns of intercellular CO_2 concentration appeared to mirror-image the patterns of net photosynthetic rate and stomatal conductance. P_n and g_s maxima were associated with the lowest intercellular CO_2 concentrations, with c_i minima for the cotyledons and Leaf 1 of 165 $\mu molCO_2\ mol^{-1}$ and 170 $\mu molCO_2\ mol^{-1}$, respectively. Post-maximal declines in P_n and g_s were associated with increases in c_i values.

5.4.2.2 Estimated Carboxylation Efficiencies and Supply Functions Under Controlled Conditions

Figure 5.15 shows a generalised net photosynthetic response to intercellular CO_2 concentration for a C_3-photosynthetic leaf at light saturation: a demand function (Farquhar and Sharkey, 1982). Carboxylation efficiency (CO_2 assimilated/intercellular [CO_2]; Ku and Edwards, 1977) is calculated as the initial slope of the demand function, and represents the relative activity of Ribulose 1,5 Bisphosphate Carboxylase-Oxygenase. The supply function is the slope from the operating P_n/c_i point to the atmospheric CO_2 concentration at zero photosynthetic rate, and describes the relative efficiency of CO_2 diffusion from the atmosphere to the intercellular spaces (Raschke, 1979).

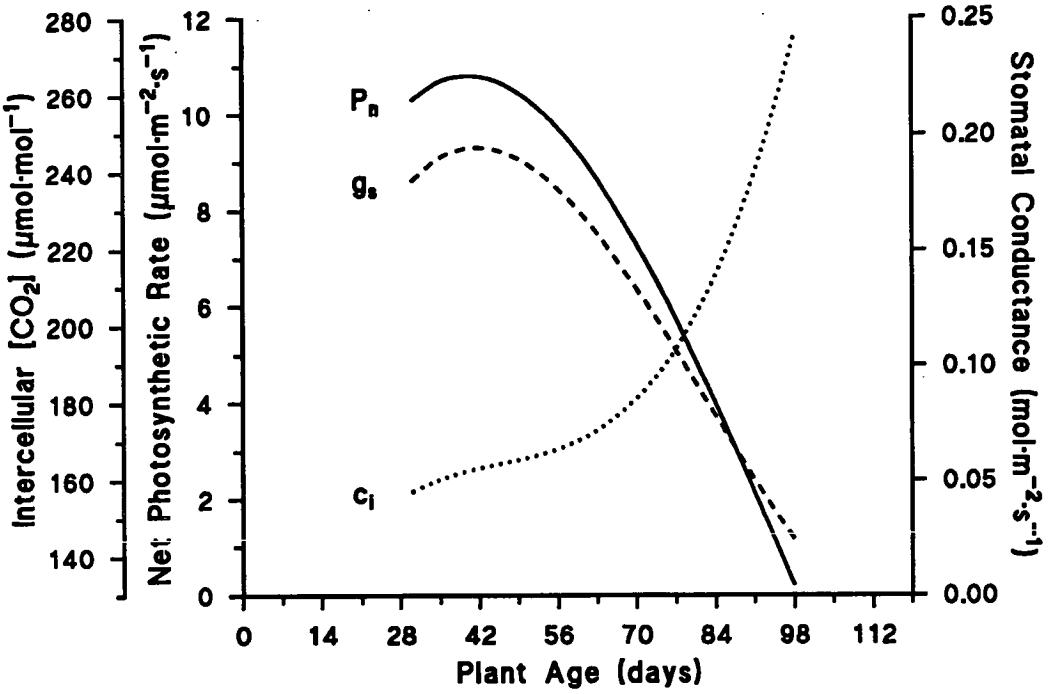


Figure 5.13 Relationships between net photosynthetic rate (P_n), stomatal conductance (g_s), intercellular CO_2 concentration (c_i) and plant age, for cotyledons of *K. coriacea* seedlings grown under controlled conditions (*C.C.*1). Free-hand curves summarise the *C.C.*1 data (see Figure 5.1), which is ommited for clarity. g_s and c_i data provided by calculation by the DL2 data logger according to functions described in Appendix 2.2.

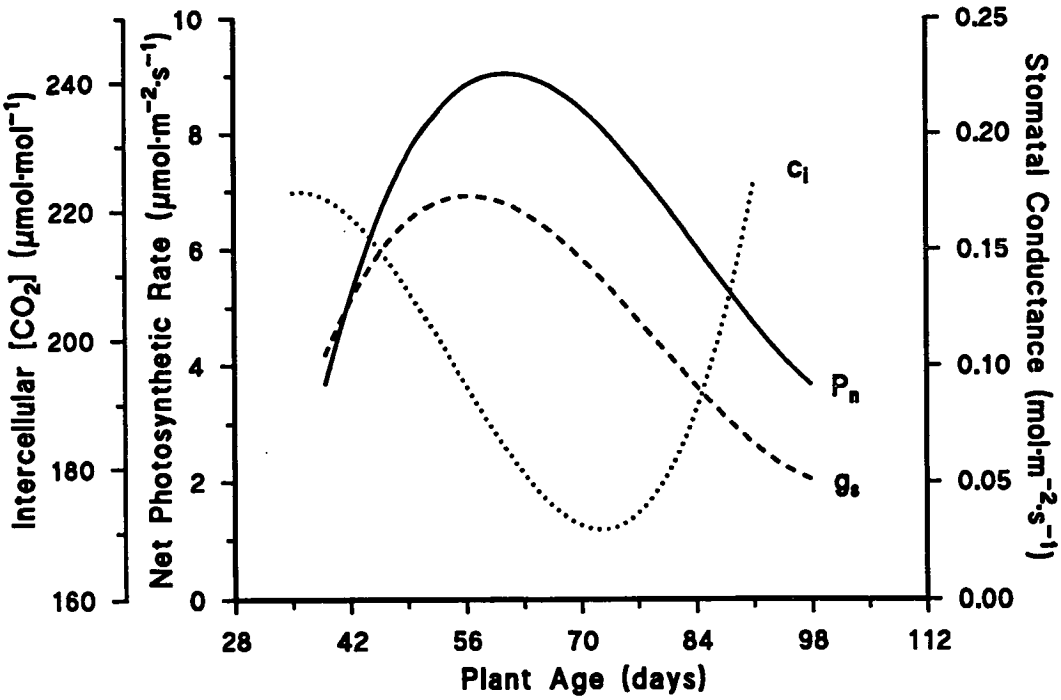


Figure 5.14 Relationships between net photosynthetic rate (P_n), stomatal conductance (g_s), intercellular CO_2 concentration (c_i) and plant age, for Leaf 1 of *K. coriacea* seedlings grown under controlled conditions (*C.C.*1). Free-hand curves summarise the *C.C.*1 data (see Figure 5.2), which is ommited for clarity. g_s and c_i data provided by calculation by the DL2 data logger according to functions described in Appendix 2.2.

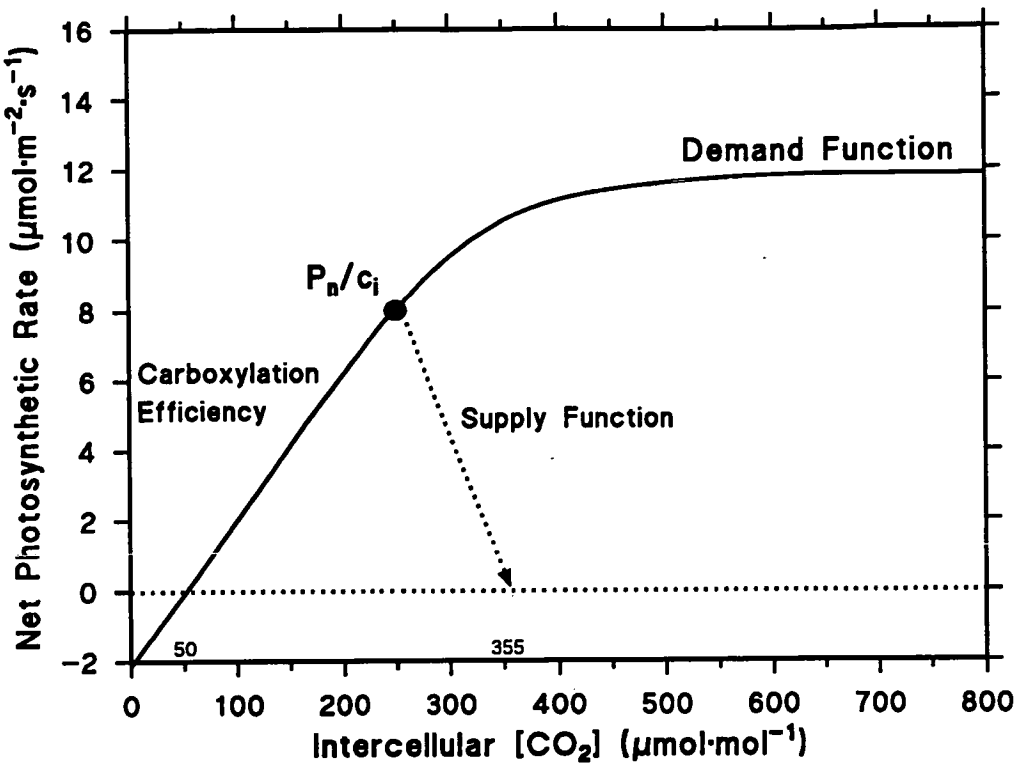


Figure 5.15 Generalised net photosynthetic response to intercellular CO_2 concentration for a C_3-photosynthetic leaf at light saturation, the demand function, showing carboxylation efficiency and supply function (after Farquhar and Sharkey, 1982).

Carboxylation efficiencies (CE) and supply functions (SF) were estimated, assuming a compensation CO_2 concentration of 50 μmol mol^{-1}, a linear demand function to the P_n/c_i point, and an atmospheric CO_2 concentration of 355 μmol mol^{-1}. These assumptions were considered reasonable for the following reasons: a compensation CO_2 concentration of 50 μmol mol^{-1} was measured for leaves under defined growth room environment conditions (see section 5.2.2.2), and this value is typical of the unstressed leaves of woody species (Schaedle, 1975); leaves operated on the initial, essentially linear, part of the demand function under growth room conditions (see section 5.2.2.2), and "*the response curve* (the demand function) *does not usually depart appreciably from linearity up to the normal operating* c_i", (Sandford and Jarvis, 1986); and net photosynthetic rate and intercellular CO_2 concentration measurements were made under ambient CO_2 concentrations approximating to 355 μmol mol^{-1}. CE and SF values are estimates of the true values, and are only used to indicate broad ontogenic trends in these sub-processes under controlled and field conditions.

Figure 5.16 and Figure 5.17 show the patterns of change of estimated carboxylation efficiency (CE) and estimated supply function (SF) for the cotyledons and Leaf 1 of *K. coriacea* seedlings grown under controlled conditions, respectively. For the cotyledons, CE declined from a value of around 0.1 mol^{-1} m^{-2} s^{-1} at day 28 to near zero by day 98. SF increased slightly from day 28 to a peak on day 42 of about 0.06 mol^{-1} m^{-2} s^{-1}, thereafter declining to 0.01 by day 98.

For Leaf 1 initial CE and SF values were similar and rapidly increased to peaks of 0.07 mol^{-1} m^{-2} s^{-1} and 0.055 mol^{-1} m^{-2} s^{-1}, respectively. As reflects the earlier peak in g_s over P_n (see section 5.4.2.1), the peak in SF for L1 slightly proceeded the peak in CE. Thereafter both declined, resulting in the decline in P_n

5.4.2.3 Cotyledon and Leaf 1 Internal Structure Under Controlled Conditions

Cotyledon internal structure at full expansion is shown in Plates 5.1-5.4. Cotyledon transverse section is shown in Plate 5.1. Internal cellular volume was dominated by spongy-mesophyll tissue, with a single pallisade layer clearly visible below the adaxial epidermis. Cotyledon thickness, from adaxial to abaxial cuticle, was typically 1100 μm (S.E. 18 μm), which included a 950 μm (S.E. 17 μm) thick spongy-mesophyll layer and a 73 μm (S.E. 2 μm) thick pallisade layer. The pallisade-mesophyll was composed of a single layer of closely packed roughly cylindrical cells of mean length 73 μm (S.E. 2 μm) and diameter 28 μm (S.E. <1 μm) (Plate 5.2). The spongy-mesophyll was composed of a number of irregular layers (typically 13-16) of roughly ovoid or spherical cells of mean diameter 54 μm (S.E. <1 μm) (Plate 5.3). The spongy-mesophyll in paradermal section is shown in Plate 5.4.

Leaf 1 internal structure at full expansion is shown in Plates 5.5-5.10. Leaf 1 transverse section is show in Plate 5.5. A large proportion of leaf cellular volume was occupied by spongy-mesophyll tissue, with a pallisade cell layer immediately below the adaxial epidermis. Leaf 1 thickness at full expansion, from adaxial to abaxial cuticle, was typically 400 μm (S.E. 14), which included a 80 μm (S.E. 2 μm) thick pallisade layer and a 234 μm (S.E. 10 μm) thick spongy-mesophyll layer. The pallisade-mesophyll was composed of a single layer of closely packed roughly cylindrical cells of mean length 80 μm (S.E. 2 μm) and diameter 25 μm (S.E. 1 μm) (Plate 5.6 and Plate 5.9). The spongy-mesophyll was composed of a number of layers (typically 4-7) of radially lobed cells (Plate 5.7). The distinct radially lobed morphology of spongy-mesophyll cells can be clearly seen in paradermal section (Plate 5.8 and Plate 5.10). Generally each cell had 4-5 projections, and a definite stacking of cells could be seen.

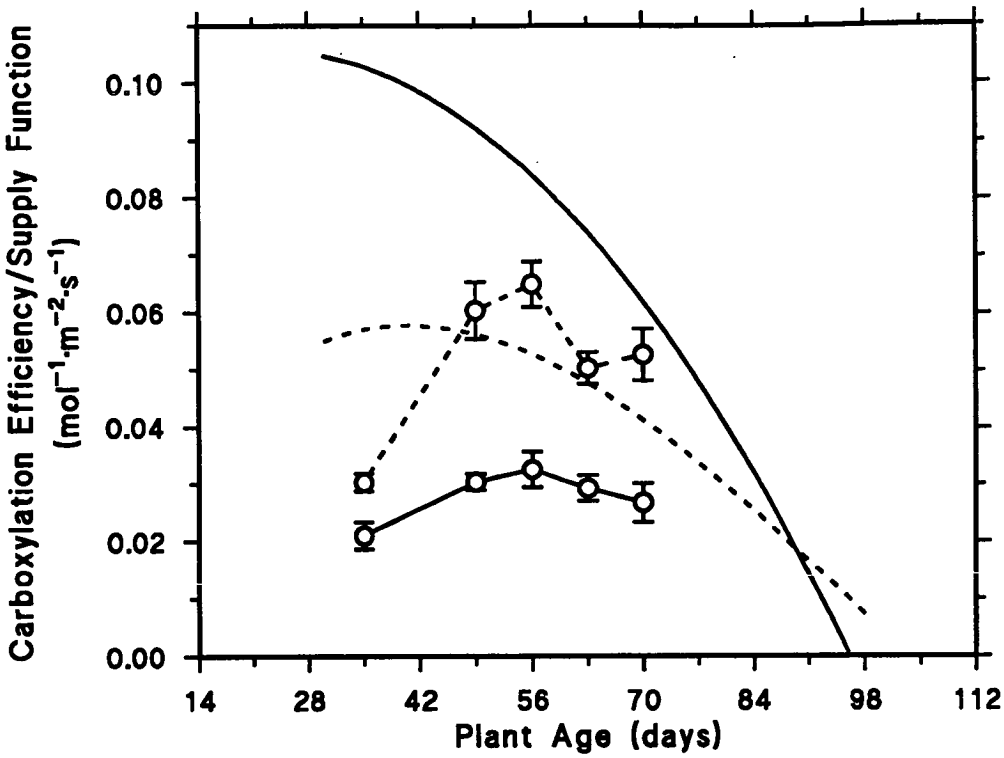


Figure 5.16 Relationships between estimated carboxylation efficiency (———), estimated supply function (- - -) and plant age, for cotyledons of *K. coriacea* seedlings grown under controlled (*C.C.*1) and field (○, *F.C.*2) conditions.

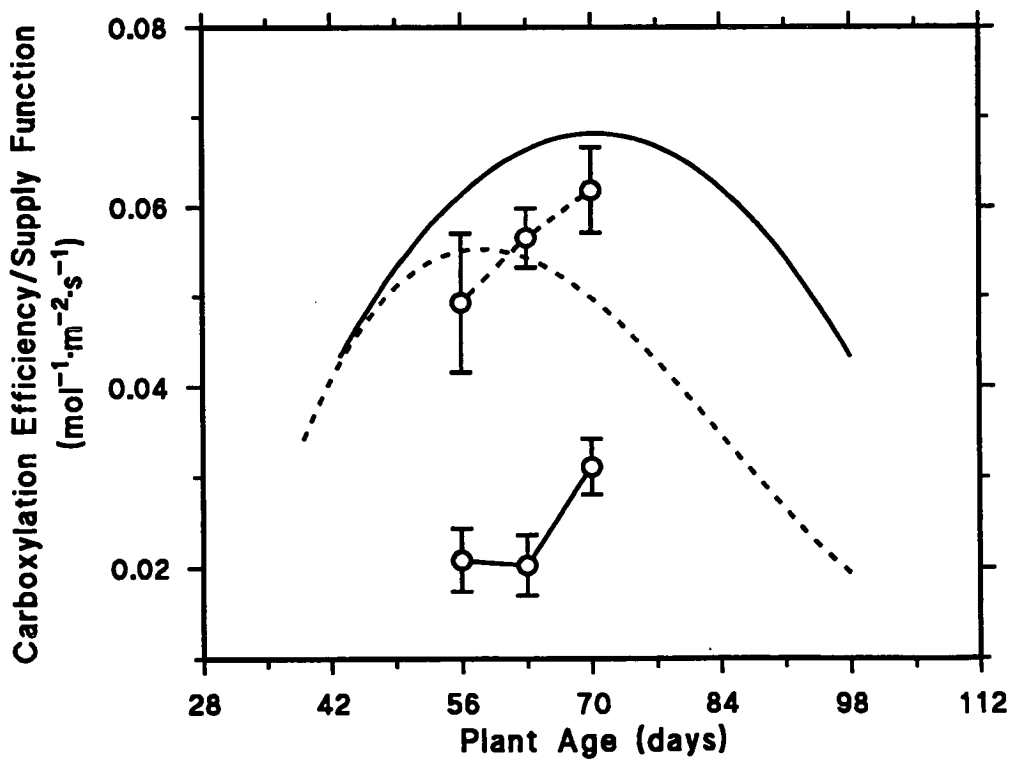


Figure 5.17 Relationships between estimated carboxylation efficiency (———), estimated supply function (- - -) and plant age, for Leaf 1 of *K. coriacea* seedlings grown under controlled (*C.C.*1) and field (○, *F.C.*2) conditions.

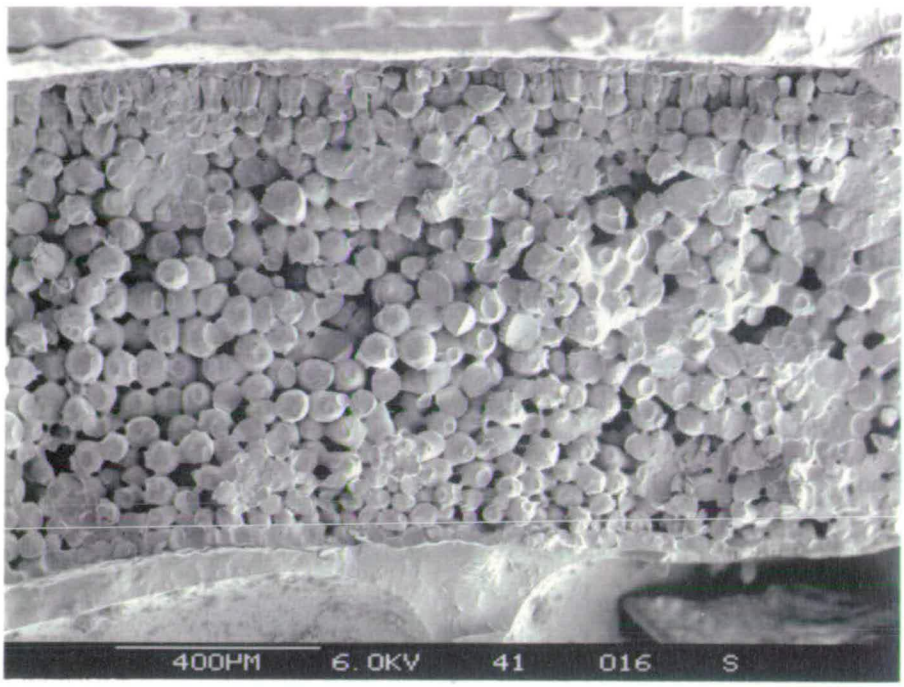


Plate 5.1 Transverse section of a *K. coriacea* cotyledon at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

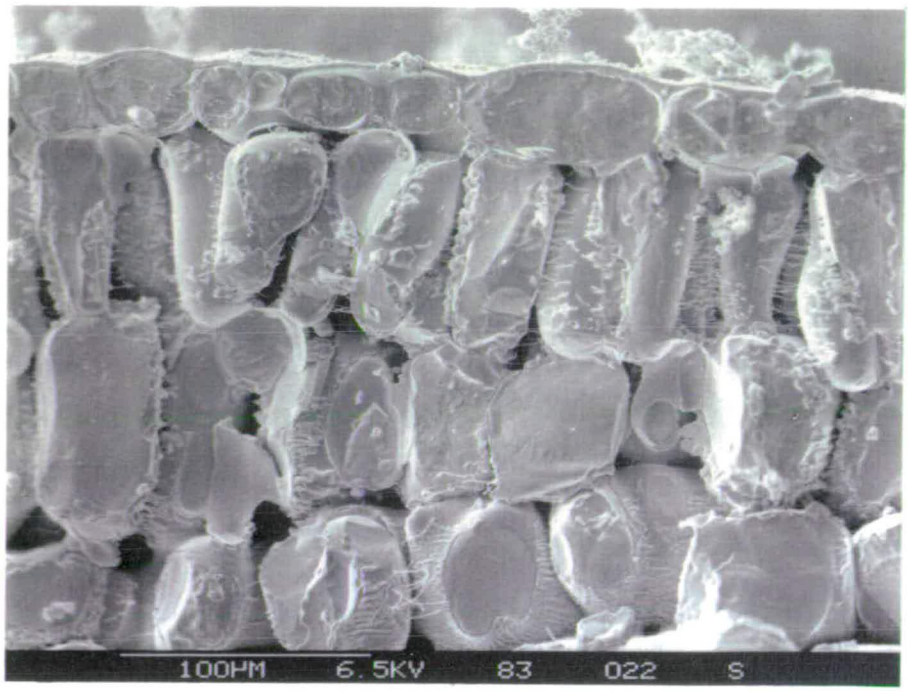


Plate 5.2 Close-up transverse section of *K. coriacea* cotyledon pallisade layer at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

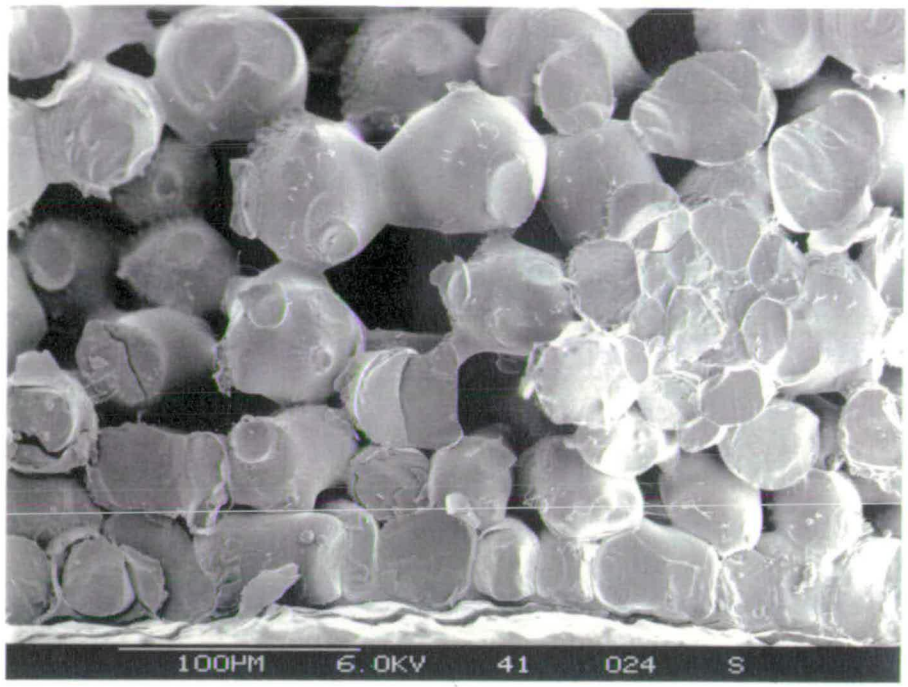


Plate 5.3 Close-up transverse section of *K. coriacea* cotyledon spongy-mesophyll layer at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

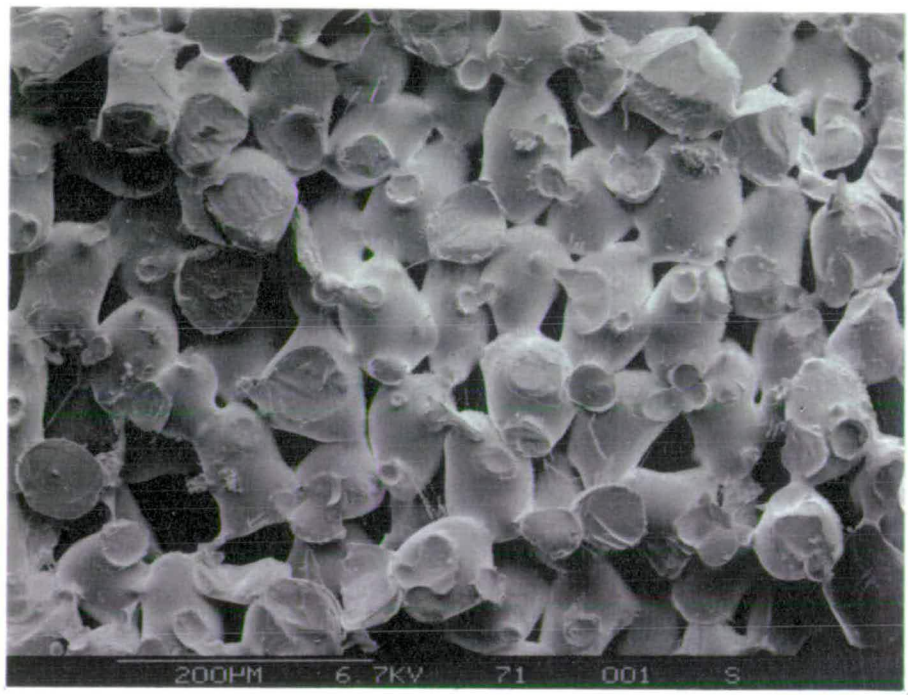


Plate 5.4 Paradermal section of *K. coriacea* cotyledon spongy-mesophyll layer at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

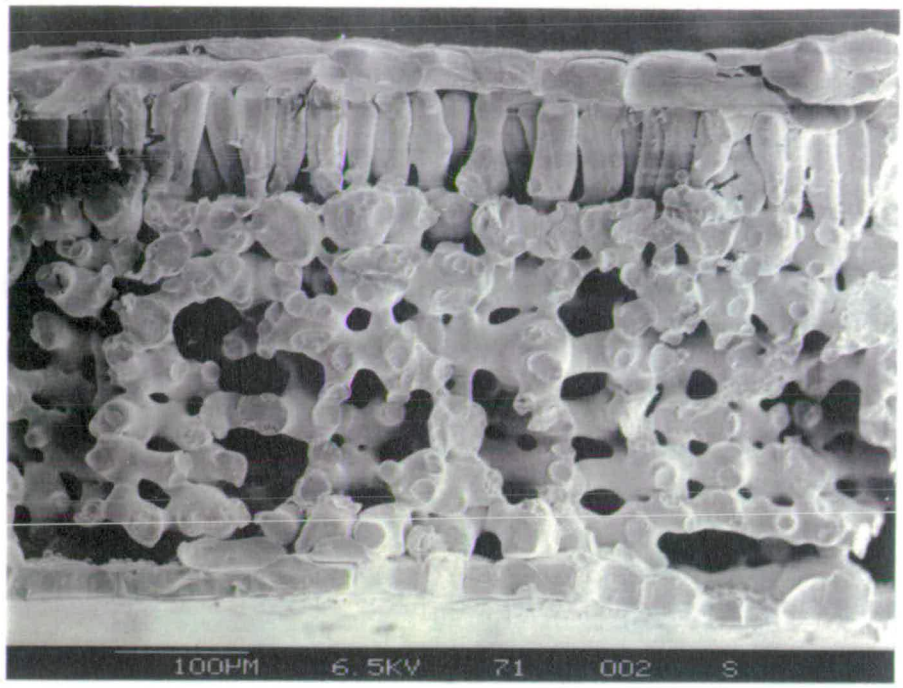


Plate 5.5 Transverse section of a *K. coriacea* Leaf 1 at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

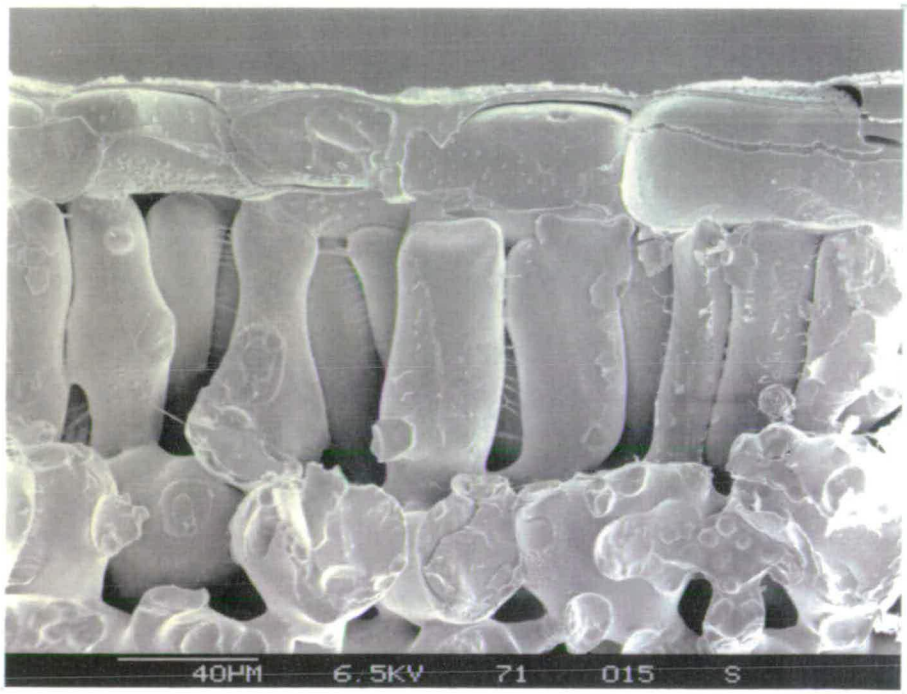


Plate 5.6 Close-up transverse section of a *K. coriacea* Leaf 1 pallisade layer at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

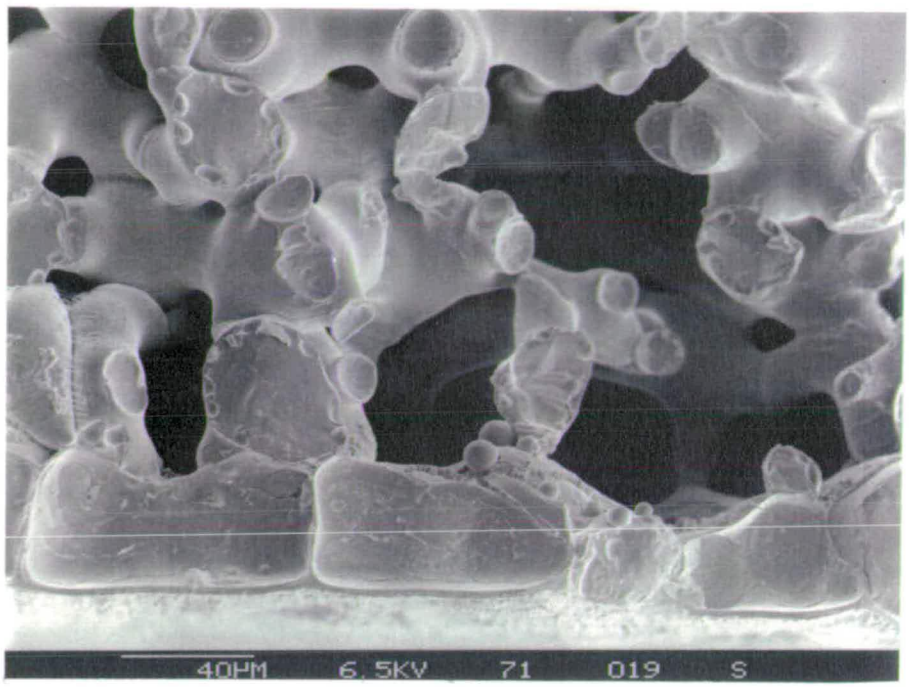


Plate 5.7 Close-up transverse section of a *K. coriacea* Leaf 1 spongy-mesophyll layer at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

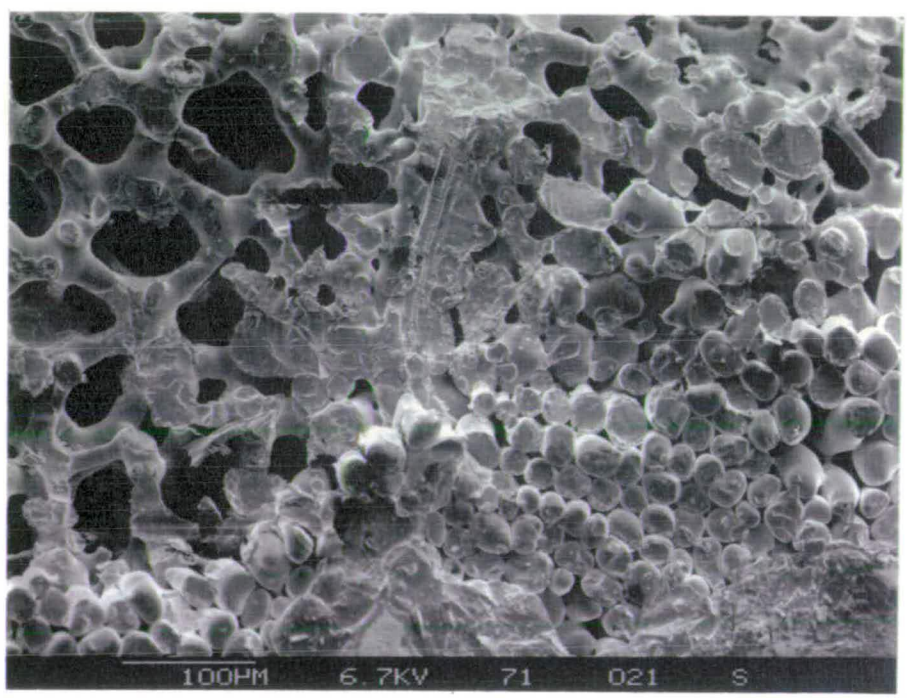


Plate 5.8 Split-level paradermal section of a *K. coriacea* Leaf 1 at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

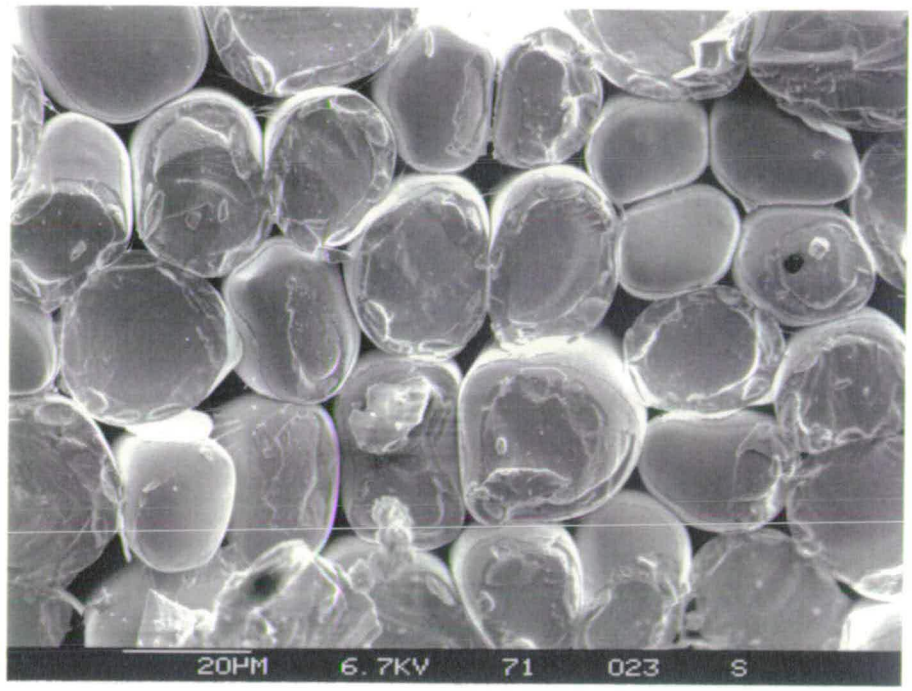


Plate 5.9 Close-up paradermal section of a *K. coriacea* Leaf 1 pallisade layer at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

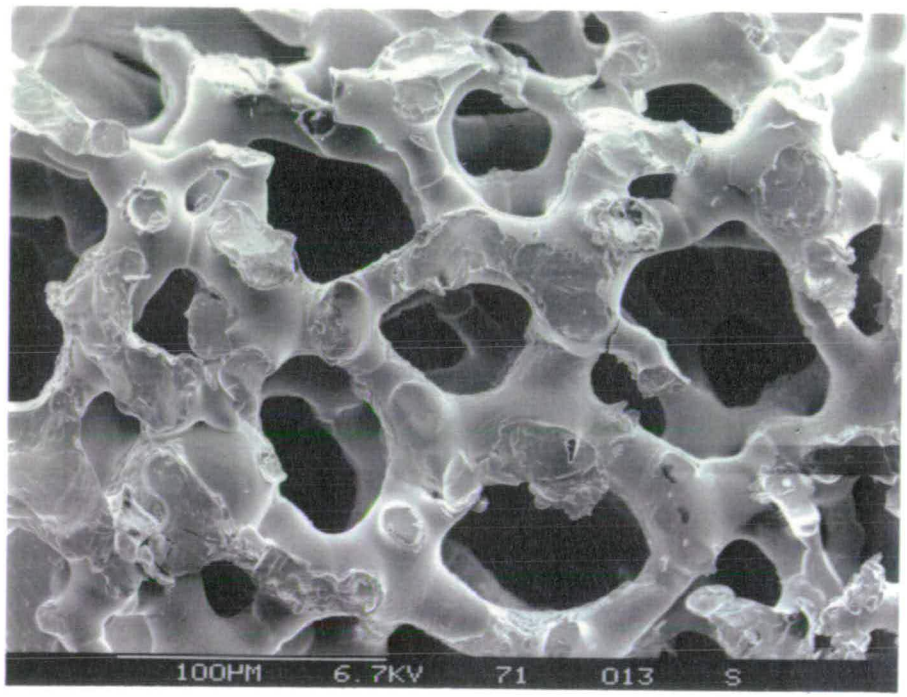


Plate 5.10 Close-up paradermal section of a *K. coriacea* Leaf 1 spongy-mesophyll layer at full expansion, from a seedling grown under controlled conditions. The plate is an electron-micrograph obtained using low temperature scanning electron microscopy. Scale-bar indicates magnification.

5.4.2.4 Estimated Photosynthetic Pigment Concentrations Under Controlled Conditions

Changes in chlorophyll concentration ([Chl *a+b*]) and the ratio between chlorophyll *a* and chlorophyll *b* (Chl *a:b*) for the cotyledons and Leaf 1 of seedlings grown under controlled conditions are shown in Figure 5.18 and Figure 5.19, respectively. From day 14 values very rapidly increased to plateau values by day 21-28, and remained at these levels until at least day 91. Plateau chlorophyll concentrations were between 0.7-0.8 mg $gFwt^{-1}$ and 45-60 $\mu g\ cm^{-2}$, when expressed on a fresh weight and an area basis, respectively. Chlorophyll *a* to chlorophyll *b* ratios remained between 2.2 and 2.8 from day 35 to day 91.

For Leaf 1, chlorophyll concentrations steadily increased from leaf emergence, around day 28, to maxima around day 77 (Figure 5.19). Values for [Chl *a+b*], expressed on a fresh weight basis, increased to 1.14 mg $gFwt^{-1}$ on day 60 and 1.43 mg $gFwt^{-1}$ by day 77. These values are high when compared with the cotyledons, because of the thick, fleshy nature of the cotyledons. Hand-sections indicated that only cells 200-300 μm below the adaxial epidermis of the cotyledon were chlorophyllous, and that the bulk of the lower spongy-mesophyll (see section 5.4.2.3 and Plate 5.1) was composed of achlorophyllous cells. This contrasts with the anatomy of foliar leaves in which the whole of the mesophyll was chlorophyllous. Values for [Chl *a+b*], expressed on an area basis, increased from 36.5 $\mu g\ cm^{-2}$ on day 60 to 48.8 $\mu g\ cm^{-2}$ on day 77. Chlorophyll *a* to chlorophyll *b* ratios remained between 2.0 and 2.6 from emergence to, and beyond, full expansion on day 56.

5.4.3 Associated Photosynthetic Sub-Processes under Field Conditions

5.4.3.1. Stomatal Conductance and Intercellular CO_2 Concentration under Field Conditions

Figure 5.20 and Figure 5.21 show ontogenic changes in net photosynthetic rate, stomatal conductance, and intercellular CO_2 concentration for the cotyledons and Leaf 1 of seedlings grown under field conditions, respectively. For the cotyledons net photosynthetic rate was closely associated with stomatal conductance. The peak in net photosynthetic rate of 6.5 $\mu mol\ m^{-2}\ s^{-1}$ on day 56 was accompanied by a peak stomatal conductance of 0.17 $mol\ m^{-2}\ s^{-1}$. Intercellular CO_2 concentration increased from 230 $\mu molCO_2\ mol^{-1}$ on day 35 to around 250 $\mu molCO_2\ mol^{-1}$ on day 49, remaining around this value to at least day 70. For Leaf 1, associations between P_n and g_s were less clear, although increasing P_n values from day 56 were accompanied by larger stomatal conductances.

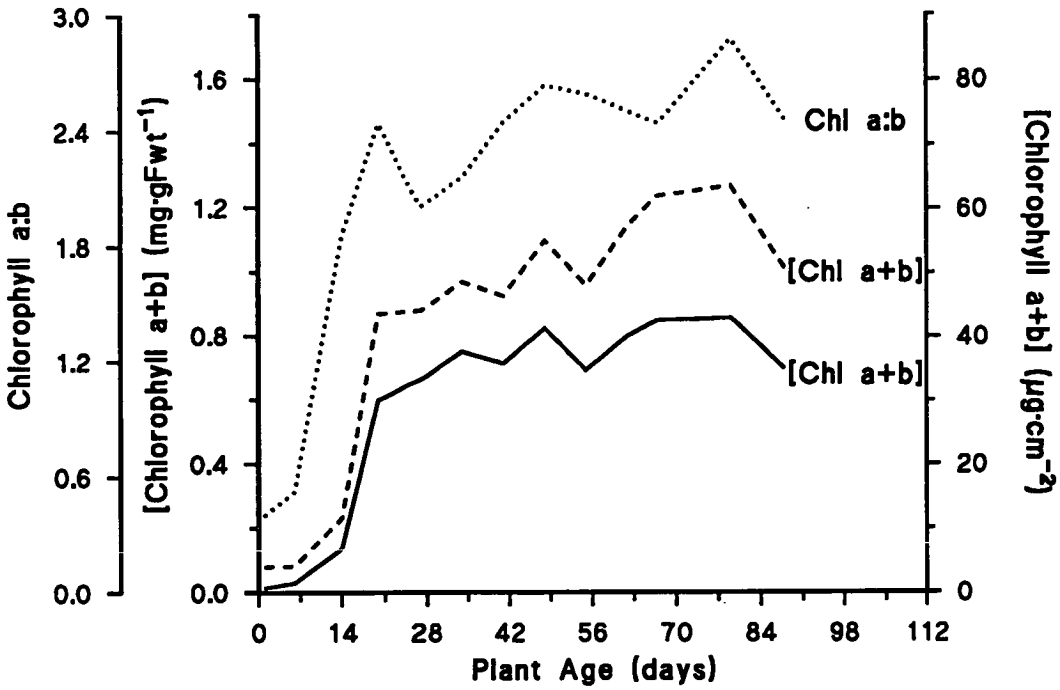


Figure 5.18 Relationships between chlorophyll concentration ([Chl a+b]), expressed on a leaf fresh-weight (—) and leaf area (- -) basis, chlorophyll *a* to chlorophyll *b* ratio (Chl a:b; ····) and plant age, for *K. coriacea* cotyledons grown under controlled conditions.

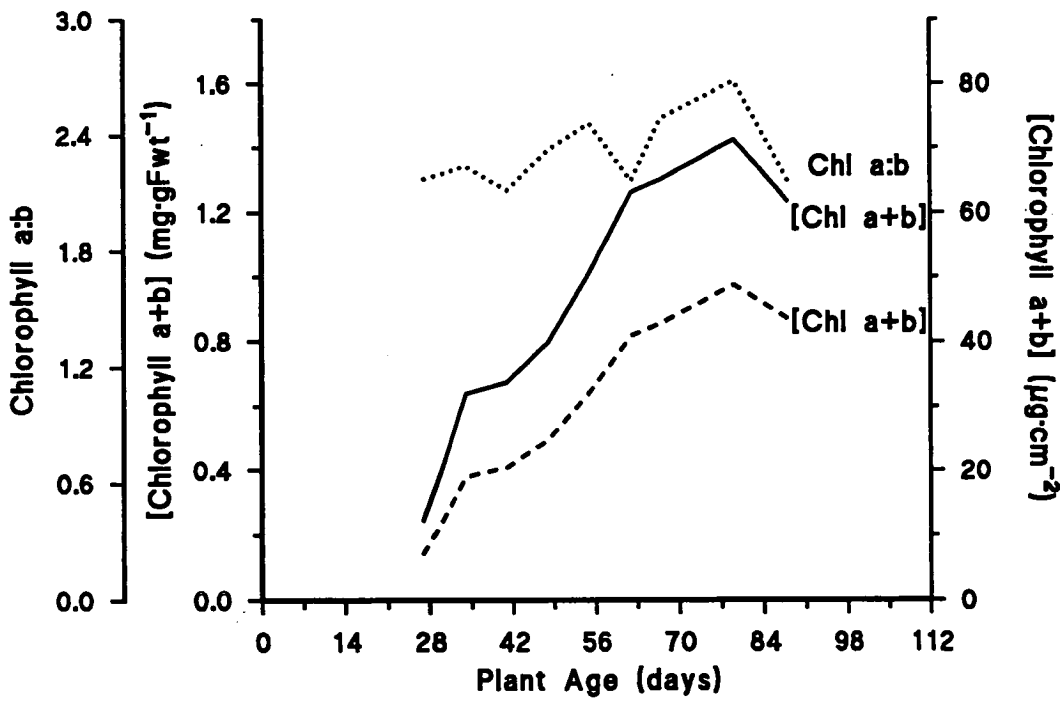


Figure 5.19 Relationships between chlorophyll concentration ([Chl a+b]), expressed on a leaf fresh-weight (—) and leaf area (- -) basis, chlorophyll *a* to chlorophyll *b* ratio (Chl a:b; ····) and plant age, for Leaf 1 of *K. coriacea* seedlings grown under controlled conditions.

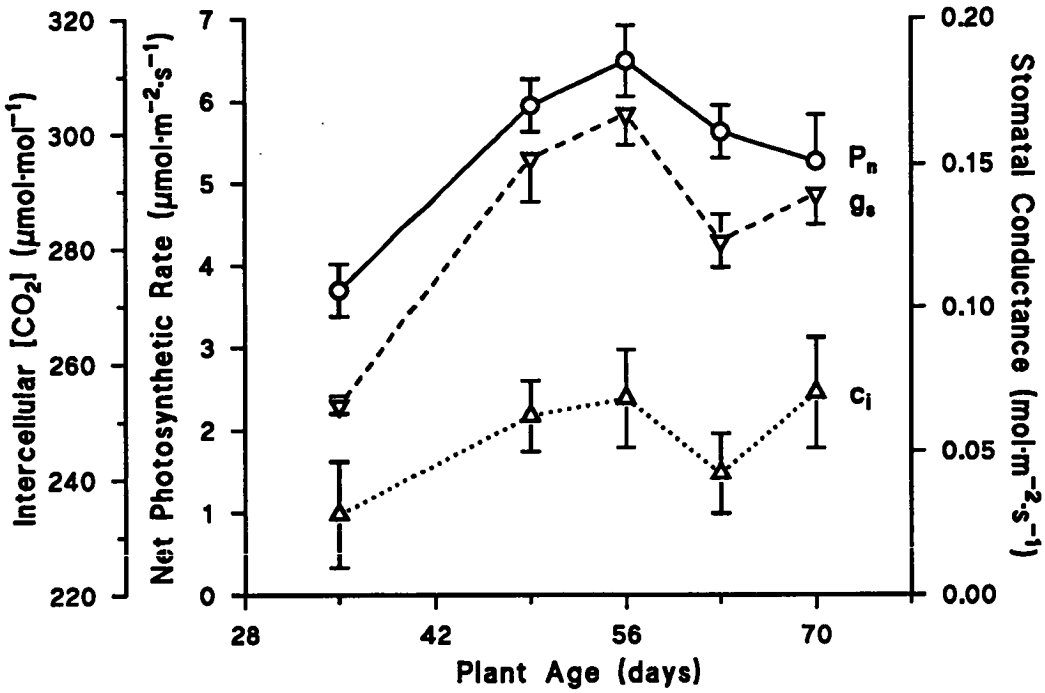


Figure 5.20 Relationships between net photosynthetic rate (P_n), stomatal conductance (g_s), intercellular CO_2 concentration (c_i) and plant age, for cotyledons of *K. coriacea* seedlings grown under field conditions (*F.C.*2).

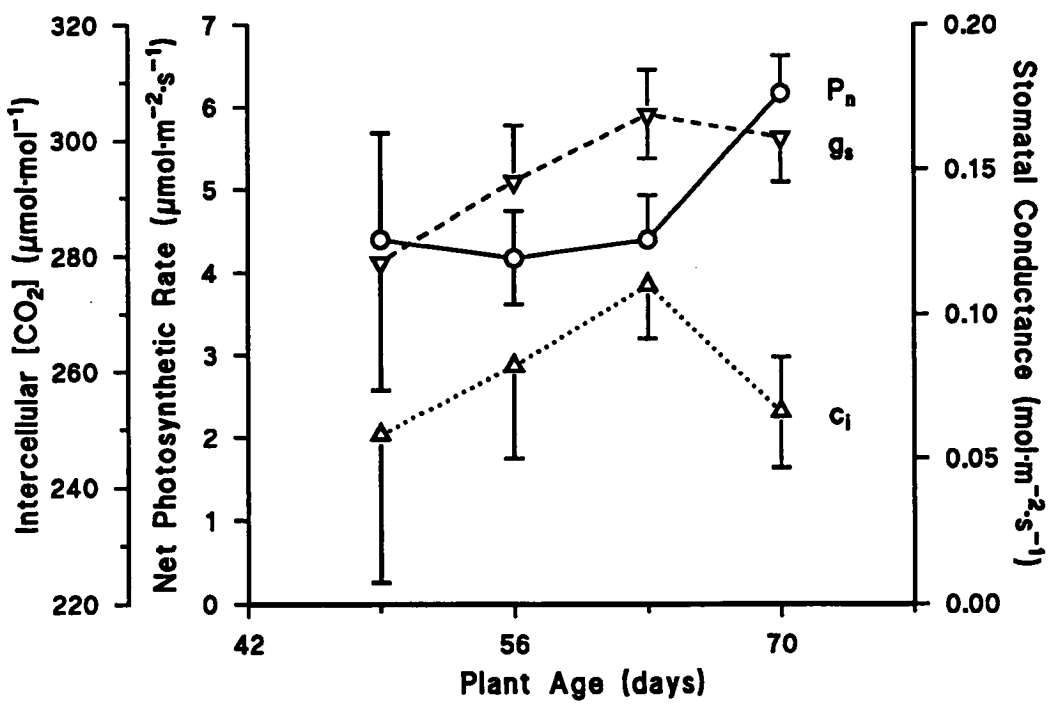


Figure 5.21 Relationships between net photosynthetic rate (P_n), stomatal conductance (g_s), intercellular CO_2 concentration (c_i) and plant age, for Leaf 1 of *K. coriacea* seedlings grown under field conditions (*F.C.*2).

5.4.3.2 Estimated Carboxylation Efficiencies and Supply Functions under Field Conditions

See section 5.4.2.2 for an explanation and justification of estimated carboxylation efficiency and estimated supply function calculation.

Figure 5.16 and Figure 5.17 show patterns of change of estimated carboxylation efficiency and estimated supply function for the cotyledons and Leaf 1, of seedlings grown under field conditions, respectively. In stark contrast to cotyledons grown under controlled conditions, in the field cotyledons showed substantially greater estimated supply functions than estimated carboxylation efficiencies from day 35 to day 70 (Figure 5.16). Peak carboxylation efficiency for the cotyledons on day 56 was around 0.03 $mol^{-1}\ m^{-2}\ s^{-1}$ and declined thereafter. This contrasts strongly with the cotyledons of seedlings grown under controlled conditions where CE declined from a value of 0.1 $mol^{-1}\ m^{-2}\ s^{-1}$ from day 28. Estimated supply functions were broadly similar for the cotyledons of seedlings grown under controlled and field conditions, although they differed in the timing of their peaks.

Similarly for Leaf 1, estimated supply functions for field grown seedlings were similar to those of controlled condition grown seedlings, but in the field carboxylation efficiencies were substantially lower (Figure 5.17). Initial ly CE values were low at 0.02 $mol^{-1}\ m^{-2}\ s^{-1}$ from day 56 to day 63, but increased to 0.03 $mol^{-1}\ m^{-2}\ s^{-1}$ by day 70. This contrasts with the peak of CE for Leaf 1 under controlled conditions of 0.07 $mol^{-1}\ m^{-2}\ s^{-1}$ around day 70.

5.4.3.3 Estimated Photosynthetic Pigment Concentrations Under Field Conditions

Changes in chlorophyll concentration ([Chl *a+b*]) and the ratio between chlorophyll *a* and chlorophyll *b* (Chl *a:b*) for the cotyledons and Leaf 1 of seedlings grown under field conditions are shown in Figure 5.22 and Figure 5.23, respectively. For the cotyledons [Chl *a+b*] values remained between 13.8-17.6 $\mu g\ cm^{-2}$ from day 35 until at least day 70, rising slightly on day 56 to the peak value of 17.6 $\mu g\ cm^{-2}$. Chlorophyll *a* to chlorophyll *b* ratios remained between 2.1 and 2.4 from day 35 to day 70.

For Leaf 1, chlorophyll concentrations increased from 9.0 $\mu g\ cm^{-2}$ on day 63, to 13.6 $\mu g\ cm^{-2}$ by day 77 (Figure 5.23). As for net photosynthetic rates (section 5.2.3.1), [Chl *a+b*] values appear unusually high on day 49 and day 56, because of the non-random selection of Leaf 1 data at these points. Chlorophyll *a* to chlorophyll *b* ratios remained between 2.0 and 2.2 from day 35 to day 70.

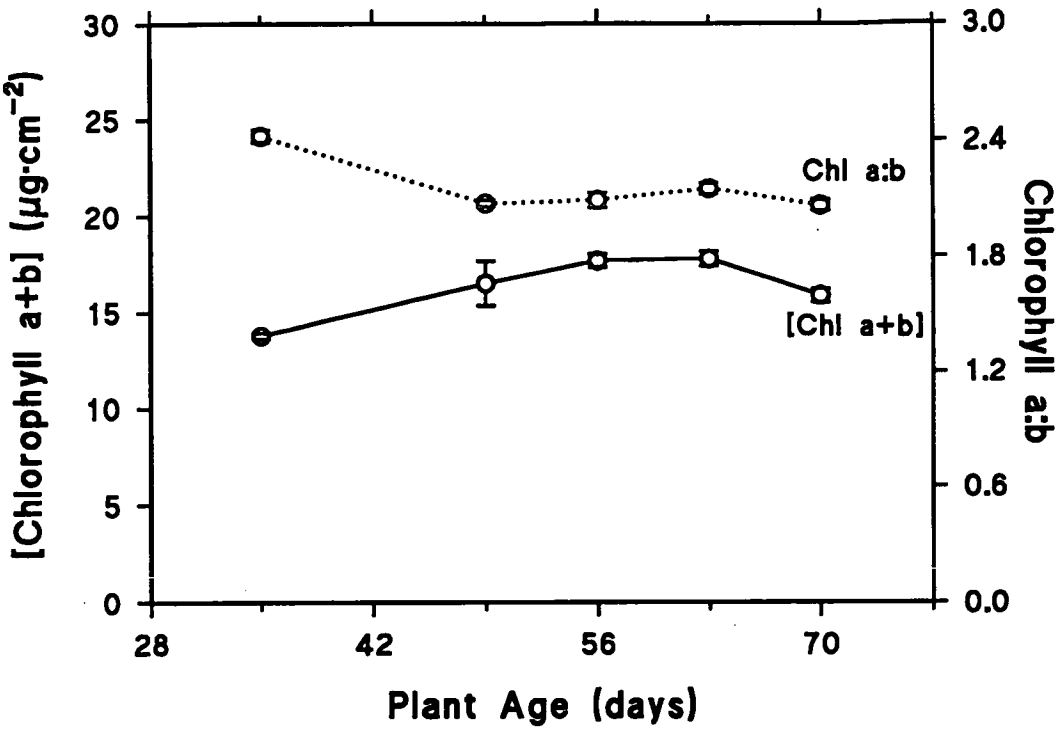


Figure 5.22 Relationships between chlorophyll concentration ([Chl a+b]), expressed on a leaf area basis (—), chlorophyll *a* to chlorophyll *b* ratio (Chl a:b; ····) and plant age, for *K. coriacea* cotyledons grown under field conditions.

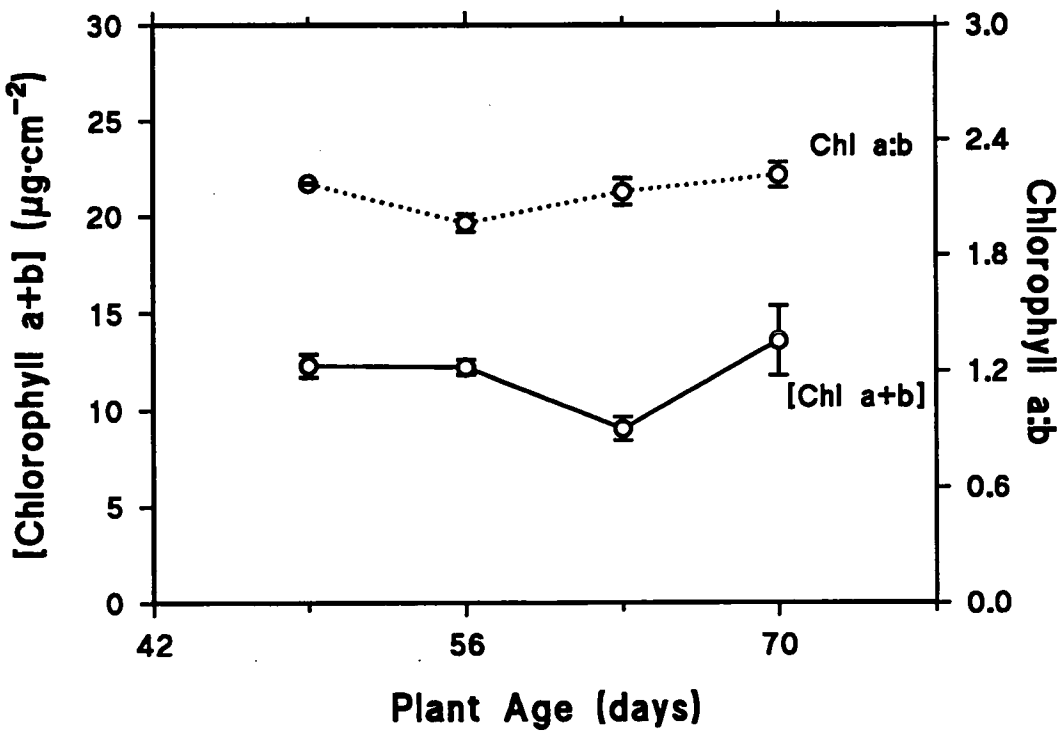


Figure 5.23 Relationships between chlorophyll concentration ([Chl a+b]), expressed on a leaf area basis (—), chlorophyll *a* to chlorophyll *b* ratio (Chl a:b; ····) and plant age, for Leaf 1 of *K. coriacea* seedlings grown under field conditions.

5.5 Discussion

Changes in leaf net photosynthetic rate (P_n) for *K. coriacea* seedlings formed low values during early growth, increasing during leaf expansion to maximum values before or at full expansion, and then declining to minimum values during senescence (Figure 5.1 and Figure 5.2). This pattern is seen in a wide range of plants (Šesták and Catsky, 1985; Tichá *et al.*, 1985).

Maximum net photosynthetic rates for the leaves of *K. coriacea* seedlings grown under controlled conditions (see Table 5.1) are comparable with those reported for seedlings of other woody species (Table 5.2).

Table 5.2 Net photosynthetic rates (P_n) for *K. coriacea* and a selection of other temperate and tropical/subtropical woody species. Values are for seedlings or young clonal material grown under controlled conditions.

Species	Net Photosynthetic Rate ($\mu mol\ m^{-2}\ s^{-1}$)
Temperate Woody Species:	
Fagus sylvatica L.[a]	3.6
Quercus rubra L.[b]	8.9
Populus trichocarpa 'Unal'[c]	12.0
Subtropical/Tropical Woody Species:	
Entandrophragma angolense (Welw.)C.DC.[d]	5.4
Terminalia sericea Burch. ex DC.[e]	5.8
Nauclea diderrichii (De Wilde.) Merrill[d]	6.9
Grewia flavescens Juss.[e]	7.1
Brachystegia spiciformis Benth.[f]	8.0
K. coriacea Leaf 1	8.9
K. coriacea Cotyledons	11.0
Eucalyptus grandis Hill ex Maiden[g]	11.6

[a] Masarovicova (1984)
[b] Hanson *et al.* (1988b)
[c] Ceulemans and Impens (1980)
[d] Riddoch *et al.* (1991)
[e] Ferrar (1980)
[f] Ernst (1988)
[g] Doley (1978)

Considering that all other values in Table 5.2 describe P_n values at light saturation (and some, *Terminalia sericea* and *Grewia flavescens*, at temperature optima), rates for *K. coriacea* determined under growth room conditions, and known to be below light saturating levels (see section 5.2.2.2), are relatively high compared with other woody species when expressed on an area basis. In particular, the cotyledons as well as serving as a store of reserves, are efficient assimilatory organs. Even when expressed on a dry weight basis, cotyledon net photosynthetic rates

(0.121 μmol g^{-1} s^{-1}) are comparable, although less than, values for Leaf 1 (0.166 μmol g^{-1} s^{-1}), Leaf 2 (0.132 μmol g^{-1} s^{-1}), and Leaf 3 (0.126 μmol g^{-1} s^{-1}).

Although there are few studies of the photosynthesis of the cotyledons of woody species (Schaedle, 1975) and particularly of tropical/subtropical woody species, Kitajima (1992) in a study of a range of Panamanian lowland forest species established a relationship between cotyledon thickness and net photosynthetic rate. In this, increasing cotyledon thickness correlated with progressively lower net photosynthetic maxima. As gross photosynthetic maxima on an area basis varied little, despite a 25-fold variation in cotyledon thickness, the amount of photosynthetic machinery per unit area was considered to be roughly constant, with thicker cotyledons having more non-photosynthetic storage mesophyll tissue.

Table 5.3 Net photosynthetic rate (P_n) and leaf thickness for the cotyledons of *K. coriacea* and a selection of other woody species.

Species	Cotyledon Thickness (mm)	P_n (μmol m^{-2} s^{-1})	P_n (μmol g^{-1} s^{-1})
Cavanillesia platanifolia H.B.K. (Bombacaceae)[a]	0.28	14.0	0.397
Tachigalia versicolor Standl. & Wms. (Caesalpinioideae)[a]	0.78	14.0	0.118
K. coriacea	1.10	11.0	0.121
Ormosia macrocalyx Ducke (Papilionoideae)[a]	2.92	9.0	0.031
Anacardium excelsum Skeels (Anacardiaceae)[a]	5.04	4.0	0.002

[a] Kitajima (1992)

The photosynthetic characteristics of *K. coriacea* cotyledons agree well with the observations of Kitajima (1992; see Table 5.3). *K. coriacea* cotyledons with a mean thickness of 1.1 mm at full expansion (see section 5.4.2.3) have a predicted net photosynthetic rate of 0.133 μmol g^{-1} s^{-1}, similar to their measured value of 0.121 μmol g^{-1} s^{-1}. In addition, only the cells 200-300 μm below the adaxial epidermis were chlorophyllous and therefore photosynthetically active. This depth may represent the limit to which efficient photosynthesis may proceed, and indeed Knapp *et al.* (1988) reported that 95% of incident light is absorbed within 200 μm of the adaxial surface in cucumber cotyledons with a total thickness of 1200 μm (1.2 mm). The higher density of stomata on the adaxial leaf surface of *K. coriacea* cotyledons (Self, 1989; unpresented data from this study) may be expected with predominantly adaxial surface gas-exchange. Cells low in the chlorophyllous layer although experiencing lower light intensities than those higher up, may experience

raised ambient CO_2 concentrations as a consequence of the adjacent metabolically active non-photosynthetic spongy-mesophyll.

The dominance of cotyledon photosynthetic productivity at the points of maximum specific growth rate under controlled (d48) and field (d56) conditions (see section 3.3.3), indicates the importance of these organs to these maxima. The predominance of cotyledon photosynthetic productivity through the development of Leaf 1 and Leaf 2 (Figure 5.11 and Figure 5.12) indicates the importance of these organs as a source of photosynthate for the early growth and survival of *K. coriacea* seedlings. The close dependency of growth of one class of foliar appendages on the capacity of the proceeding class to synthesise growth requirements, such as that between first foliar leaves and cotyledons has previously been noted for woody angiosperms (Kramer and Kozlowski, 1979).

The pattern of successive peaks in net photosynthetic rate for successive leaves seen in *K. coriacea* seedlings under controlled conditions is typical of many species (Hodáňová, 1981; Tichá *et al.*, 1985)). A few such 'insertion gradients' (Šesták and Catsky, 1985) have been determined for woody species such as *Populus* (Furukawa, 1973; Dickman *et al.*, 1975)), *Prunus* (Sams and Flore, 1982) and *Quercus* (Hanson *et al.*, 1988[b]). From the maximum net photosynthetic rates for the cotyledons and L1 to L5 measured under controlled conditions, *K. coriacea* appears to have a basipetal insertion gradient of maximum net photosynthetic rate, with maximum P_n in the lowest leaves, at least for those leaves measured.

The cotyledons and L1, L2 and L3 show common declines in net photosynthetic rate towards d98 which were associated with the end of the expansion of leaves of flush 2 (F2; see section 4.2.1 and Figure 4.2). The significant post-d98 increase in P_n seen in the cotyledons and L1, L2, and L3, which were associated with leaf flush 3 (F3), may be response to this increased assimilate demand, and similar to the enhanced net photosynthetic rates seen in pre-existing leaves due to the increase in sink demand, as reported for *Populus* and *Quercus* species (Shiba, 1978; Hanson *et al.*, 1988[a,b]). Previous studies on other species have shown that these P_n enhancements were never as high as the initial peaks coinciding with leaf maturity (Woodward and Rawson, 1976; Fujii and Kennedy, 1985).

Despite similar areas and specific leaf areas at full expansion, cotyledons under controlled conditions reached peak net photosynthetic rates 14 days in advance of those seen under field conditions, and maximum values were nearly double those seen in the field (Table 5.4). Thus environmental conditions were associated with

enhanced assimilatory capacity of these preformed organs. Under field conditions, Leaf 1 is fully expanded by day 75, and therefore P_n values obtained at day 70 (6.2 μmol m^{-2} s^{-1}) must approach peak P_n, estimated to be between 6.5 μmol m^{-2} s^{-1} and 7.5 μmol m^{-2} s^{-1} (assuming coincident peak P_n and full expansion, as was seen under controlled conditions). Thus in contrast to the cotyledons, although areas for Leaf 1 under field and controlled conditions are significantly and substantially different, maximum net photosynthetic rates, although lower, are similar.

Table 5.4 Mean individual leaf areas (A_i, cm^2) and net photosynthetic rates (P_n, μmol m^{-2} s^{-1}) at full expansion, for *K. coriacea* seedlings grown under controlled (*C.C.*1) and field conditions (*F.C.*2). *n.d.* indicates no data available.

Assimilatory Organ	Field Conditions		Controlled Conditions	
	A_i	P_n	A_i	P_n
Cotyledons	19.3	6.5	15.3	11.0
Leaf 1	4.5	6.5-7.5	32.1	8.9
Leaf 2	*n.d.*	*n.d.*	34.3	7.2
Leaf 3	*n.d.*	*n.d.*	41.2	7.0

Estimates of carboxylation efficiency and supply function for the leaves of *K. coriacea* seedlings grown under controlled and field conditions indicate that observed differences in net photosynthetic rate are due primarily to differences in carboxylating activity. For seedlings grown under controlled and field conditions, supply functions are broadly similar (see sections 5.4.2.2 and 5.4.3.2). In contrast, carboxylating efficiencies under controlled conditions are approximately 3 and 2 times greater than under field conditions for the cotyledons and Leaf 1, respectively (see Figure 5.16 and Figure 5.17). Although estimated SF and CE values under controlled conditions were calculated based upon measurements made in the growth room, which were therefore non light-saturating, differences between light saturating and measured values (*c.* 10-20%, see section 5.2.2.2) are insufficient to account for the substantial differences in CE values between controlled and field conditions. These must therefore indicate real differences in carboxylating capacity. This conclusion is supported by chlorophyll concentrations in seedling cotyledons and leaves under controlled and field conditions (Table 5.5).

Table 5.5 Net photosynthetic rates (P_n; $\mu mol\ m^{-2}\ s^{-1}$), estimated carboxylation efficiencies (CE; $mol^{-1}\ m^{-2}\ s^{-1}$), and chlorophyll concentrations ([Chl *a+b*]) for cotyledons and Leaf 1 of *K. coriacea* seedlings grown under controlled and field conditions.

Assimilatory Organ	P_n	CE	[Chl *a+b*]	
			mg $gFwt^{-1}$	$\mu g\ cm^{-2}$
*C.C.*1:				
Cotyledon (d42)	11.0	0.099	0.71	46.3
Leaf 1 (d60)	8.9	0.065	1.14	36.5
*F.C.*2:				
Cotyledon (d56)	6.5	0.030	*n.d.*	17.6
Leaf 1 (d70)	6.2	0.030	*n.d.*	13.6

Leaf chlorophyll concentrations ([Chl *a+b*]) correlate well with estimated carboxylation efficiencies, both between assimilatory organs (cotyledons and Leaf 1) and growing conditions (controlled and field conditions). Cotyledon and Leaf 1 chlorophyll concentrations under controlled conditions are approximately 3 and 2 times those for cotyledons under field conditions, very similar to the ratios for carboxylation efficiency between these conditions. Further research to establish the activity of other carboxylating processes, such as RuBisCO activity (see section 5.4.1), is required to further support these conclusions.

Chlorophyll concentrations of cotyledons of *K. coriacea* are comparable with those reported for photosynthetically active cotyledons of other herbaceous (Lovell and Moore, 1970) and woody species (Ampofo *et al.*, 1976). Maximum chlorophyll concentrations for cucumber and *Acer platanoides* were 38 $\mu g\ cm^{-2}$ and 62 $\mu g\ cm^{-2}$ respectively (Lovell and Moore, 1970; Ampofo *et al.*, 1976), as compared with 46.3 $\mu g\ cm^{-2}$ for *K. coriacea* cotyledons (Table 5.5). Interestingly, *K. coriacea* cotyledons showed a doubling in total cell number (from 3.6E6 to 7.2E6 cells $cot.^{-1}$) from the seed to full expansion, which is rare in angiosperm seedlings, although has been noted for cucumber (Lovell and Moore, 1970).

From the calculated unit leaf rate productivities (Figure 5.10) and unit leaf rates (Figure 3.5, Figure 3.7 and Figure 3.8), estimates can be made of respiration rates on a plant and dry weight basis. This may allow comparison between respiration rates under controlled and field conditions, and thereby establish if the differences in net photosynthetic rates, and therefore plant productivity reported above, are accompanied by significant differences in respiratory loads.

Plant dry weight is assumed to be essentially composed of carbohydrate. Figure 5.10 (inset) shows unit leaf rate productivity (**EP**, on a CO_2 basis) for the *C.C.*1 data. Conversion to productivity on a gramme carbohydrate basis is achieved by multiplication by 0.682, according to:

$$n\mathrm{CO_2} + n\mathrm{H_2O} = (\mathrm{CH_2O})n + n\mathrm{O_2}$$

$$44\ \mathrm{g} + 18\ \mathrm{g} = 30\ \mathrm{g} + 32\ \mathrm{g}$$

For every 44 g CO_2 uptake 30 g CH_2O is produced, that is, for every 1 g CO_2 uptake 0.6818 g of CH_2O is produced.

Figure 5.20 (**A**) shows the relationship between unit leaf rate productivity (**EP**) and unit leaf rate (**E**) and plant age, for *K. coriacea* seedlings grown under controlled conditions (*C.C.*1), both expressed on an area basis. Change in leaf-area with plant age is also indicated (L_A). **E** relates to **EP** according to,

$$\mathbf{E} = \mathbf{EP} - R_D$$

where R_D is respiration rate ($gCH_2O\ m^{-2}\ d^{-1}$). Thus,

$$R_D = \mathbf{EP} - \mathbf{E}$$

Respiration may be expressed on an individual plant basis (R_i) by multiplication by leaf area (L_A),

$$R_i = R_D \cdot L_A$$

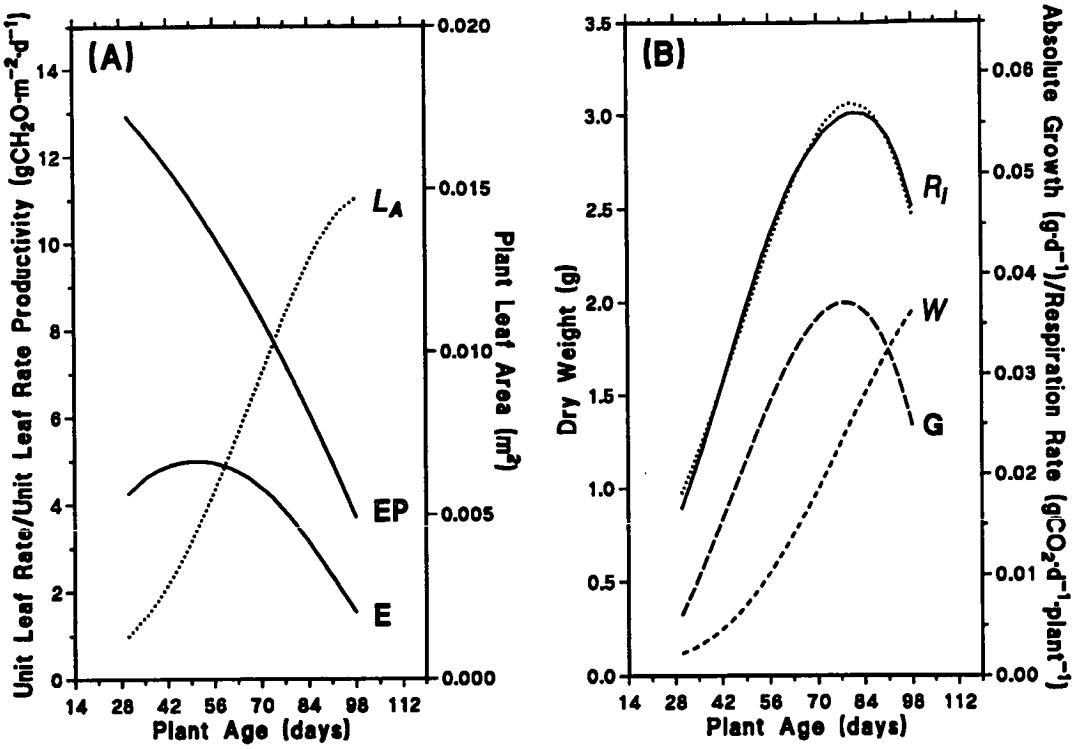


Figure 5.20 **(A)** Relationship between, unit leaf rate productivity (**EP**, from the best fit regression shown in inset, Figure 5.10) and unit leaf rate (**E**, from Figure 3.5) (Y1), and leaf-area (L_A, from Figure 3.3) (Y2), with plant age.

(B) Relationship between, calculated respiration rate (R_i, expressed on a per plant basis) and absolute growth rate (**G**) (Y2), and plant dry weight (*W*) (Y1), with plant age. Line immediately adjacent to R_i (····) represents the estimated individual plant respiration based on relationship (4) and associated parameters in Table 5.6.

Figure 5.20 **(B)** shows the relationship between R_i and plant age, expressed as grammes CO_2 produced per day, calculated by multiplication by 1.466, according to,

$$(CH_2O)n + nO_2 = nCO_2 + nH_2O$$

$$30\ g + 32\ g = 44\ g + 18\ g$$

For every 30 g CH_2O respired 44 g CO_2 is released, that is, for every 1 g CH_2O respired 1.466 g of CO_2 is produced.

Respiration may be resolved into two components, that involved in the production of new tissue, and that involved in the maintenance of existing biomass. These will related to R_i according to,

$$R_i = \mathbf{G} \cdot R_g + W \cdot R_m$$

Plant Respiration = Growth Respiration + Maintenance Respiration

where G and W are the absolute plant growth rate and plant dry weight respectively, and R_g is respiration per unit absolute growth rate and R_m is respiration per unit plant dry weight.

As net photosynthetic rates include the 12 hour photoperiod dark respiration, the maintenance respiration component is more correctly $(^1/_2 L_W + (W - L_W)) \cdot R_m$, where L_W is leaf dry weight. Table 5.6 shows the correlations between R_i and three predictors, G, W, and $^1/_2 L_W + (W - L_W)$, in four possible relationships. Regressed parameter values for R_g and R_m are also displayed.

Table 5.6 Regressed growth respiration (R_g) and maintenance respiration (R_m) coefficients, with correlation coefficients (r^2), for 4 possible relationships between calculated respiration rate (R_i), and absolute growth rate (G), and plant weight components (W) and $(^1/_2 \cdot L_W + (W - L_W))$.

Relationship	R_g (g CO_2 g^{-1})	R_m (g CO_2 g $plant^{-1}$ d^{-1})	r^2
(1) $R_i = R_m \cdot W$	-	0.0161	0.624
(2) $R_i = R_g \cdot \mathbf{G}$	1.27	-	0.977
(3) $R_i = R_g \cdot \mathbf{G} + R_m \cdot W$	1.09	0.0039	0.996
(4) $R_i = R_g \cdot \mathbf{G} + R_m \cdot (^1/_2 \cdot L_W + (W - L_W))$	1.11	0.0050	0.996

Stepwise regression of R_i on the three predictors G, W, and $^1/_2 \cdot L_W + (W - L_W)$, results in preferential selection of two predictors, G and $^1/_2 \cdot L_W + (W - L_W)$ (relationship (4), Table 5.6). The closeness of this correlation is shown in Figure 20(B), where calculated R_i and the estimated respiration rate, based on regressed R_g and R_m values, are plotted adjacently.

These regressed parameter values suggest that the great majority of daily respiration is due to growth and that only a small proportion is due maintenance, from 5% on day 48 (the point of maximum specific growth rate), and 10% on day 77 (the point of maximum absolute growth rate), to 21% by day 98.

The maintenance respiration coefficient, R_m, for $R_i = R_g \cdot G + R_m \cdot (1/2 \cdot L_W + (W - L_W))$ equates to 54 $ngCO_2$ $gplant^{-1}$ s^{-1}. This value provides a mean for all dry weight. However, it is known that woody tissue is laid down in *K. coriacea* from an early age (Self, 1989). Thus this respiration rate will be an under-estimate for the non-woody tissue. Indeed, dark respiration rates for Leaf 1 at full expansion (*i.e.* in the absence of growth) are between 340-410 $ngCO_2$ $gplant^{-1}$ s^{-1} (section 5.2.2.2). This higher value may be explained by the high physiological activity of this organ. Direct respiratory measurements of all *K. coriacea* plant organs are required to confirm these suggestions. Such measurements for different plant organs on a variety of other species (Penning de Vries and Van Laar, 1982; Penning de Vries *et al.*, 1989) indicate a maintenance respiration rate for foliar tissue of 0.03 gCO_2 g^{-1} d^{-1} (347 $ngCO_2$ g^{-1} s^{-1}) (Table 5.7). This value is within the range found for Leaf 1 of *K. coriacea*. Similarly estimated R_g and R_m values for *K. coriacea* are comparable to those presented in Table 5.7. As *K. coriacea* shows substantial root, and particularly storage-root development, estimated R_m (0.005 g CO_2 g $plant^{-1}$ d^{-1}) has a slightly low bias within the range seen for organs with high and low metabolic activity (0.03-0.003 g CO_2 g $plant^{-1}$ d^{-1}). Estimated R_g is of the same order, but slightly lower, than previously reported.

Table 5.7 Respiration coefficients for different plant organ groups (Penning de Vries and Van Laar, 1982; Penning de Vries *et al.*, 1989).

Plant Organs	Growth Requirements (R_g) (gCO2 g $plant^{-1}$)	Maintenance Requirements (R_m) (g CO_2 g $plant^{-1}$ d^{-1})
Leaves	1.46	0.03
Stems	1.51	0.015
Fibrous Roots	1.44	0.015
Storage Organs	1.29	0.003

Calculations made using the same procedure, were used to estimate R_g and R_m values for the field data (Table 5.8). A stepwise regression preferentially selected G and $^1/_2 \cdot L_W + (W - L_W)$ as predictors, and provided R_g and R_m values similar to those for controlled conditions. Values were expected to be high, because photosynthetic productivities under field conditions were based on light-saturating P_n values and not operating values. This would lead to slight over-estimates of PP, R_D, R_i, and therefore R_g and R_m.

Table 5.8 Regressed growth respiration (R_g) and maintenance respiration (R_m) coefficients, with correlation coefficients (r^2), for *K. coriacea* seedlings grown under controlled and field conditions. Estimated R_g and R_m values calculated, based upon the preferential predictors of calculated respiration rate (R_i), absolute growth rate (G) and plant weight component ($^1/_2 \cdot L_W + (W - L_W)$).

Relationship	R_g (g CO_2 g^{-1})	R_m (g CO_2 g $plant^{-1}$ d^{-1})	r^2
Controlled Conditions $R_i = R_g \cdot G + R_m \cdot (^1/_2 \cdot L_W + (W - L_W))$	1.11	0.0050	0.996
Field Conditions $R_i = R_g \cdot G + R_m \cdot (^1/_2 \cdot L_W + (W - L_W))$	1.59	0.0260	0.879

Although R_m values under field conditions are higher than those under controlled conditions (Table 5.8), this may in part be explained by the differing morphologies of the plants during the sampling periods. Under controlled conditions the maintenance respiration was calculated based on plant development from day 28 to day 98. The rapid growth of *K. coriacea* seedlings under controlled conditions meant that this period included a large proportion of the phase of main root favoured development (section 3.4.3), and therefore a considerable period with plant dry weight substantially composed of xylopodium storage-tissue. The slower growth of seedlings under field conditions meant that the period over which R_m was calculated, was largely composed of the initial phase of cotyledon dominated plant dry weight. This would heavily 'weight' the value of R_m for metabolically highly active leaf tissue, *i.e.* higher values.

Net photosynthetic rates for cotyledons and leaves of *K. coriacea* seedlings were comparable with those reported for other woody species. Leaves have a basipetal insertion gradient of maximum net photosynthetic rate, with highest P_n values for cotyledons. Declining P_n values for the cotyledons and Leaf 1, 2, 3 towards d98, increased in association with leaf flush 3 (F3), suggesting a response to increased sink demand. The cotyledons were very important to early growth, providing the majority of photosynthate for seedling development up to day 56, and therefore for Leaf 1 and Leaf 2 formation. Under field conditions net photosynthetic rates were lower and peaked later than under controlled conditions. These lower net photosynthetic rates were due to lower carboxylation efficiencies, and not supply functions. This was indicated by estimated carboxylation efficiencies, and the levels of photosynthetic pigments. Estimates of respiration rate suggest that growth and maintenance respiration coefficients (R_g and R_m, respectively) are similar to those reported for other species, and that there was no significant differences in R_g and R_m between controlled and field conditions.

CHAPTER 6

Photosynthesis in Trees of *Kielmeyera coriacea* Mart. and Other Cerrado Woody Species.

6.1 Introduction

This chapter describes the results of photosynthetic analyses of *Kielmeyera coriacea* trees and other Cerrado woody species under field conditions. All measurements were made on adult material using the methodology described in section 2.2.6.3. The aim of these analyses was to investigate the photosynthetic characteristics of mature *K. coriacea* plants, and to contrast these with those of *K. coriacea* seedlings (see Chapter 5) and other Cerrado woody species. Objectives were to determine, for *K. coriacea* trees and a representative selection of other Cerrado woody species: (1) the photosynthetic performance, that is the response of net photosynthetic rate, stomatal conductance and intercellular CO_2 concentration to incident photosynthetic photon flux; (2) the photosynthetic behaviour, that is net photosynthetic rate, stomatal conductance and intercellular CO_2 concentration, through the course of the day.

Existing photosynthetic studies of Cerrado woody species under field conditions are few and concern a limited number of species: *Caryocar brasiliense* Camb. (Caryocaraceae) (Pereira Netto and Hay, 1986), *Didymopanax macrocarpum* (C. & S.) Seem. (Araliaceae) (Franco, 1983; Johnson *et al.*, 1983), and *Ouratea hexasperma* (St. Hil.) Baill. (Ochnaceae) (Johnson *et al.*, 1983).

Gas-exchange measurements were made during the period 25/01/91 to 15/03/91. Eight species were investigated for photosynthetic performance by making spot measurements at random. Four of these species were considered further in time-course photosynthetic analyses to determine photosynthetic behaviour. Species for random spot measurements were selected on the basis of being important Cerrado species (Goodland and Ferri, 1979), being locally abundant, having an entire leaf shape, and having a related or distinct ecology to that of *K. coriacea*. As a consequence the following eight species were investigated: *Anacardium humile* St. Hil. (Anacardiaceae), *Annona coriacea* Mart. (Annonaceae), *Bauhinia holophylla* Steud. (Leguminosae/Caesalpinoideae), *Byrsonima coccolobifolia* Kunth (Malpighiaceae), *Kielmeyera coriacea* Mart., *Kielmeyera variabilis* Mart. (Guttiferae), *Ouratea spectabilis* (Mart.) Engl (Ochnaceae), and *Xylopia aromatica* Lam. (Annonaceae). This ecologically diverse group includes: a locally dominant and characteristic Cerrado species (*K. coriacea*; Goodland and Ferri, 1979), a legume (*Ba. holophylla*), a hemi-cryptophyte (*Ana. humile*) and a cerrado/cerradão border species (*X. aromatica*).

6.2 Random Spot Photosynthetic Measurements

Random measurements were made on healthy leaves, typically between the hours of 10:00 and 14:00 hr. Leaves were selected from high and low positions, sun and shade locations on the trees, and measurements were made on a number of separate occasions. Although data was collected under a range of environmental conditions, in terms of atmospheric CO_2 concentrations and air temperatures, measurements are only considered further here if made under atmospheric CO_2 concentrations of 340-370 μmol mol^{-1} and air temperatures of 27-33°C.

6.2.1 The Relationship between Net Photosynthetic Rate and Incident Photosynthetic Photon Flux Density

Net photosynthetic rates (P_n) varied substantially within and between species, most notably in response to differing incident photosynthetic photon flux densities ($PPFD_i$). The relationships between photosynthetic rate and incident photosynthetic photon flux for different Cerrado species could be separated into two groups: those in which P_n increased more or less linearly with increasing $PPFD_i$ to a plateau value at light saturation, such as that seen for *Bauhinia holophylla* (Figure 6.1) and *Byrsonima coccolobifolia* (Figure 6.2); and those in which the relationship was more diffuse *i.e. Kielmeyera coriacea* (Figure 6.3), *Anacardium humile* (Figure 6.4), *Annona coriacea, Xylopia aromatica, Kielmeyera variabilis,* and *Ouratea spectabilis.* For this second group, as photon flux increased the range of P_n values increased, from low values to an upper limit. Reference to the $P_n/PPFD_i$ relationship for *K. coriacea* (Figure 6.3) shows that at high light intensities a range of sub-maximal P_n values obscure the clearer type of relationship seen for *Ba. holophylla* and *By. coccolobifolia.* For all species, these sub-maximal photosynthetic rates were often associated with lower stomatal conductances. Minimum light-saturating photon fluxes varied between species, ranging from around 800 μmol Quanta m^{-2} s^{-1} for *By. coccolobifolia* and *Ana. humile,* to around 1400-1500 μmol Quanta m^{-2} s^{-1} for *Ba. holophylla* and *K. coriacea.*

Net photosynthetic rate, stomatal conductance and intercellular CO_2 concentration data at saturating light intensities (defined as $PPFD_i$>1500 μmol Quanta m^{-2} s^{-1}) are summarised and displayed in Figures 6.5, 6.6, and 6.7, respectively.

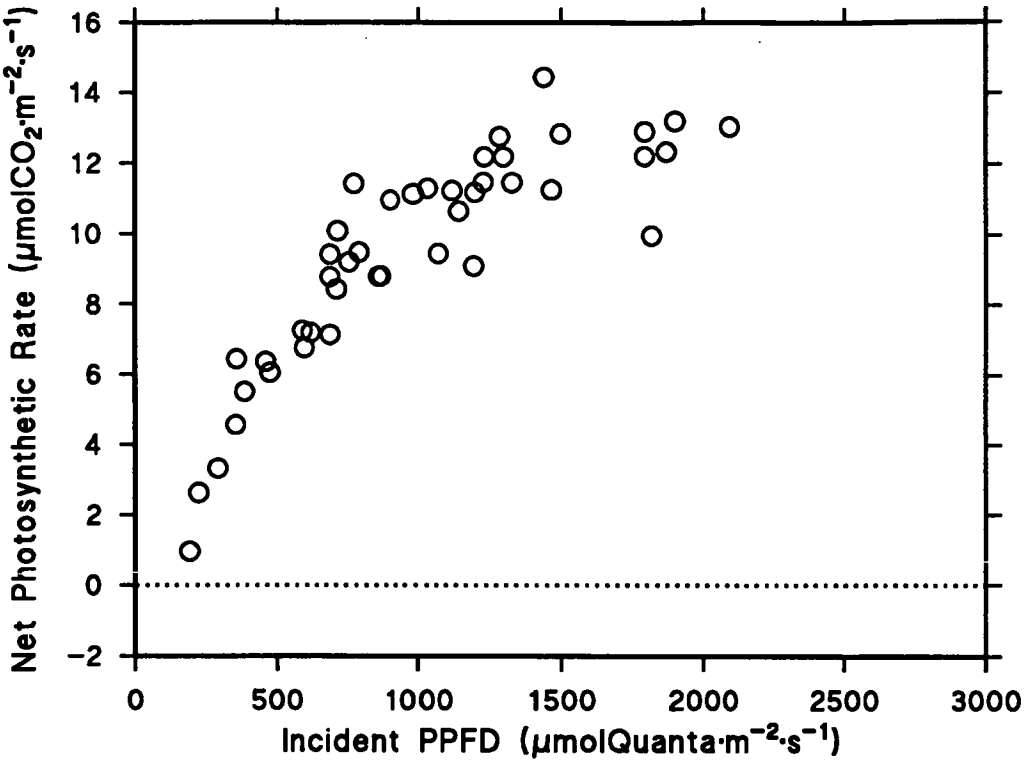


Figure 6.1 Scatter diagram showing the relationship between net photosynthetic rate (P_n) and incident photosynthetic photon flux density ($PPFD_i$) for *Bauhinia holophylla* in the field. Data are restricted to air temperatures of 27-33°C and ambient CO_2 concentrations of 340-370 μmol mol^{-1}. Each point is P_n for a single leaf.

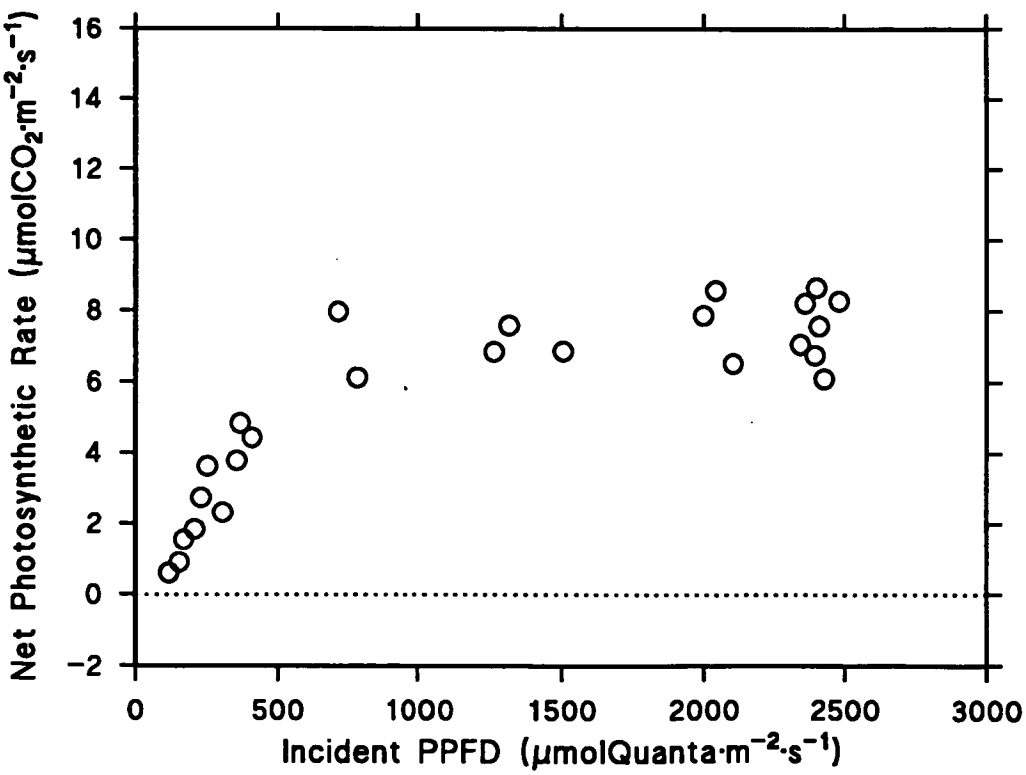


Figure 6.2 Scatter diagram showing the relationship between net photosynthetic rate (P_n) and incident photosynthetic photon flux density ($PPFD_i$) for *Byrsonima coccolobifolia* in the field. Data are restricted to air temperatures of 27-33°C and ambient CO_2 concentrations of 340-370 μmol mol^{-1}. Each point is P_n for a single leaf.

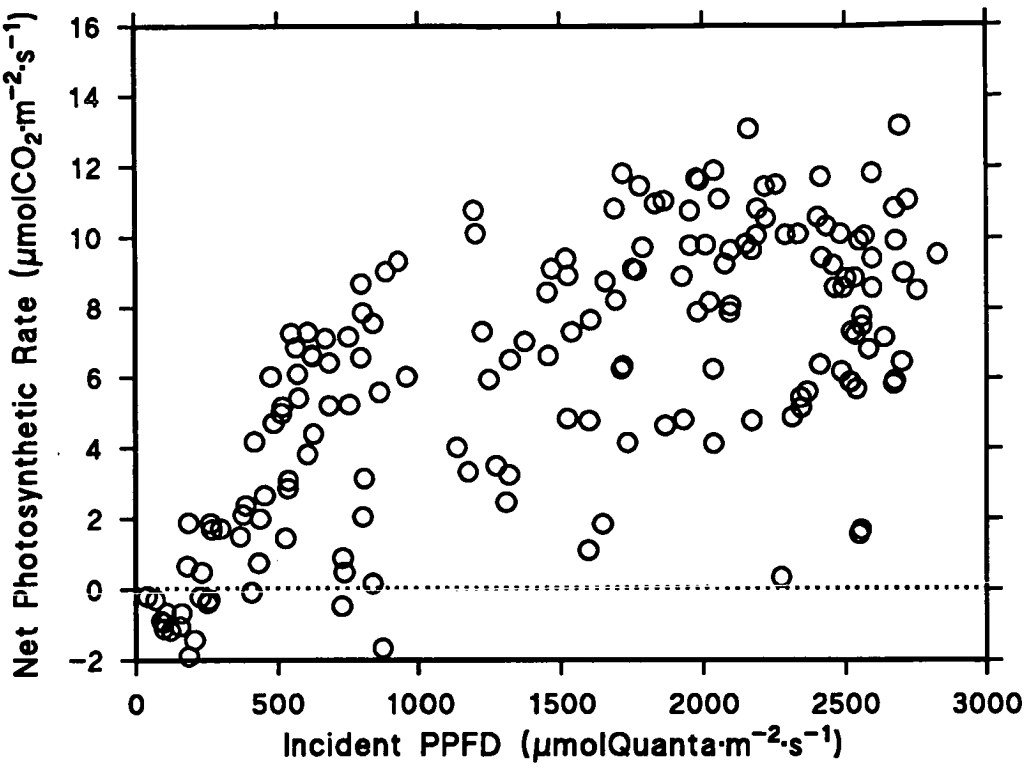


Figure 6.3 Scatter diagram showing the relationship between net photosynthetic rate (P_n) and incident photosynthetic photon flux density ($PPFD_i$) for *Kielmeyera coriacea* in the field. Data are restricted to air temperatures of 27-33°C and ambient CO_2 concentrations of 340-370 μmol mol^{-1}. Each point is P_n for a single leaf.

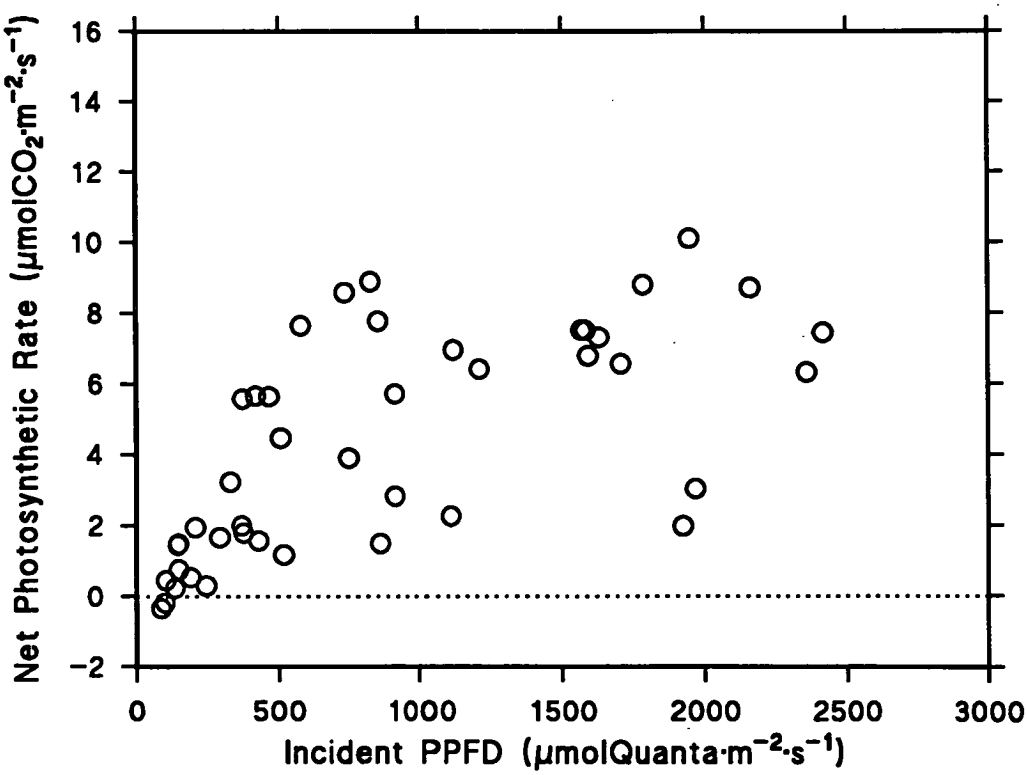


Figure 6.4 Scatter diagram showing the relationship between net photosynthetic rate (P_n) and incident photosynthetic photon flux density ($PPFD_i$) for *Anacardium humile* in the field. Data are restricted to air temperatures of 27-33°C and ambient CO_2 concentrations of 340-370 μmol mol^{-1}. Each point is P_n for a single leaf.

6.2.2 Gas-Exchange Behaviour at Saturating Photon Flux

6.2.2.1 Net Photosynthetic Rate

Mean net photosynthetic rates at saturating photon flux densities are, acknowledging the favourable sampling conditions, field determined approximations of photosynthetic capacities (P_c) by definition (see section 5.2.1). P_c values and their 95% confidence limits, for the eight species considered are shown in Figure 6.5. This range is continuous from the leguminous *Ba. holophylla* (P_c=12.2 μmol m^{-2} s^{-1}) and the cerrado/cerradão border species *X. aromatica* (P_c=10.5 μmol m^{-2} s^{-1}), to the hemi-cryptophyte *Ana. humile* (P_c=7.4 μmol m^{-2} s^{-1}) and *K. variabilis* (P_c=6.5 μmol m^{-2} s^{-1}). *K. coriacea* with a photosynthetic rate of 9.2 μmol m^{-2} s^{-1} is central in this almost two-fold range of values (range mean=9.1 μmol m^{-2} s^{-1}).

6.2.2.2 Stomatal Conductance

Mean stomatal conductances (g_s) range from 0.15 mol m^{-2} s^{-1} for *Ana. humile* to 0.34 mol m^{-2} s^{-1} for *Ann. coriacea*, with a mean for all the species of 0.26 mol m^{-2} s^{-1} (Figure 6.6). *K. coriacea* has a small spread of g_s values, with a low mean of 0.19 mol m^{-2} s^{-1}.

6.2.2.3 Intercellular CO_2 Concentration

Mean intercellular CO_2 concentration (c_i) varied between species (Figure 6.7), from a minimum for *X. aromatica* of 228 μmol mol^{-1} to a maximum of 270 μmol mol^{-1} for *K. variabilis*, with *K. coriacea* at the lower edge of the range with 240 μmol mol^{-1}.

6.2.3 Estimated Carboxylation Efficiencies and Supply Functions

Carboxylation efficiencies (CE) and supply functions (SF) were estimated as for section 5.4.2.2, assuming a compensation CO_2 concentration of 50 μmol mol^{-1}, a linear demand function to the P_n/c_i points, and an atmospheric CO_2 concentration of 355 μmol mol^{-1}. A CO_2 compensation concentration of 50 μmol mol^{-1} is typical of the unstressed leaves of mature woody species (Schaedle, 1975), and as this value is common to all species considered, real interspecific variation would have minimal relative effect on estimated CE and SF values.

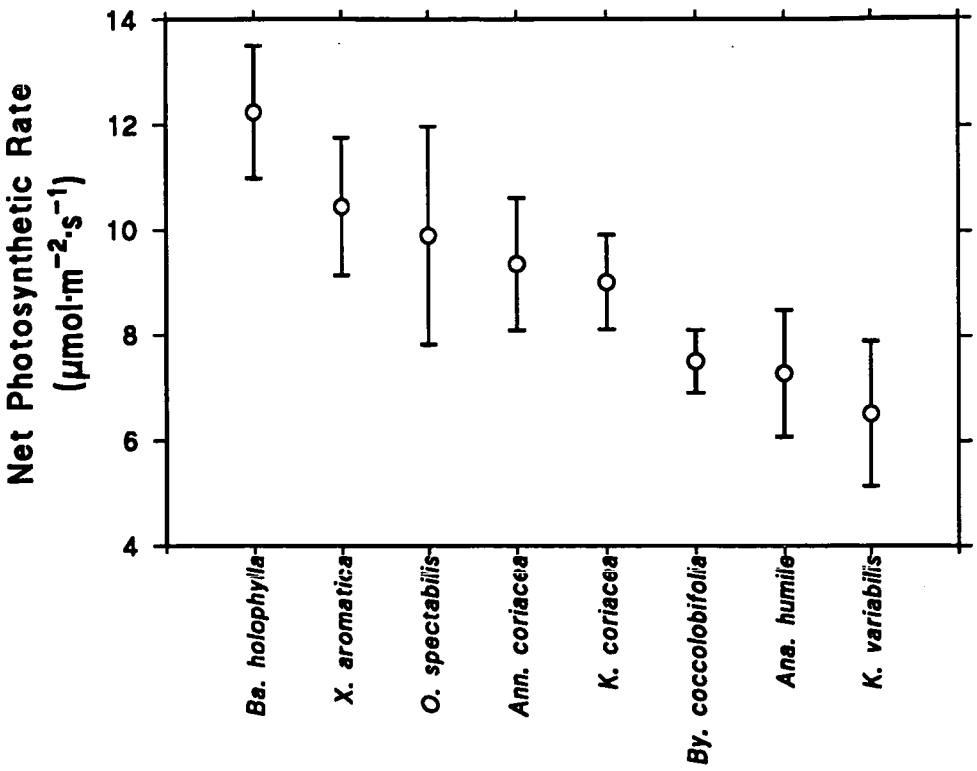


Figure 6.5 Net photosynthetic rates at saturating light intensities (>1500 μmol Quanta m^{-2} s^{-1}) for several Cerrado woody species in the field. Values are sample means, with bars indicating 95% confidence intervals.

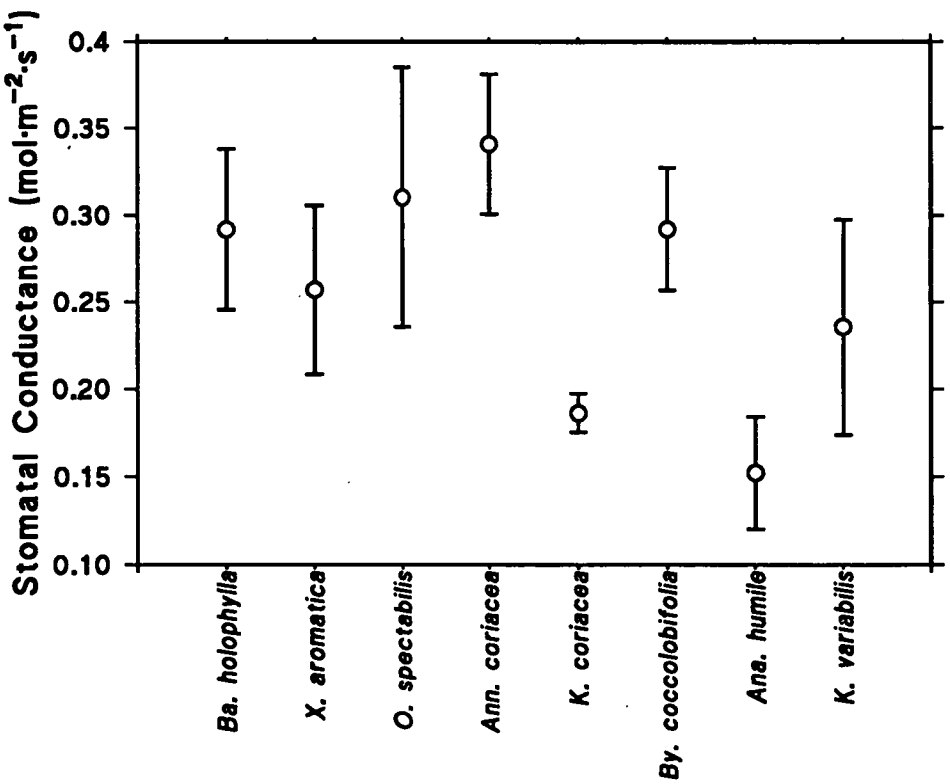


Figure 6.6 Stomatal conductances at saturating light intensities (>1500 μmol Quanta m^{-2} s^{-1}) for several Cerrado woody species in the field. Values are sample means, with bars indicating 95% confidence intervals.

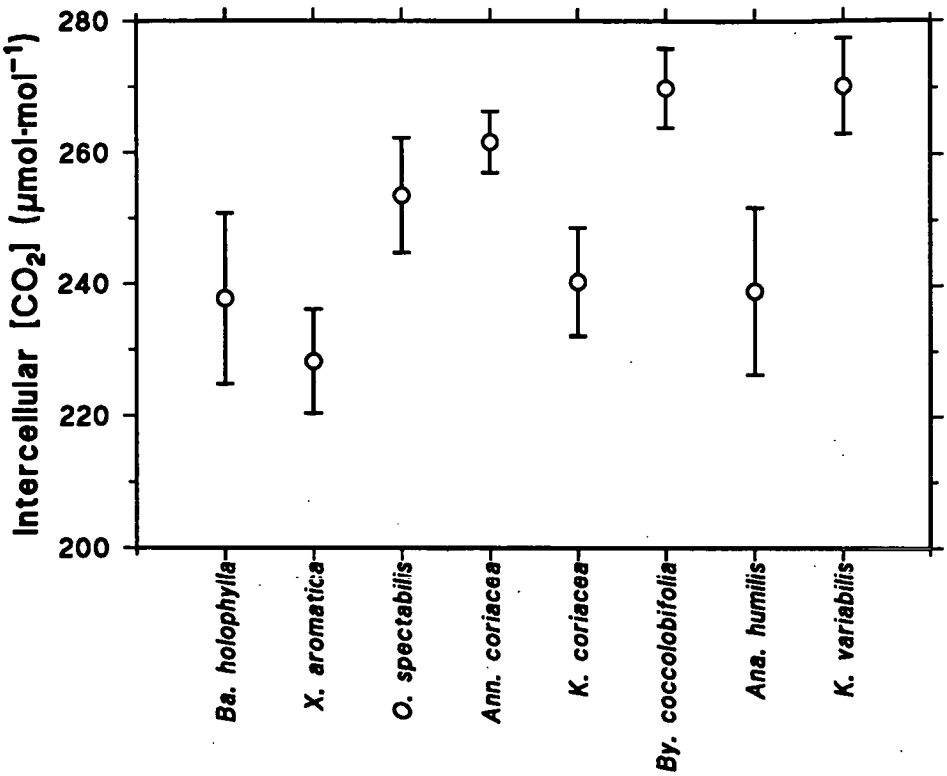


Figure 6.7 Intercellular CO_2 concentrations at saturating light intensities (>1500 µmol Quanta m^{-2} s^{-1}) for several Cerrado woody species in the field. Values are sample means, with bars indicating 95% confidence intervals.

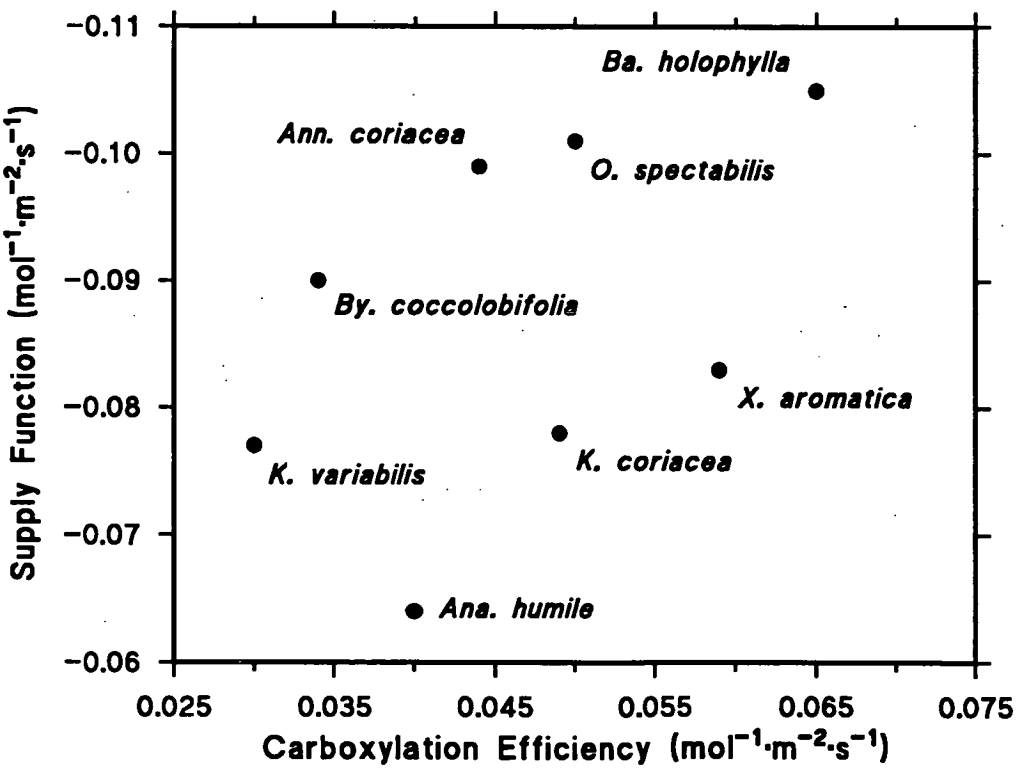


Figure 6.8 Estimated carboxylation efficiencies (CE) and supply functions (SF) for several Cerrado woody species in the field. Values are sample means. Details of CE and SF calculation are provided in section 6.2.3.

For efficient allocation of leaf nitrogen to photosynthesis von Caemmerer and Farquhar (1981) suggest that plants should operate in the region of transition between Ribulose Bisphosphate (RuBP) limited (initial linear slope) and RuBP regeneration limited (plateau) portions of the demand function (see Figure 5.15), such that the two processes are co-limiting and excess nitrogen is allocated to neither. This has been shown in certain crop species, such as *Phaseolus vulgaris* L. (Caemmerer and Farquhar, 1981) and Soybean (Harley *et al.*, 1985). However, field studies for *Acacia ligulata* (Schulze *et al.*, 1982), *Arbutus unedo* (*Harley et al.*, 1986), *Dodonaea angustissima* (Schulze *et al.*, 1982), *Quercus coccifera* (Tenhun en *et al.*, 1984a) and *Quercus suber* (Tenhun en *et al.*, 1984b) have shown that a variety of seasonally arid and semi-arid woody species operate on the linear part of the demand function, sometimes low on this initial slope (Tenhun en *et al.*, 1984b), even at the time of highest daily CO_2 uptake (Schulze *et al.*, 1982). Indeed, the response curve does not usually depart appreciably from linearity up to the normal operating value of c_i (Jarvis and Sandford, 1986). This is thought to be an adaptation to the mean light environment experienced by the plants. An atmospheric CO_2 concentration of 355 μmol mol^{-1} was considered reasonable, as this is the mid-point of the selected data set of atmospheric CO_2 concentrations used (see section 6.2).

Figure 6.8 shows estimated carboxylation and supply function values for the eight species considered. Increasing values indicate increasing carboxylation efficiencies and supply functions, however supply functions are negative as a consequence of their derivation. Clearly different species achieve their photosynthetic rates as a consequence of differing reliances on CO_2 supply and carboxylation processes. The maximal photosynthetic rate of *Ba. holophylla* (P_n=12.2 μmol m^{-2} s^{-1}) is a product of maximal supply function (-0.105 mol m^{-2} s^{-1}), and maximal carboxylation efficiency (0.065 mol m^{-2} s^{-1}). *K. coriacea* and *Ann. coriacea*, achieve their similar net photosynthetic rates (9.2 and 9.3 μmol m^{-2} s^{-1} respectively) by contrasting means: *K. coriacea* has a low supply function (-0.078 mol m^{-2} s^{-1}) and high carboxylation efficiency (0.049 mol m^{-2} s^{-1}) whereas *Ann. coriacea*, with its large stomatal conductance, has a high supply function (-0.099 mol m^{-2} s^{-1}) but lower carboxylation efficiency (0.044 mol m^{-2} s^{-1}).

6.3 Time-course Photosynthetic Measurements

Of the eight species selected for random spot measurements, four were selected to establish their photosynthetic behaviour through the course of a day by time-course analysis. These were *Kielmeyera coriacea* Mart., *Bauhinia holophylla* Steud., *Annona coriacea* Mart., and *Anacardium humile* St. Hil..

Time-course analysis involved repeated photosynthetic measurement of a specific leaf, *in situ*, typically at 60-90 min. intervals. The first measurement was normally made immediately before dawn, and the analysis continued thereafter for the experimental day. For each occasion and each leaf measured, environmental conditions and leaf orientation were recorded, respectively.

6.3.1 Environmental Conditions

Values for the three environmental variables, ambient photosynthetic photon flux (PPFD), atmospheric CO_2 concentration ($[CO_2]$) and air temperature (T_A) were recorded at 30 min. intervals for all time-course experiments.

6.3.1.1 Ambient Photosynthetic Photon Flux

The months of January, February and March 1991 showed an increase in monthly rainfall over the previous summer months, with associated reduced amounts of sunshine (see Appendix 2.1), as is usual. The increased cloud cover often resulted in rapidly varying ambient photon flux levels at the field site, from maximum values possible for the time of day ((a), Figure 6.9) to minima of 100-200 μmol Quanta m^{-2} s^{-1} ((b), Figure 6.9). The two loci shown in Figure 6.9 ((a) and (b)) represent the two extremes seen, of clear and cloudy days, and experimental days typically consisted of a combination of clear sky and intermittent cloud.

6.3.1.2 Air Temperature and Atmospheric CO_2 Concentration.

Pre-dawn air temperatures of 15-20°C rose steadily from daybreak reaching maximum values of 30-35°C between 12:30-13:30, remaining high until late afternoon when values began to decline (T_A, Figure 6.10).

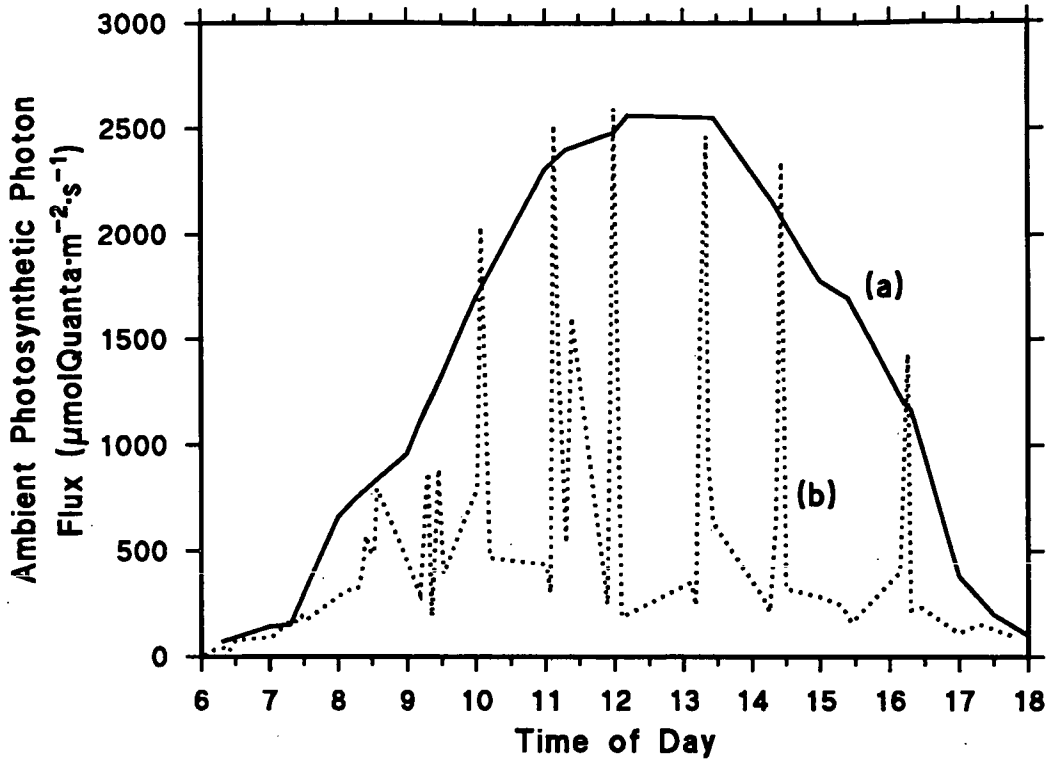


Figure 6.9 Ambient photosynthetic photon flux levels for two separate days at the Reserva Biológica de Mogi-Guaçú field site: (a) cloudless day with a slight haze; (b) cloudy day with occasional cloud breaks, both recorded during the period 25/01/91 to 15/03/91.

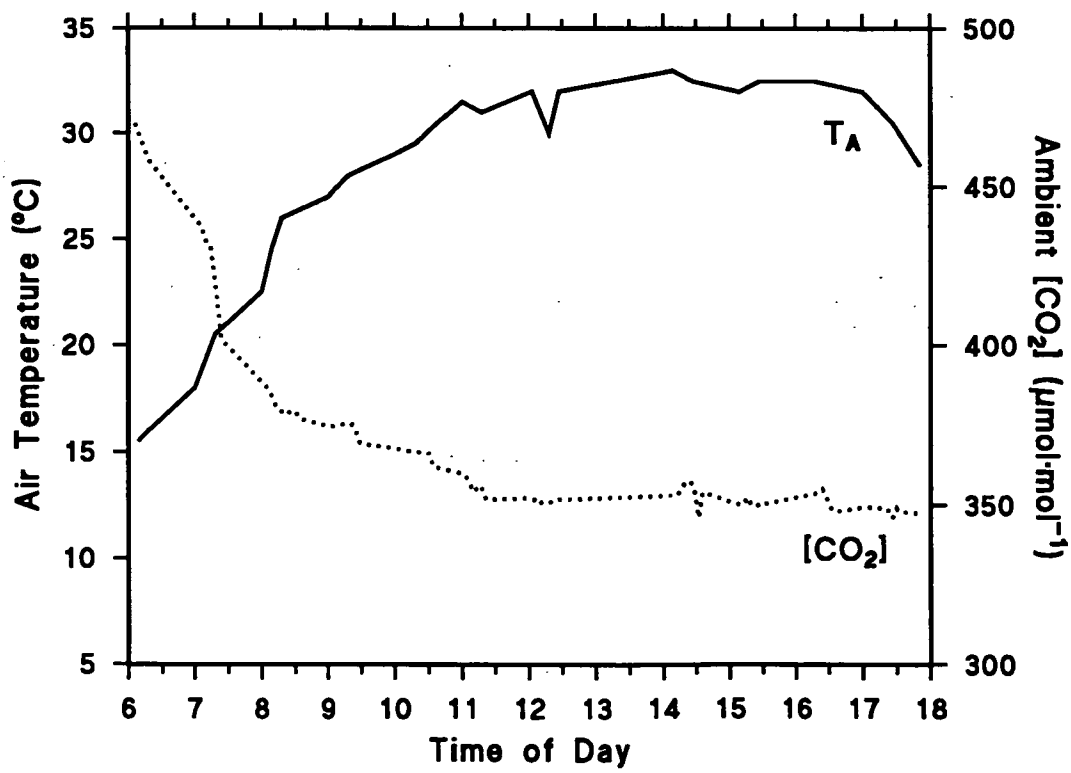


Figure 6.10 Air temperatures (T_A) and atmospheric CO_2 concentrations ($[CO_2]$) for a typical day at the Reserva Biológica de Mogi-Guaçú field site, recorded during the period 25/01/91 to 15/03/91.

Pre-dawn and early morning atmospheric CO_2 concentrations over the vegetation were always above the global mean of 353 μmol mol^{-1} (IPCC, 1990), typically to levels of around 450 μmol mol^{-1} (Figure 6.10). From dawn (05:00-06:00) levels declined rapidly, to around 350-360 μmol mol^{-1} by 10:00-11:00, thereafter remaining constant until sunset (19:00-20:00). This pattern was seen on all experimental days, variation only seen in the rate of early morning CO_2 concentration decline. This was thought to be increased by high early morning photon fluxes and higher wind speeds.

6.3.2 Limitations of the Measurement Technique

Concern was expressed as to the effect leaf handling had on photosynthetic behaviour, and so values for any one measurement were considered in view of the known performance of the species from random spot measurements, and the preceding behaviour of the leaf. Of the four species investigated only one showed sensitivity and changes in behaviour thought to be due to handling (see section 6.3.7).

6.3.3 Leaf Orientation and Photosynthetic Behaviour

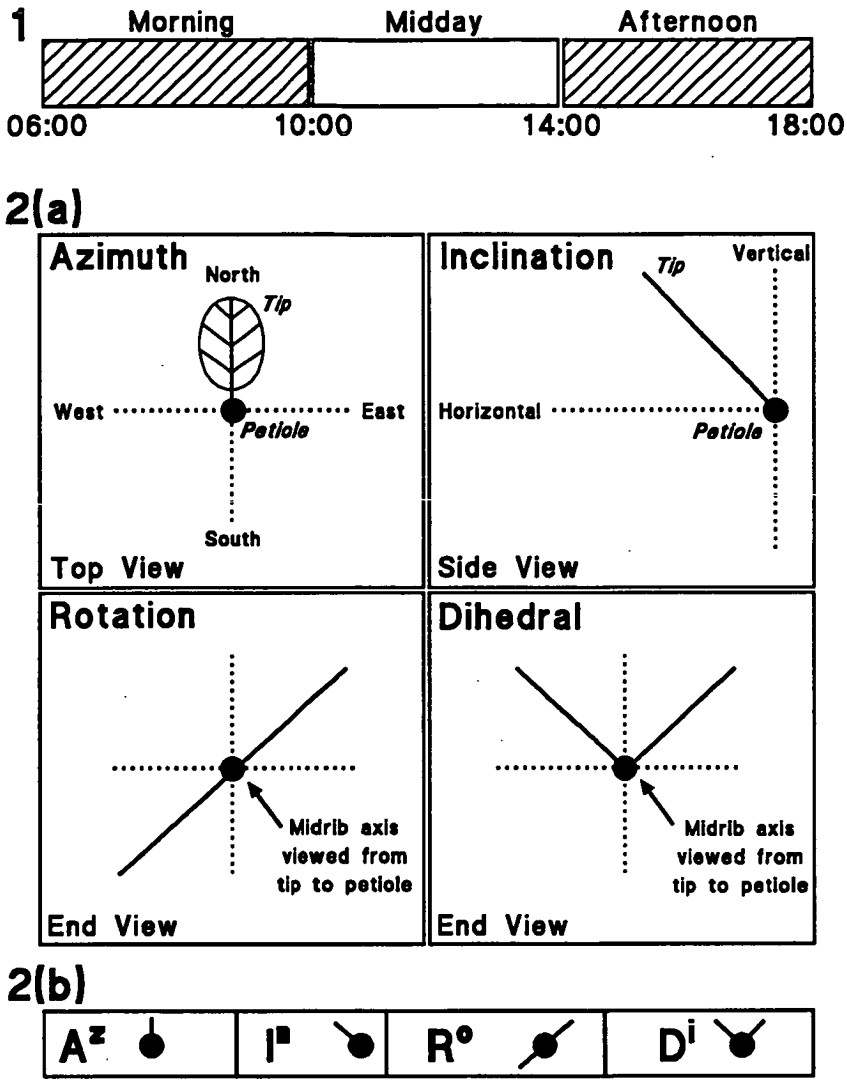
All leaves showed changes in photosynthetic behaviour through the course of the day, most often in association with changes in incident photon flux, atmospheric CO_2 concentration and possibly air temperature.

Solar radiation incident on a leaf may vary substantially depending on specific leaf orientation. The orientation of the leaf affects three separate aspects of solar radiation interception by the lamina: (1) daily integral radiation, (2) peak instantaneous irradiance, and (3) diurnal distribution of instantaneous incident irradiance (Ehleringer and Werk, 1986). The diurnal distribution on a steeply angled leaf facing East-West is heavily weighted toward the early morning and late afternoon, reducing midday irradiance. The steeper the angle the more the irradiance is shifted away from noon. This contrasts with a horizontal lamina which has a simple parabolic distribution of solar irradiance over the course of a day.

Incident photosynthetic photon flux ($PPFD_i$), defined as the amount of photosynthetically active radiation incident on the leaf surface, is determined by ambient photosynthetic photon flux, plant location, leaf position on the plant, and leaf orientation. Plant location and leaf position refer to shading by surrounding vegetation (determined by the stature of the plant and adjacent vegetation), and shading by the parent plant, respectively. For each division of the photoperiod:

morning (06:00-10:00), midday (10:00-14:00) and afternoon (14:00-18:00), any substantial shading of the leaf (>50%) due to leaf location and/or leaf position was recorded. Leaf orientation, referring to the 3-dimensional orientation of the leaf, was characterised by azimuth, inclination from the horizontal, rotation about the midrib axis, and lamina dihedral. The orientation of *Bauhinia holophylla* leaves was determined against the pulvinus at its junction with the leaf laminae. The orientation of the pulvinus does not represent the actual orientation of the leaf unless the leaf laminae are without a dihedral (*i.e.* in a flat plane; Forseth and Ehleringer, 1980).

Figure 6.11 Key explaining leaf shading and orientation diagrams,



1 shows the division of the daily photoperiod in to three parts: morning, midday and afternoon, separated at 10:00 and 14:00. Substantial shading (>50%) in any one part due to location or position is indicated by diagonal hatching, whereas unobstructed insolation is indicated by an open box. The shading diagram shown in **1** represents substantial morning and afternoon shading.

2(a) shows the determination of azimuth (A^z), inclination (I^n), rotation (R^o) and dihedral (D^i). Azimuth or compass bearing, and inclination, elevation or depression from the horizontal were determined from petiole to leaf tip. Rotation of the leaf lamina and dihedral, inclination between the lamina planes, were determined by looking down the midrib from leaf tip to petiole. All leaf orientations were measured to the nearest 22.5° band, *i.e.* for a horizontal leaf inclination could be +/- 11.25°.

2(b) shows the orientation diagram for the leaf shown in 2(a): a North pointing leaf, elevated to 45°, rotated anti-clockwise 45°, with a 90° dihedral between the lamina planes.

6.3.4 Photosynthetic Behaviour of *Kielmeyera coriacea* Mart. Leaves

The photosynthetic behaviour of 22 leaves from 11 *Kielmeyera coriacea* plants was measured on three separate days. The mature plants ranged from 2.0 to 3.5 m in height and were not subject to shading by the surrounding vegetation. The growing shoots were generally oriented within an inverted cone subtending 45°C from the vertical, although occasionally beyond this to the horizontal (*i.e.* in a hemisphere). Growing tips have a spiral phyllotaxis on a short shoot, resulting in the characteristic rosette growth form of *K. coriacea* shoots. Consequently leaves were oriented randomly with respect to azimuth, elevation and rotation, and had no dihedral.

The great variety of leaf orientations, even for a single growing tip, meant that diurnal photosynthetic patterns for *K. coriacea* leaves varied substantially. Leaf orientations largely determined incident photon fluxes as the canopies of *K. coriacea* trees are generally open.

Net photosynthetic rates were closely associated with incident photon flux levels (Figures 6.12, 6.13, 6.14, 6.15). Horizontal leaves receiving a single peak $PPFD_i$ exhibited a corresponding single peak of high P_n values, as in leaf KC1 (Figure 6.12), where the peaks are offset from midday because of a slight leaf rotation to face the morning sun. Vertically oriented, East-West facing leaves received a bimodal pattern of $PPFD_i$ with a corresponding bimodal pattern of net photosynthetic rate (KC2, Figure 6.13). The wide variety of alternative leaf orientations observed in the field resulted in a greater variety of leaf photosynthetic behaviours than the two examples provided here.

Leaf position was occasionally important to incident photon flux level, despite the open nature of the *K. coriacea* canopy (Figure 6.14 and Figure 6.15). Leaf KC4 (Figure 6.15) had an orientation similar to that of leaf KC2 (Figure 6.13) but did not show the second afternoon peak in $PPFD_i$, and so P_n. This was because the leaf was positioned on the east side of the tree, and was subject to self-shading at this time.

Differences were seen in the photosynthetic activity of different *K. coriacea* leaves, as was suggested by Figure 6.3. Under very similar environmental conditions of $PPFD_i$, atmospheric CO_2 concentration, and air temperature, leaf KC1 had a P_n of 10 $\mu mol\ m^{-2}\ s^{-1}$ (at 10:30, Figure 6.12), as compared with 6 $\mu mol\ m^{-2}\ s^{-1}$ for leaf KC3 (at 11:00, Figure 6.14).

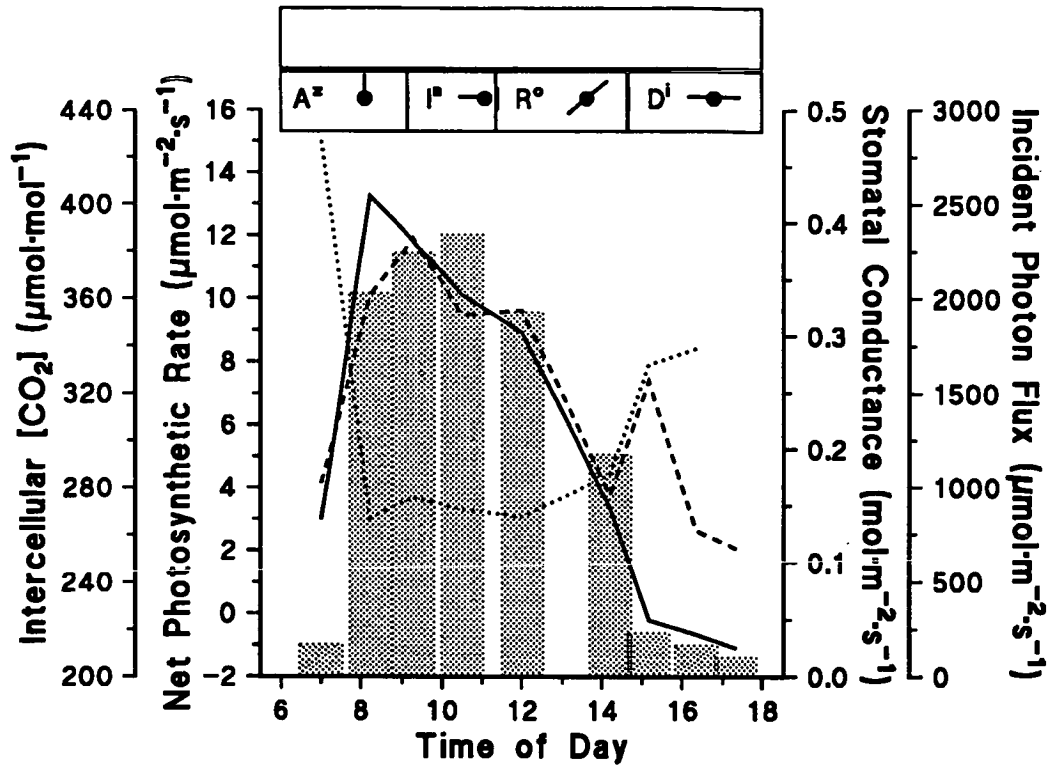


Figure 6.12 Photosynthetic behaviour of leaf KC1, an essentially horizontal *Kielmeyera coriacea* leaf rotated slightly to face the morning sun, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day.

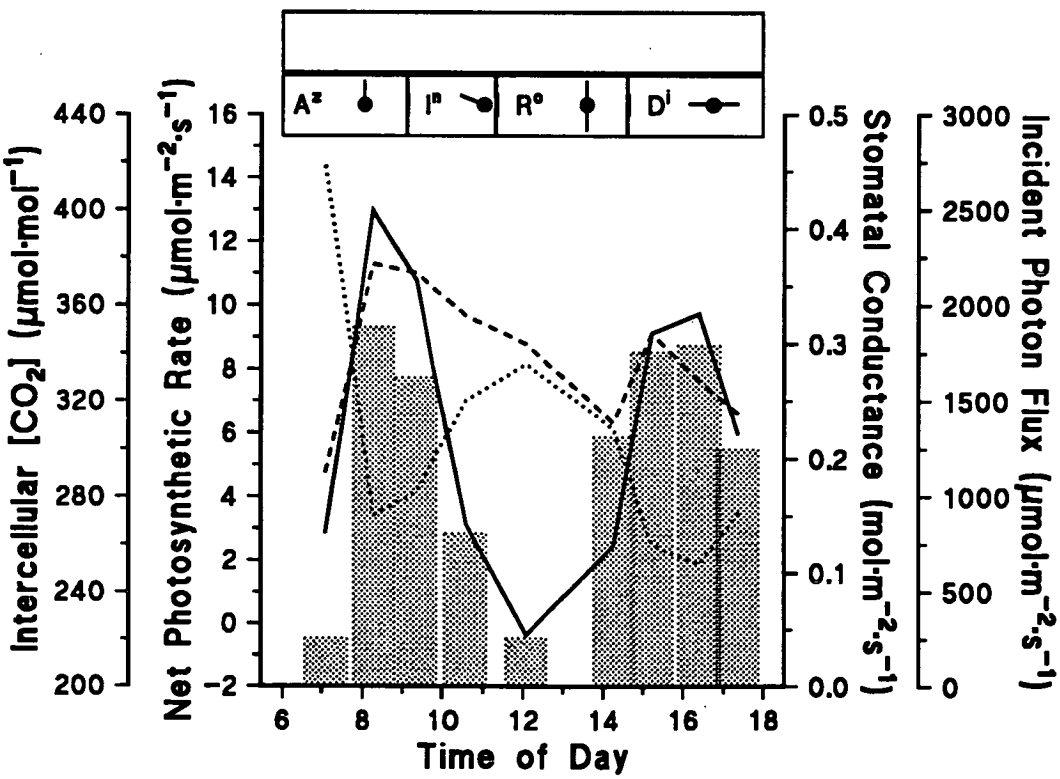


Figure 6.13 Photosynthetic behaviour of leaf KC2, a vertical East-West facing *Kielmeyera coriacea* leaf, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day.

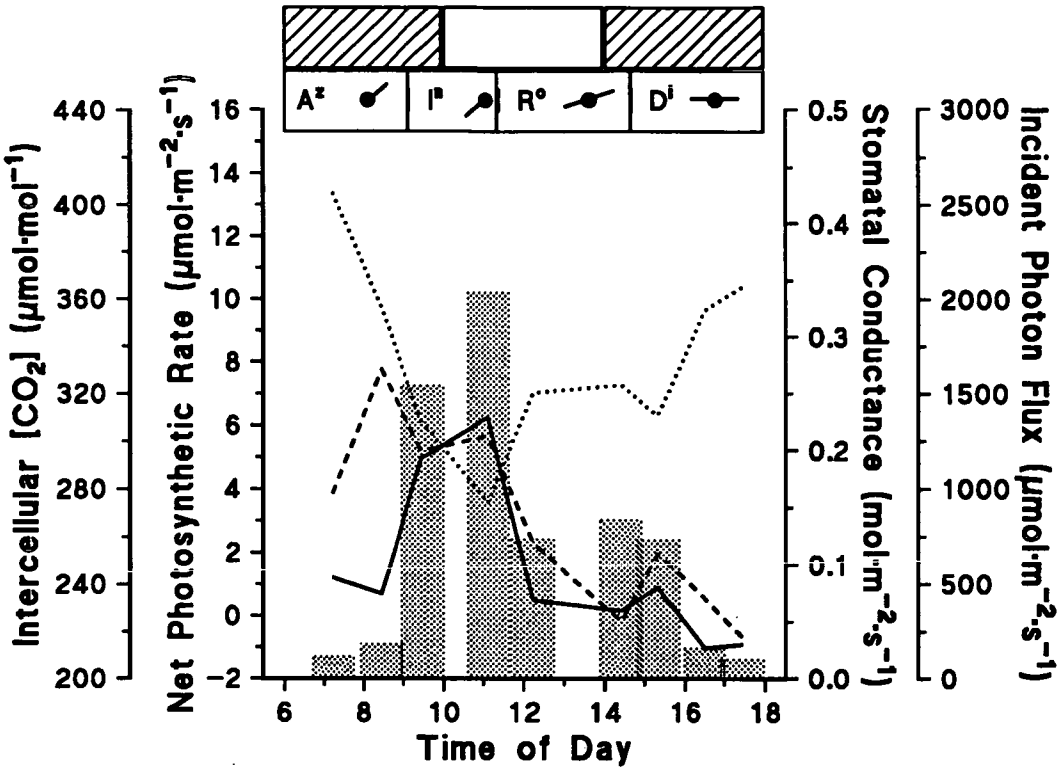


Figure 6.14 Photosynthetic behaviour of leaf KC3, a *Kielmeyera coriacea* leaf of relatively low photosynthetic activity, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day. Note morning and afternoon shading.

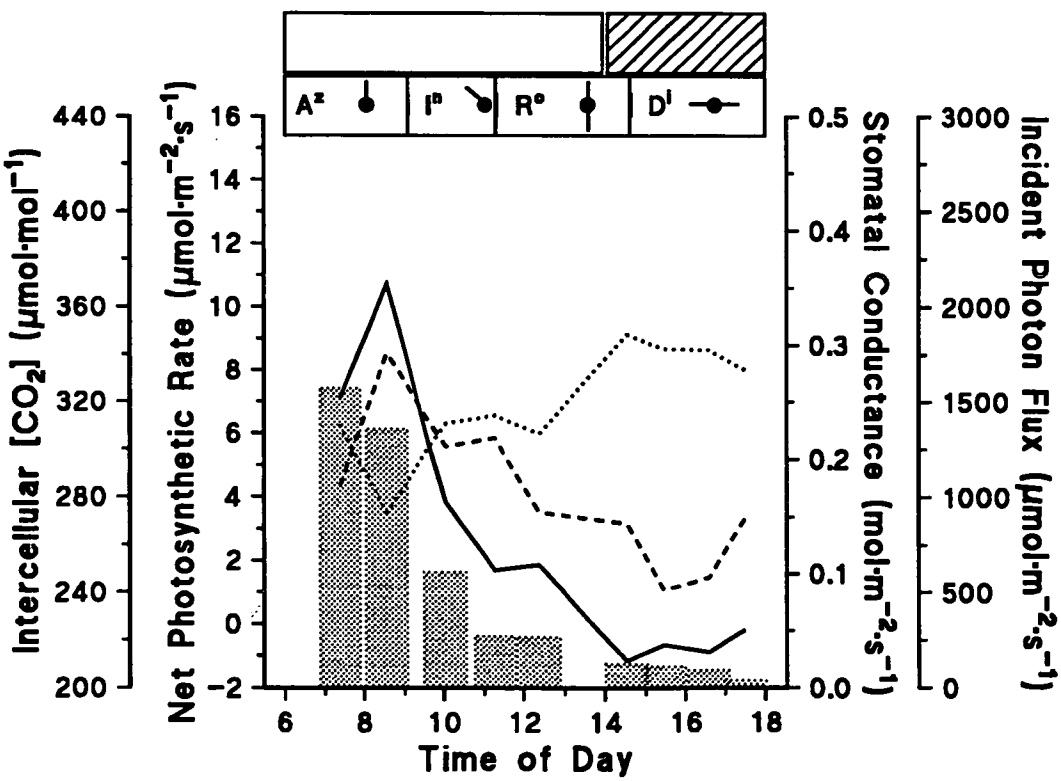


Figure 6.15 Photosynthetic behaviour of leaf KC4, an afternoon shaded *Kielmeyera coriacea* leaf, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day.

The high early morning atmospheric CO_2 concentrations meant that many suitably positioned and oriented leaves exhibited maximal net photosynthetic rates at this time. These were often considerably greater than the calculated mean for the species of 9.2 μmol m^{-2} s^{-1} (see Figure 6.5). For example leaves KC1 and KC2 (Figure 6.12 and Figure 6.13 respectively) both reached peak P_n values of 13 μmol m^{-2} s^{-1} at 08:30.

Stomatal conductance showed close coupling to incident photon flux level, with g_s increasing in response to increasing $PPFD_i$ (Figures 6.12, 6.13, 6.14). As for P_n, stomatal conductance was generally greatest in the early morning.

Intercellular CO_2 concentration was generally high before dawn, but declined rapidly from daybreak to values of 240-320 μmol mol^{-1}, as photosynthetic rate increased and ambient concentration declined. Values remained constant (KC1, Figure 6.12), or varied (KC2, Figure 6.13) in association with changing environmental conditions, although values never declined below 240 μmol mol^{-1} during the course of a day.

6.3.5 Photosynthetic Behaviour of *Bauhinia holophylla* Steud. Leaves

The photosynthetic behaviour of 7 leaves from 4 *Bauhinia holophylla* plants was measured on one single day. The mature plants ranged from 1.5 to 2.0 m in height, and the leaves measured were subject to some shading by the surrounding vegetation and some self-shading. The upright growth habit *Ba. holophylla* stems is accompanied by an alternate phyllotaxis (Ferri, 1969). Leaves were generally oriented randomly with respect to azimuth, inclined to -45°, not rotated, and had a 90° dihedral. Photosynthetic measurements were made on the leaf lamina receiving the greater incident photon flux. No change in leaf orientation due to pulvinus movement was detected for any of the leaves measured.

As a result of previous overnight rain, the early morning vegetation was particularly wet and the atmosphere particularly humid. This made initial stomatal conductance measurements impossible, a problem exacerbated by the slow drying of the heavily pubescent abaxial *Ba. holophylla* leaf surface. From 13:00 hr complete cloud cover at the field site reduced afternoon ambient photon fluxes to 150-250 μmol Quanta m^{-2} s^{-1}, and lowered air temperatures to 25-26°C (Figure 6.16 and Figure 6.17).

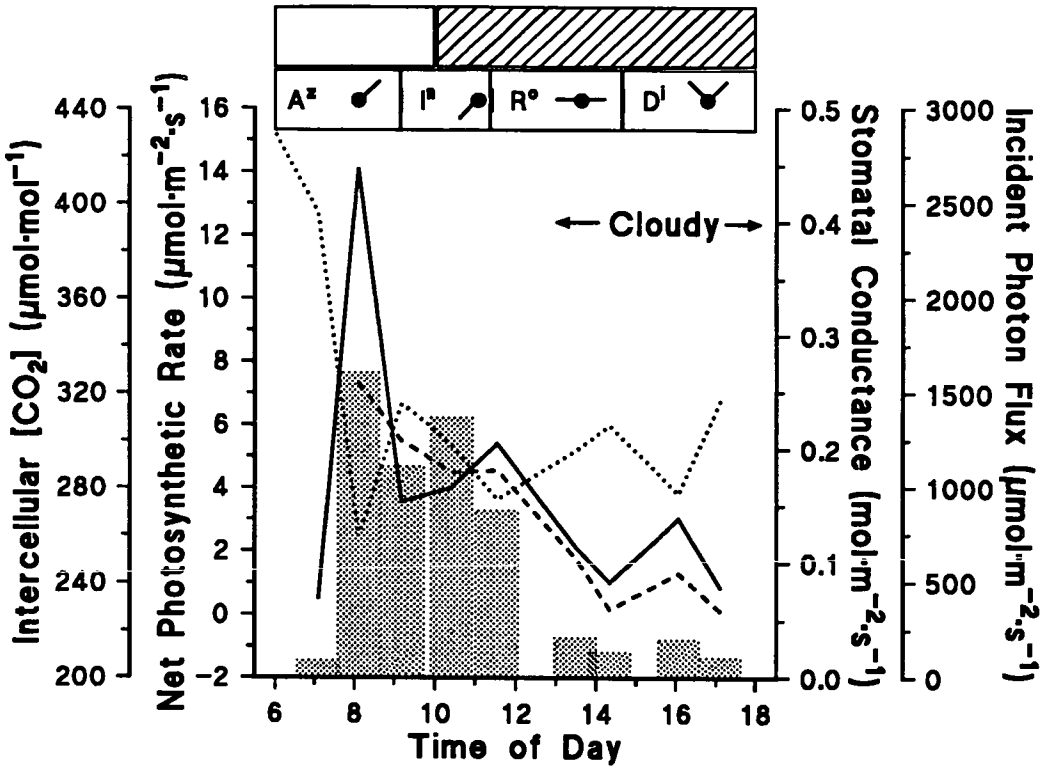


Figure 6.16 Photosynthetic behaviour of leaf BH1, a midday and afternoon shaded *Bauhinia holophylla* leaf, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day.

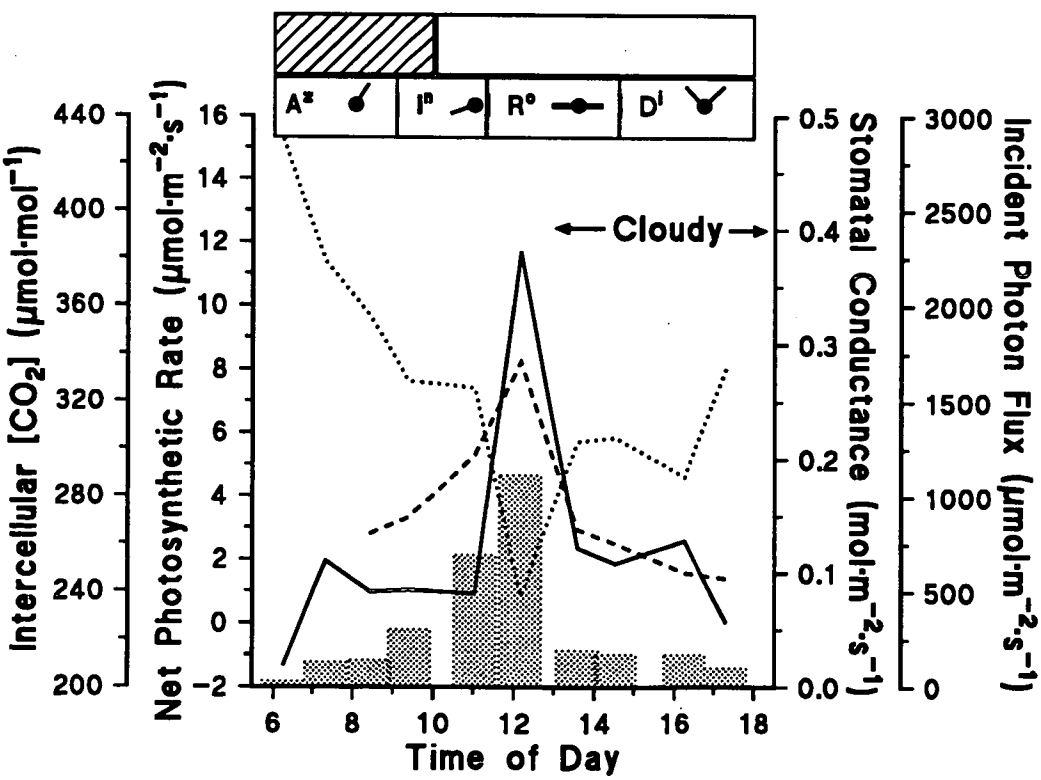


Figure 6.17 Photosynthetic behaviour of leaf BH2, a morning shaded *Bauhinia holophylla* leaf, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day. Afternoon ambient quantum fluxes were low due to cloud.

Differences in photosynthetic activity were seen between different *Ba. holophylla* leaves for comparable environmental conditions, although all leaves measured showed high activities. Incident photon fluxes and net photosynthetic rates were generally unimodal, a consequence of the species leaf orientation and plant morphology. Leaves were not vertically oriented to receive a bimodal $PPFD_i$ pattern, and the species dense hemispherical canopy normally prevented early morning and late afternoon irradiance. Indeed, self-shading and shading by the surrounding vegetation appeared to be more important for *Ba. holophylla* than for *K. coriacea.* Leaves BH1 and BH2 (Figures 6.16 and 6.17 respectively) have similar leaf orientations but quite distinct photosynthetic behaviours due to differences in leaf positioning (note leaf shading diagrams). Suitably oriented leaves benefited from the high early morning atmospheric CO_2 concentrations to produce high peaks of net photosynthesis (BH1, Figure 6.16). The high photosynthetic capacity of *Ba. holophylla* meant that leaves maintained high net photosynthetic rates even at low incident photon flux levels. This is shown by leaf BH1 (Figure 6.16), which despite low morning and afternoon $PPFD_i$, maintained a positive net photosynthetic rate from dawn to dusk.

Net photosynthetic rate showed close coupling to incident photon flux, as did stomatal conductance. Both responded to gradual declines in $PPFD_i$ (BH1, Figure 6.16) and short-lived periods of high irradiance (BH2 at 12:00, Figure 6.17). The rapid decrease in stomatal conductance in the afternoon for leaf BH2 (Figure 6.17) contrasts with the slow decrease seen for leaf KC2 (Figure 6.13) through the midday period when the bimodal pattern of $PPFD_i$ reduced fluxes to near zero.

Intercellular CO_2 concentrations were initially high but decreased as photosynthesis proceeded. Values varied in response to photosynthetic rate but remained between 240 and 340 $\mu mol\ mol^{-1}$ for the greater part of the day.

6.3.6 Photosynthetic Behaviour of *Annona coriacea* Mart. Leaves

The photosynthetic behaviour of 17 leaves from 6 *Ann. coriacea* plants was investigated on two separate days. The juvenile plants ranged from 0.5 to 1.0 m in height, and most were subject to some early morning shading by the surrounding vegetation. Stems were generally vertical, with an alternate phyllotaxis (Ferri, 1969). Leaves were oriented randomly with respect to azimuth, generally elevated to 45/67.5°, not rotated, and with no dihedral (Figure 6.18 and Figure 6.19).

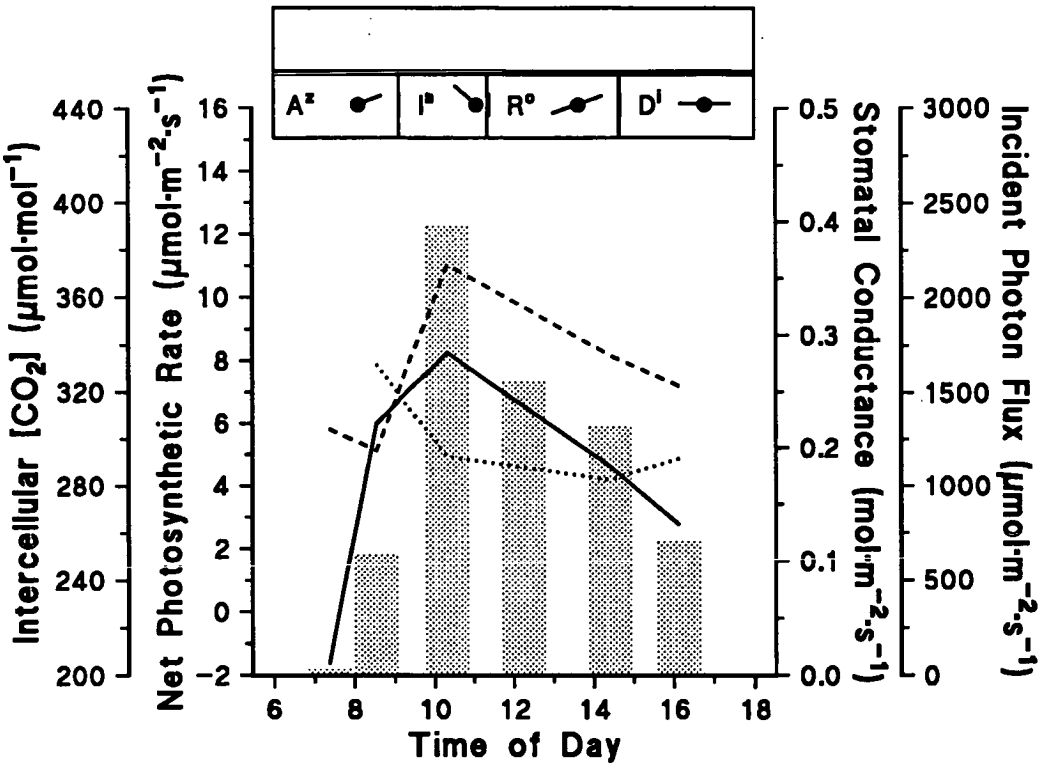


Figure 6.18 Photosynthetic behaviour of leaf AC1, a steeply inclined *Annona coriacea* leaf rotated slightly to face the morning sun, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day.

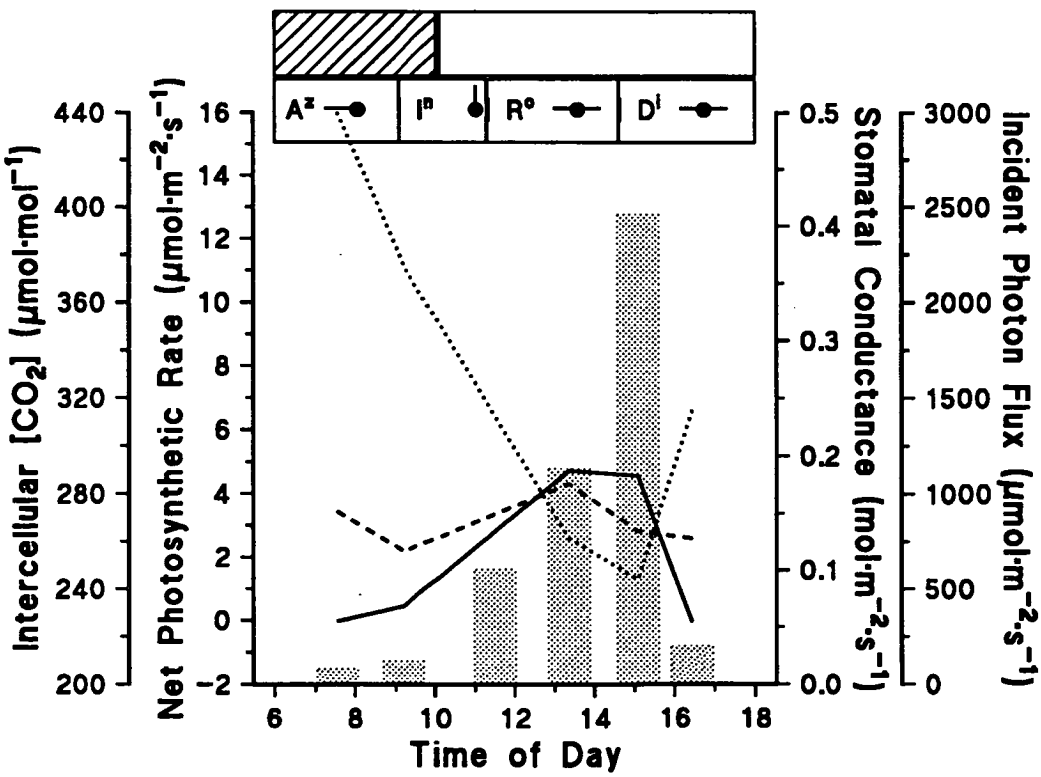


Figure 6.19 Photosynthetic behaviour of leaf AC2, a morning shaded *Annona coriacea* leaf, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day.

Although randomly oriented for azimuth, leaves were consistently oriented for inclination, rotation and dihedral. Thus, although most leaves experienced a unimodal pattern of incident photon flux, the steep inclination of some *Ann. coriacea* leaves often resulted in non-symetrical bimodal patterns of $PPFD_i$ with associated P_n and g_s patterns.

Differences in photosynthetic activity were seen for different *Ann. coriacea* leaves although P_n values were within the range of the random spot measurements, and early morning net photosynthetic rates were often high as a result of high atmospheric CO_2 concentrations.

Stomatal conductances were generally high (AC1, Figure 6.18) compared with *K. coriacea* and *Ba. holophylla*, although some leaves did show lower conductances and photosynthetic rates (AC2, Figure 6.19). Intercellular CO_2 concentrations were initially high and decreased as photosynthesis proceeded, but values remained above 240 $\mu mol\ mol^{-1}$.

6.3.7 Photosynthetic Behaviour of *Anacardium humile* St. Hil. Leaves

The photosynthetic behaviour of 12 leaves from 6 *Anacardium humile* plants was investigated on two separate days. Plants were generally 0.25 to 0.5 m in height, and most were subject to some shading by the surrounding vegetation. Stems were generally vertical, with an alternate phyllotaxis (Ferri, 1969). Leaves were oriented randomly with respect to azimuth, generally elevated to 45/67.5°, occasionally rotated, and with no dihedral.

Most *Ana. humile* leaves maintained low stomatal conductances through-out the day, despite increases in incident photon flux. These particularly low conductances were inconsistent with values obtained for random spot measurements (see Figure 6.6) and simultaneous measurements on adjacent leaves, and were thought to be a consequence of leaf handling. Only a small number of leaves were thought to show handling-independent behaviour and are described below.

The steep inclination of many *Ana. humile* leaves often resulted in bimodal patterns of $PPFD_i$ with associated P_n and g_s patterns (AH1, Figure 6.20). However, the greatest determinant of incident photon flux level for most *Ana. humile* leaves was shading by the surrounding vegetation, often for both morning and afternoon periods (AH2, Figure 6.21), but occasionally for the whole day (AH1, Figure 6.20).

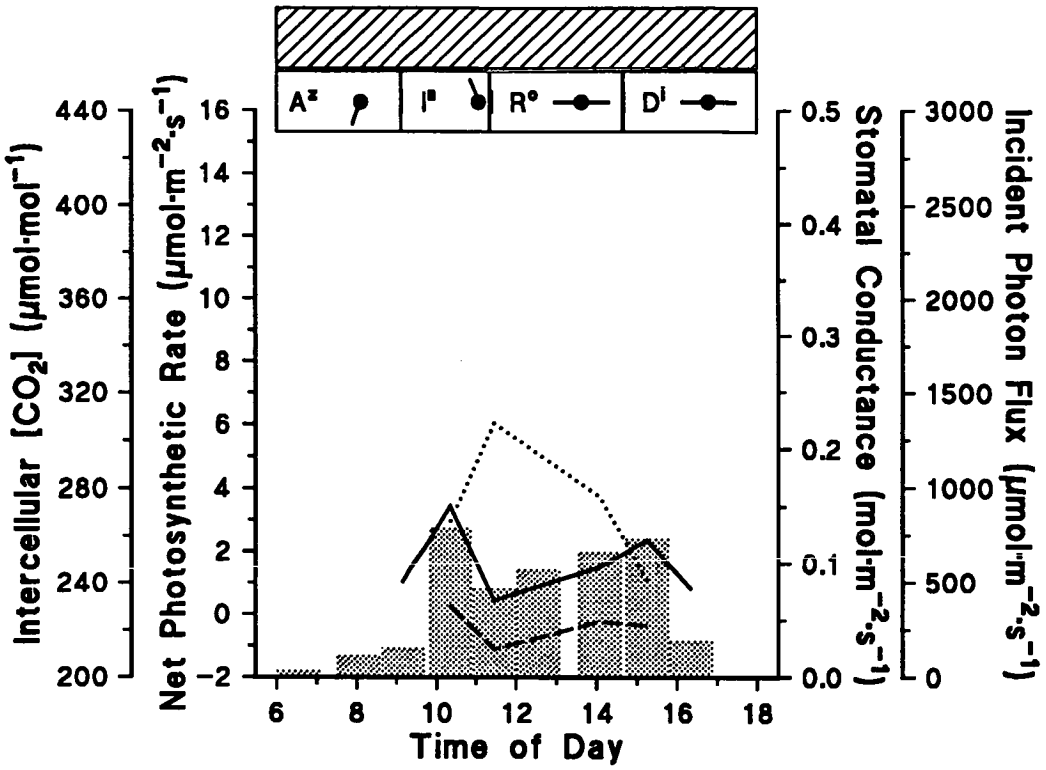


Figure 6.20 Photosynthetic behaviour of leaf AH1, a shaded *Anacardium humile* leaf, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day.

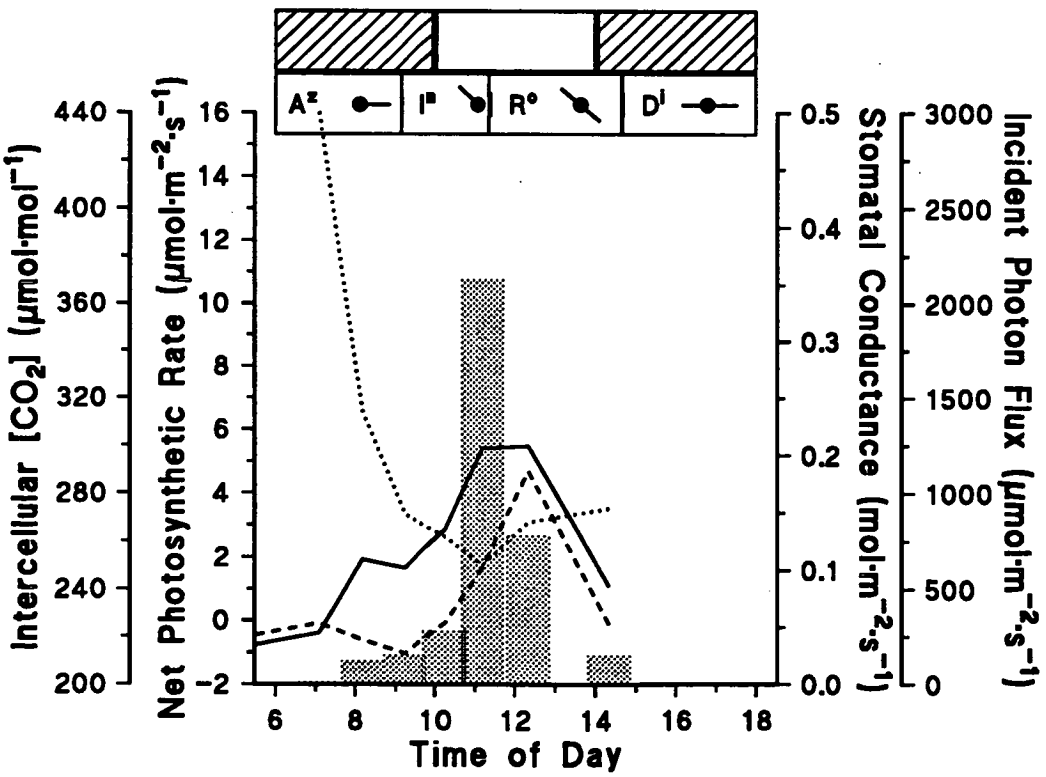


Figure 6.21 Photosynthetic behaviour of leaf AH2, a morning and afternoon shaded *Anacardium humile* leaf, showing relationships between net photosynthetic rate (—), stomatal conductance (- -), intercellular CO_2 concentration (···), incident photon flux (▒), and time of day.

Net photosynthetic rates and stomatal conductances were generally low (AH1 and AH2, Figure 6.21 and Figure 6.22 respectively) compared with *K. coriacea*, although some high values were occasionally seen (AH2 at 12:00, Figure 6.22). Intercellular CO_2 concentrations varied in response to photosynthetic rate but remained above 240 μmol mol^{-1} for the greater part of the day.

6.4 Discussion

The response of net photosynthetic rate to increasing light intensity exhibited by *K. coriacea* and the other Cerrado woody species investigated (Figures 6.1, 6.2, 6.3 and 6.4), is typical of the saturating response of leaf photosynthesis to increasing incident photon flux (Larcher, 1969; Lawlor, 1987). The more common diffuse relationship between incident photosynthetic photon flux ($PPFD_i$) and net photosynthetic rate, seen for *K. coriacea* (Figure 6.3), *Anacardium humile* (Figure 6.4) and others (section 6.2.1), would be expected from the random sampling technique used. Leaves known to have differing physiological activities, such as sun and shade leaves (Larcher, 1969), and old and young leaves (Šesták and Catsky, 1985; Tichá *et al.*, 1985) would be measured together, and therefore a range of photosynthetic activities would be expected for any given species. Although lower net photosynthetic rates at high $PPFD_i$ were associated with lower stomatal conductances (section 6.2.1), these are not thought to be causal, as these were also associated with similar intercellular CO_2 concentrations and therefore lower estimated carboxylation efficiencies. The tighter relationships between incident photosynthetic photon flux and net photosynthetic rate seen in *Byrsonima coccolobifolia* and *Bauhinia holophylla* (Figure 6.1 and Figure 6.2 respectively) may be due to a narrow degree of physiological variation, or to a failure of random sampling. Further research is needed to clarify this point.

Photosynthetic light saturation occurs at high light intensities in early successional temperate plants, but at much lower light intensities (≈10-15% of full sunlight) in late successional species (Bazzaz, 1979; Bazzaz and Carlson, 1982), such as beech (Ducrey, 1981), oak (Bazzaz and Carlson, 1982; Koike, 1986) and maple (Wuenscher and Kozlowski, 1970; Bazzaz and Carlson, 1982). As the Cerrado species examined had light saturation points ≥800 μmol Quanta m^{-2} s^{-1}, and two species did not reach light saturation until photon fluxes of 1500 μmol Quanta m^{-2} s^{-1} (section 6.2.1), light-saturating photon fluxes are considerably higher for Cerrado woody species than for comparable late successional temperate species. Similar high light-saturating photon fluxes have been reported for other woody savanna species (Tuohy *et al.*, 1991).

Although of the same magnitude, maximum photosynthetic rates for mature *K. coriacea* tree leaves are approximately 50 percent greater than those for seedling cotyledons and Leaf 1 (Table 6.1).

Table 6.1 Maximum net photosynthetic rates (P_n, $\mu mol\ m^{-2}\ s^{-1}$), stomatal conductances (g_s, $mol\ m^{-2}\ s^{-1}$), intercellular CO_2 concentrations (c_i, $\mu mol\ mol^{-1}$), estimated supply functions (SF, $mol^{-1}\ m^{-2}\ s^{-1}$) and estimated carboxylation efficiencies (CE, $mol^{-1}\ m^{-2}\ s^{-1}$) for fully expanded leaves of *Kielmeyera coriacea* seedlings and mature trees in the field. Seedling data taken from section 5.4.3.1, and Figures 5.8, 5.16 and 5.17. *n.d.* indicates no data available.

Leaf Type (Plant Age)	P_n	g_s	c_i	SF	CE
Seedling Leaf 1 (d70)	6.2	*n.d.*	*n.d.*	-0.062	0.031
Seedling Cotyledons (d56)	6.5	0.17	250	-0.064	0.033
Tree Leaf (Mature)	9.2	0.19	240	-0.078	0.049

Net photosynthetic rates, stomatal conductances (g_s), and intercellular CO_2 concentrations (c_i) show that leaf photosynthetic rates for mature trees are associated with slightly greater g_s values, and slightly reduced c_i values (Table 6.1). Estimated supply functions and carboxylation efficiencies indicated that the 42% greater net photosynthetic rate of mature tree leaves as compared with cotyledons, is associated with a 22% higher supply function and a 48% higher carboxylation efficiency.

Based on the range of species considered in this research and that of previous studies, Cerrado woody species have a range of photosynthetic capacities (see section 6.2.2.1) from 4.2 to 15.2 $\mu mol\ m^{-2}\ s^{-1}$, with a range mean of 9.6 $\mu mol\ m^{-2}\ s^{-1}$ (Table 6.2). This range of species includes a number of characteristic and ecologically important Cerrado genera and species, such as *Byrsonima* sp., *Annona* sp., *Kielmeyera* sp., *Bauhinia holophylla*, *Caryocar brasiliense*, and *Curatella americana* (Goodland, 1970), and therefore provides a representative sample of the Cerrado woody flora. The value for *Byrsonima crassifolia* is for material collected from the Venezuelan Llanos and measured in the laboratory under CO_2-saturating conditions ($c_i = 300\ \mu mol\ mol^{-1}$), and therefore may represent an over-estimate of photosynthetic capacity as compared with values for the other species.

Table 6.2 Maximum net photosynthetic rates for Cerrado woody species.

Species	Net Photosynthetic Rate ($\mu mol\ m^{-2}\ s^{-1}$)
Ouratea hexasperma (St. Hil.) Baill.[a]	4.2
Kielmeyera variabilis Mart.	6.5
Anacardium humile St. Hil.	7.4
Byrsonima coccolobifolia Kunth	7.5
Kielmeyera coriacea Mart.	9.2
Annona coriacea Mart.	9.3
Ouratea spectabilis (Mart.) Engl	9.9
Caryocar brasiliense Camb.[b]	10.2
Xylopia aromatica Lam.	10.5
Curatella americana L.[c]	11.0
Byrsonima crassifolia (L.) (H.B.K.)[d]	11.8*
Bauhinia holophylla Steud.	12.2
Didymopanax macrocarpum (C.& S.) Seem.[e]	15.2

* material collected from the Venezuelan Llanos, and measured at CO_2-saturation (c_i = 300 $\mu mol\ CO_2\ mol^{-1}$).
[a] Johnson *et al.* (1983)
[b] Pereira Netto and Hay (1986)
[c] San José (1977)
[d] Medina (1982)
[e] Franco (1983), Johnson *et al.* (1983)

Leaf photosynthetic capacities (P_c) for woody species range from 3 to 30 $\mu mol\ m^{-2}\ s^{-1}$ (Ceulemans and Saugier, 1991). Late successional woody species, such as oak, beech, *Triplochiton scleroxylon*, and *Copaifera venezuelana*, have relatively low photosynthetic capacities (Bazzaz, 1979; Bazzaz and Carlson, 1982), typically less than 10 $\mu mol\ m^{-2}\ s^{-1}$, and generally between 2 and 6 $\mu mol\ m^{-2}\ s^{-1}$. Early successional or pioneer woody species, such as poplar, willow, eucalypt, have relatively high photosynthetic capacities (Bazzaz, 1979; Bazzaz and Carlson, 1982), with P_c values always above 10 $\mu mol\ m^{-2}\ s^{-1}$ (Ceulemans and Saugier, 1991). From this analysis, Cerrado woody species have photosynthetic capacities which are neither typical of pioneer nor late successional species, but have values that range in to both categories. As the Cerrado is generally considered to be a late successional or 'climax' vegetation (Ratter, 1992), certain Cerrado woody species appear to have photosynthetic capacities higher than expected.

Figure 6.22 shows photosynthetic capacities for, (a) the three major ecological groups of woody species, and (b) species from the Cerrado and other related scleromorphic vegetations. The range of photosynthetic capacities found for evergreen broad-leaf species is clearly intermediate between that for deciduous broad-leaf species and coniferous species, and is approximately from 2 to 20 $\mu mol\ m^{-2}\ s^{-1}$.

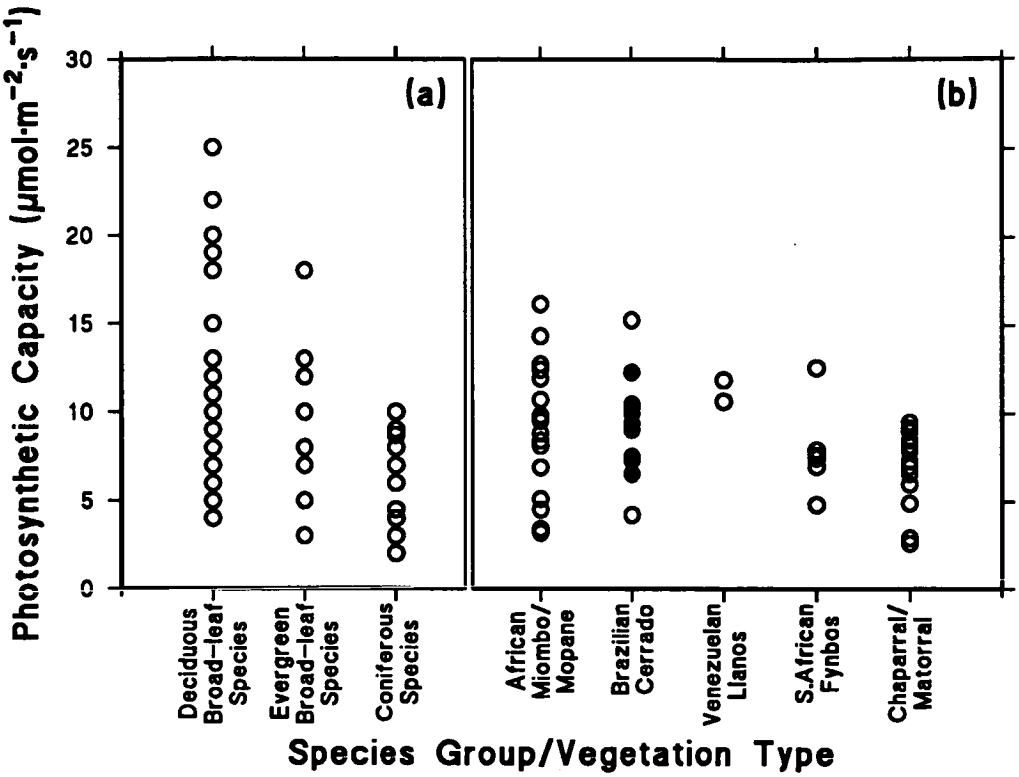


Figure 6.22 Scatter diagram of photosynthetic capacities for, (a) an important selection of deciduous broad-leaf, evergreen broad-leaf, and coniferous woody species, and (b) a selection of woody species from the Cerrado and other related scleromorphic vegetations. Each symbol represents the photosynthetic capacity for a single species determined under 'natural' conditions (field, nursery, or *in situ*). Filled symbols are values determined in this study. Species included are listed below.

Deciduous broad-leaf species: *Acer saccharinum, Acer hippocastanum, Betula ermanii, Betula pendula, Betula platyphylla, Carya illinoensis, Castanea sativa, Crataegus* x *macrocarpa, Fagus sylvatica, Fraxinus lanuginosa, Fraxinus pennsylvanica, Malus domestica, Populus deltoides, Populus tremula, Populus tremuloides, Populus trichocarpa, Populus euramericana, Prunus persica, Prunus spinosa, Pyrus communis, Quercus macrocarpa, Quercus velutina, Vitis vinifera* (references in Ceulemans and Saugier, 1991).
Evergreen broad-leaf species: *Eucalyptus behriana, Eucalyptus deglupta, Eucalyptus globulus, Eucalyptus maculata spp. globoidea, Hevea* sp., *Quercus coccifera, Quercus ilex, Quercus suber* (references in Ceulemans and Saugier, 1991).
Coniferous Species: *Abies lasiocarpa, Juniperus communis, Larix dicidua, Lagarostrobos franklinii, Picea abies, Picea sitchensis, Pinus halepensis, Pinus radiata, Pinus taeda, Podocarpus oleifolius, Podocarpus rospigliosii, Pseudotsuga menziesii* (references in Ceulemans and Saugier, 1991).

African Miombo/Mopane: *Acacia nigrescens, Albizia antunesiana, Bolusanthus speciosus, Brachystegia spiciformis, Burkea africana, Colophospermum mopane, Combretum apiculatum, Dalbergia melanoxylon, Euclea divinorum, Julbernardia globiflora, Lannea stuhlmannii, Monotes glaber, Terminalia sericea, Ziziphus mucronata* (Tuohy *et al.*, 1991).
Brazilian Cerrado: *Caryocar brasiliense, Didymopanax macrocarpum, Ouratea hexasperma* (Franco, 1983; Johnson *et al.*, 1983; Pereira Netto and Hay, 1986).
Venezuelan Llanos: *Curatella americana, Byrsonima crassifolia* (San José, 1977; Medina, 1982).
S. African Fynbos: *Protea repens, Protea neriifolia, Protea nitida, Protea acaulos, Rhus tomentosa, Maytenus oleoides* (Mooney *et al.*, 1983).
Chaparral/Matorral: *Prunus ilicifolia, Rhus ovata, Heteromeles arbutifolia, Lithraea caustica, Kageneckia oblonga, Colliguaya odorifera, Pistacia lentiscus, Rhamnus alaternus, Phillyrea media, Arbutus menziesii, Quillaja saponaria, Quercus ilex, Olea europaea* (references in Mooney, 1981).

Cerrado woody species have a range of photosynthetic capacities similar to those reported for other related scleromorphic vegetations, such as the Venezuelan Llanos, South African Fynbos, Chilean/Californian/Mediterranean Chaparral/Matorral, and particularly the African Miombo/Mopane. All species from these vegetations have photosynthetic capacities within the range 2 to 16 $\mu mol\ m^{-2}\ s^{-1}$, with most centred around 8 to 12 $\mu mol\ m^{-2}\ s^{-1}$. Chaparral/Matorral species appear to have a slightly lower range of P_c values, which is thought to be due to the particularly low nutrient status of these habitats (Mooney, 1981). None-the-less, all woody species from these scleromorphic vegetations have photosynthetic capacities typical of evergreen broad-leaf species.

In a study of leaf conductance, Körner *et al.* (1979) listed the maximum leaf conductance to water vapour for 246 species belonging to 13 morphologically and/or ecologically comparable groups. In herbaceous plants values of maximum leaf conductance for water vapour ranged from 0.16 to 1.13 $mol\ m^{-2}\ s^{-1}$ with values around 0.48 $mol\ m^{-2}\ s^{-1}$ occurring most frequently (all values expressed on a projected leaf-area basis). For most woody species a range of 0.08 to 0.40 $mol\ m^{-2}\ s^{-1}$ was obtained, with most values at about 0.24 $mol\ m^{-2}\ s^{-1}$. As the Cerrado species measured had a mean stomatal conductance to water vapour of 0.26 $mol\ m^{-2}\ s^{-1}$ (section 6.2.2.2) this would suggest that their values are fairly typical for woody plants. However this value obscures the facts that, six of the eight species measured had values above 0.24 $mol\ m^{-2}\ s^{-1}$, and that species such as *Annona coriacea* (g_s = 0.34 $mol\ m^{-2}\ s^{-1}$) had mean stomatal conductances approaching the upper limit of the above range. Indeed Goldstein *et al.* (1986) report that conductances higher than 0.4 $mol\ m^{-2}\ s^{-1}$ have been measured for Neotropical savanna woody species on a few occasions. Thus as reported for other savanna species (see section 1.6), Cerrado woody species also generally have high stomatal conductances.

It is now generally considered that leaves adjust their stomatal conductances so that they are not limiting to leaf internal carbon-dioxide assimilation. Estimated supply functions and carboxylation efficiencies for the Cerrado species investigated (Figure 6.8) suggest that the observed differences in net photosynthetic rate are due not only to differences in stomatal conductance, but also to the internal carboxylating processes of the leaf. The latter may be associated with differences in structural resistances to CO_2-transfer, or differing activities of enzymes of the carboxylating process, such as RuBisCO. Further research is needed to establish the basis of these differences in carboxylating efficiency.

Woody species of the African Miombo/Mopane are ecologically, and appear to be physiologically, very similar to those of the Cerrado. As well as photosynthetic capacity (Figure 6.22 (b)), the photosynthetic performance (*sensu* section 6.1) of woody species of the Cerrado is very similar to that of woody species from the Miombo/Mopane (Tuohy and Choinski, 1990; Tuohy *et al.*, 1991). Photosynthetic capacities for African Miombo/Mopane species range from 3.2 μmol m^{-2} s^{-1} for *Lannea stuhlmanni* to 16.1 μmol m^{-2} s^{-1} for *Acacia nigrescens*, with a mean photosynthetic capacity of 8.7 μmol m^{-2} s^{-1} (Tuohy *et al.*, 1991). Light-saturating photon fluxes for all species are >700 μmol Quanta m^{-2} s^{-1}, with *Acacia nigrescens* reaching light saturation at light intensities ≥1500 μmol Quanta m^{-2} s^{-1}.

In a study of the relationship between CO_2-assimilation rate and leaf nitrogen content in the African Miombo/Mopane woodlands (Tuohy *et al.*, 1991), higher leaf nitrogen content was found to correlate positively with higher CO_2-assimilation rates, and non-nodulating legumes had significantly ($p<0.05$) higher leaf nitrogen contents than non-legumes. Nodulating legumes had still higher nitrogen contents than non-nodulating legumes (significant at $p<0.05$). Interestingly, these woodlands are dominated by non-nodulating members of the Caesalpinoideae sub-family (Leguminosae) rather than by nodulating species (Corby, 1974; Corby, 1990). This is thought to be related to the fact that the major limiting mineral element in these habitats is phosphorus, rather than nitrogen (Högberg, 1986). Consequently the flora is biased towards species with ectomycorrhizal associations rather than nitrogen-fixing nodules.

The Cerrado contains a great diversity of legumes, many of which are woody. The number of woody legume species is not only high (Felfili and Silva, 1992), but many important and/or dominant trees are legumes which has lead Goodland (1970) to conclude that the Leguminosae are the second most important family in the Cerrado. The legume investigated as part of this study, *Bauhinia holophylla* (Caesalpinoideae) is non-nodulating (Sutherland pers. com., 1991). In view of the recognised correlation between leaf photosynthetic capacities and nitrogen contents (Field and Mooney, 1986; Evans, 1989), and the higher nitrogen concentrations found in legume leaves, this has significant implications for the productive capacity of Cerrado species, such as *Ba. holophylla.*

The saturating response of leaf photosynthesis to incident photosynthetic photon flux at levels between 800 and 1500 μmol Quanta m^{-2} s^{-1} (Figures 6.1, 6.2, 6.3 and 6.4), the light-saturated stomatal conductances of 0.15 to 0.34 mol m^{-2} s^{-1} (Figure 6.6),

and the light-saturated intercellular CO_2 concentrations of 228 to 270 μmol mol^{-1} (Figure 6.7) observed for the Cerrado species investigated, are all characteristic of plants of the C_3 photosynthetic pathway (Black *et al.*, 1969; Black, 1971).

The current work has indicated that leaf diurnal carbon dioxide exchange is determined not only by photosynthetic capacity, but also the diurnal pattern of environmental factors, such as ambient photon flux and atmospheric CO_2 concentration. The influence of ambient photon fluxes on leaf photosynthesis is heavily modified by leaf characteristics such as location, position and orientation (*sensu* section 6.3.3). Position and orientation are directly determined by parent plant morphology, and location is determined by the interaction of parent plant morphology and that of surrounding species. The relative importance of location, position and orientation varies with the individual leaf. However the inherent morphology of a species, as modified by age and history, will generally result in one or more of these characters assuming greatest importance.

Plants of relatively small stature, such as seedlings and low growing species, like *Anacardium humile*, are principally influenced by leaf location, that is the degree of shading caused by the surrounding vegetation (Figure 6.20 and Figure 6.21). These plants are often limited to a short period, or window, of over-head solar radiation through the midday period, receiving little or no lateral irradiance due to the surrounding vegetation (Figure 6.21).

Plants which form their own dense canopy, such as *Bauhinia holophylla*, although more efficiently intercepting light, will shade their own leaves as a consequence of diurnal solar movement (Figures 6.15, 6.16, 6.17). Assuming a roughly spherical, hemi-spherical or ovoid canopy, this effect will only be avoided by leaves positioned on the solar apex of the canopy.

Plant morphologies which result in diverse leaf orientations, such as the large leaf inclinations, rotations or dihedrals found for *K. coriacea* and *Ann. coriacea*, will result in a variety of patterns of incident photon flux. This will include bimodal patterns of $PPFD_i$, such as that exhibited by the *K. coriacea* leaf KC2 (Figure 6.13), and unimodal patterns of $PPFD_i$, such as that exhibited by the *K. coriacea* leaf KC1 (Figure 6.12). These three leaf characteristics, location, position and orientation may be seen as a sequence of screens determining the ultimate pattern of $PPFD_i$ experienced by the leaf.

Leaf orientation, size and shape are major factors determining the magnitude of the boundary layer, that is the still layer of air adhering to the leaf surface through which all energy and gas-exchange between the leaf and its environment must take place. Leaf energy relationships are particularly important for woody species in high energy environments, such as the Cerrado. Many Cerrado species, like *K. coriacea*, which have large leaves would soar in temperature to dangerously super-ambient levels were it not possible to reduce radiation inputs through leaf orientation, or dissipate heat energy through transpirational cooling. In a study of Amazonian sclerophyll species, Medina *et al.* (1978) indicated how alteration of the normal orientation of one species leaves could result in increases in leaf temperature of over 5°C. Reducing leaf transpiration rate, by detaching the leaf, was shown to increase this value still further.

Previous photosynthetic studies of Cerrado woody species have indicated the importance of leaf orientation. In the study of the photosynthesis of *Didymopanax macrocarpum* and *Ouratea hexasperma* (Johnson *et al.*, 1983), the importance of leaf orientation was recognised for the effect it had on the diurnal pattern of intercepted photosynthetic photon flux. A horizontal *D. macrocarpum* leaf increased net photosynthetic rate in association with increasing ambient photon flux reaching a maximum value at around 09:00 (1300 μmol Quanta m^{-2} s^{-1}). P_n then gradually declined to 15:00 hr, at which point values rapidly declined in association with dropping ambient photon flux levels. The peak in photosynthetic rates in the early morning may also possibly be a response to the greater atmospheric CO_2 concentrations at this time (see section 6.3.1.2). This unimodal behaviour shows many parallels with that exhibited by the *K. coriacea* leaf KC1 (Figure 6.12). Stomatal conductances for this *D. macrocarpum* leaf remained constant from 09:00 until 15:00, at which point g_s began to decline. This contrasts with the stomatal behaviour of *K. coriacea* and the other Cerrado woody species measured for photosynthetic behaviour, which showed a much more dynamic response to varying incident photon flux (*K. coriacea*, Figure 6.12; *Bauhinia holophylla*, Figure 6.16). The original M.Sc. thesis from which much of the paper was drawn (Franco, 1983), provides further examples of this type of photosynthetic behaviour, and also describes leaves exhibiting bimodal patterns of incident photon flux and net photosynthetic rate. Franco (1983) similarly concludes that photosynthetic rate is principally influenced by the daily course of solar radiation. Schulze (1970) drew a similar conclusion in an indepth analysis of the gas-exchange behaviour of *Fagus sylvatica*, and established that >95 percent of the daily depression below photosynthetic capacity was due to non-saturating light intensities (Schulze and Hall, 1982).

Whole-plant diurnal carbon dioxide exchange is an integration of the individual patterns of leaf diurnal carbon dioxide exchange for all constituent leaves (Ceulemans and Saugier, 1991). The influence of leaf orientation, position and location on leaf diurnal CO_2-exchange was clearly shown in this study, and will be reflected in the diurnal patterns of carbon-dioxide exchange seen for whole plants.

Patterns of individual leaf orientation play an important role in canopy architecture and are known to have a marked effect on plant growth rate (Hinckley *et al.*, 1992). The display of leaves within a canopy affects light penetration and interception, and its repartitioning between different levels or layers of leaves at different depths. Foliage display is a strategy that increases the number of leaves operating near full capacity by reducing the number of leaves that have more light than they need to photosynthesise at maximum rates (Sprugel, 1989). The broad range of leaf orientations seen in Cerrado trees, and the frequently open nature of tree canopies will increase the efficiency of light interception by the plant as a whole, by increasing the number and duration of leaves receiving sun-light and reducing the number experiencing super-saturating light intensities.

Chapter 7

Summary and General Discussion

Summary and General Discussion

This thesis has sought to address some of those areas of Cerrado woody species growth and photosynthesis which require further research. This chapter provides a summary of the salient points of the previous introduction and results chapters, and a brief general discussion.

The ecology of the Cerrado is dominated by three major environmental factors: soil nutrient status, soil water status, and fire. The transient nature of surface drought and fire stresses, on the background of low nutrient availabilities demands specific morphological and functional responses from woody species, and particularly their seedlings. Associations have been drawn between gradients of these environmental factors and variations in Cerrado floristic composition, and therefore physiognomy. The regeneration phase, and particularly seedling establishment, is most sensitive to variation in such environmental factors. Cerrado woody species exhibit characteristic morphologies and behaviours as adaptations to this ecology, at all stages of their life cycle. Most obvious of these are their short stature, and the scleromorphic nature of their leaves, however other important adaptive features include the formation of an extensive root system, and the development of woody xylopodia. Cerrado woody species appear well adapted to their environment, however these adaptations are not achieved without some cost.

This research has shown that the growth of Cerrado woody species under field conditions is slow, but within the range seen for other woody species. Seedlings of *K. coriacea* do exhibit some growth rate plasticity in response to favourable nutritional conditions, however this is limited to a doubling of maximum specific growth rate from 0.026, to 0.054 d^{-1}. The apparent lack of growth rate plasticity in certain aluminium-accumulating Cerrado woody species (*i.e. Qualea grandiflora*, Paulilo (1991)) may be an artifact of an aluminium requirement for healthy growth under nutritionally favourable conditions.

Maximum potential specific growth rate for *K. coriacea* is similar to that reported for other late successional woody species. However, when compared with other species of comparable growth rate, Cerrado woody species have similar, or relatively high unit leaf rates, but distinctly low leaf area ratios. These low leaf area ratios are primarily due to the low specific leaf areas, characteristic of savanna woody species. The high frequency of epigeal germination and the large photosynthetically active

cotyledons of many Cerrado woody species, ensure high initial leaf weight ratios during establishment. However, high biomass partitioning to the root system, which leads to rapidly increasing root to shoot ratios, results in rapid ontogenic declines in leaf weight ratios. These declining leaf weight ratios compound the inherently low specific leaf areas, to produce particularly low and declining leaf area ratios. As well as reducing leaf area ratio, declining leaf weight ratios also increase the burden of respiring non-leaf biomass. *K. coriacea*, like many Cerrado woody species, shows rapid root development, and exhibits a particularly high, but constant, biomass partitioning to the root system. Within the root and shoot systems partitioning is two phased. The first 'establishment' phase, involves high partitioning to lateral root development within the root system, and very high partitioning for Leaf 1 and Leaf 2 development within the shoot. The secondary phase of growth consists of a reduced partitioning to foliar leaf development, and a switch to substantial partitioning from lateral root to xylopodium formation.

Leaf-area development for *K. coriacea* is irregular and associated with a rhythmic pattern of leaf emergence, or leaf flushing. Leaf flushes are associated with the emergence of specific leaf positions, and individual leaves vary in area depending on, their leaf position and their position within the flush. Leaf flush 1 (F1) is associated with the emergence of Leaf 1 and Leaf 2, F2 with L3-L7, F3 with L8 -L13, and F4 with L14-L22. This flushing leaf emergence is similar to that exhibited by mature trees in the field (Arasaki, 1993), as is the associated pattern of individual leaf areas produced. Flushing leaf emergence is associated with a similar pattern of leaf primordium production, which maintains an approximately constant number of unemerged leaf primordia at the shoot apex (3-4 under controlled conditions).

The substantial partitioning of biomass to root development in Cerrado woody species, restricts the amount of dry matter available for leaf development. As a consequence, many Cerrado species show little stem development, in order to maximise their leaf to stem dry weight ratio. This is clearly illustrated by reference to the morphology of *K. coriacea*, which has an almost rosette growth form. Potential mutual shading effects between leaves are reduced by changes in leaf phyllotaxis and leaf orientation, and some limited stem elongation associated with later flushes of leaf emergence. These shading effects may be minimised up to the production of Leaf 6 (*i.e.* the end of F2), the last leaf normally produced in the first growing season in the field.

This research has clearly shown the importance of the cotyledons to early development, and therefore seedling establishment. As well as providing an initial store of reserves, the high photosynthetic activity of the cotyledons provides the majority of photosynthate through the 'establishment' phase, including the period of maximum specific growth rate, and a substantial proportion beyond this point, into the secondary phase of xylopodium development. Cotyledon photosynthetic productivity provides the capital for Leaf 1, Leaf 2, and initial lateral root development. *K. coriacea* seedlings have a basipetal insertion gradient of maximum net photosynthetic rate, with highest P_n values in the cotyledons. Net photosynthetic rates for the cotyledons and first leaves are similar or higher, than those of comparable late successional woody species. Only the upper layers of the cotyledon mesophyll are chlorophyllous, and CO_2-assimilation appears to occur predominantly through the adaxial leaf surface. Photosynthetic activities appear to respond to changes in sink demand. Net photosynthetic rates for the cotyledons and L1-L5, and therefore whole plant photosynthetic productivities, decline in association with the end of the second flush of leaf emergence (F2), and show a resurgence of activity with the beginning of the third flush (F3).

Differences in specific growth between controlled and field conditions are primarily due to differences in unit leaf rates, and, to a lesser degree, leaf area ratios. These lower unit leaf rates are associated with lower net photosynthetic rates. Estimated growth and maintenance respiration coefficients are similar to measured values for other species, and indicate no differences between controlled and field conditions. Lower net photosynthetic rates under field conditions are associated with lower estimated carboxylation efficiencies. Supply functions are broadly similar. These differences in estimated carboxylation efficiency were supported by differences in the levels of photosynthetic pigments.

In the field, leaf-area development after cotyledon expansion, is very slow. Foliar leaf emergence is delayed, slow, and accompanied by small leaf areas at full expansion. Mean phyllochron under field conditions was 12.4 d, as compared with 8.7 d under controlled conditions. This slow leaf emergence was associated with slower leaf primordia production at the shoot apex (mean plastochron of 16.4 d, as compared with 7.2 d under controlled conditions). However, substantially reduced individual leaf areas at full expansion under field conditions are the primary cause of low absolute rates of leaf-area increase in the field, although slower rates of leaf

emergence are also important. Net photosynthetic rates for the leaves of mature *K. coriacea* trees in the field are approximately 50% greater than those of seedling cotyledons and Leaf 1. This higher assimilatory capacity is associated with a higher carboxylation efficiency.

Field measurements made in this study established that photosynthetic capacities for a selection of Cerrado woody species range from 4.2 μmol m^{-2} s^{-1} to 15.2 μmol m^{-2} s^{-1}, with a range mean of 9.6 μmol m^{-2} s^{-1}. This range of values overlaps those ranges typical of pioneer and late successional species, and is comparable for those of other related scleromorphic vegetations. Differences in photosynthetic capacities for Cerrado species are associated with differences in estimated carboxylation efficiency and supply function. Stomatal conductances for Cerrado woody species are high, but within the range reported for other woody species. Light saturating photon fluxes for Cerrado species are higher than those of late successional species, but similar to those of other related savanna woody species. Indeed, the photosynthetic characteristics of Cerrado woody species appear very similar to those of ecologically related vegetations, such as the African Miombo/Mopane. As is characteristic of seedling growth, tree growth appears to be limited to a greater extent by biomass partitioning rather than assimilatory capacity per unit area.

This study has shown that the photosynthetic behaviour of leaves of Cerrado trees is principally influenced by the diurnal pattern of incident photosynthetic photon flux ($PPFD_i$). Leaf characteristics, such as leaf location, leaf position and leaf orientation (*sensu* section 6.3.3) interact with ambient photon flux levels to determine the ultimate pattern of $PPFD_i$ experienced by the leaf. Leaf location refers to the degree of shading experienced by the leaf due to the surrounding vegetation, and has been shown to be particularly important to plants of low stature. Leaf position refers to shading of the leaf by other leaves of the parent plant, and was shown to be important to species which form dense canopies. Leaf orientation refers to the 3-dimensional orientation of the leaf, and is particularly important to leaves that show large inclinations and rotations.

These leaf characteristics will be equally important for the leaves of seedlings: leaf location, because of the low stature of seedlings; leaf position, because of the lack of substantial stem development in seedlings; and orientation, because of the changes in phyllotaxis and leaf elevation seen with development.

This establishment strategy, of developing a storage/perennating organ to survive unfavourable periods of resource capture, has been recognised for other perennial plants (Schulze and Chapin, 1987). The costs involved in the development of the xylopodium may be illustrated by reference to a study by Schulze and Chapin (1987). These authors compared photosynthetic capacities and maximum potential specific growth rates found in different plant types (based on data by Grime and Hunt (1975), and Larcher (1983)), and established a significant linear correlation. Based on the regression of this correlation, *K. coriacea* seedlings, with a photosynthetic capacity of 11.0 $\mu mol\ m^{-2}\ s^{-1}$ are predicted to have a maximum specific growth rate of 0.118 d^{-1}. This is more than double the measured value, of 0.054 d^{-1}. This **R** value places *K. coriacea* on the extreme lower limit of the range of specific growth rates seen for species with comparable photosynthetic capacities.

Partitioning within Cerrado woody seedlings must be balanced to maximise the development of the xylopodium, in order to ensure survival through the dry season. This must involve a compromise between, the need to develop leaf-area and fine root structure for resource capture, and the need to partition biomass to xylopodium development, within the restricted growing season. *K. coriacea* solves this dilemma through a biphasic partitioning pattern, and efficient use of its restricted leaf biomass.

Future Research

A greater number of studies of the establishment of Cerrado woody species is required for a better understanding of the diverse ecologies exhibited by its woody species. A greater understanding of the development of Cerrado seedlings, such as *K. coriacea*, under field conditions is required. In particular direct measurements of the carboxylation efficiency, and the activity of carboxylating enzymes, such as RuBisCO, are required. Suitable techniques, taking into account the high phenolic and latex content of seedling leaves, will need to be developed for the latter assay.

Further research in to the photosynthetic performance and behaviour of Cerrado trees is required, particularly with regard to ontogenic changes in leaf activity, and relationships between leaf nitrogen concentration and photosynthetic capacity.

APPENDICES

Appendix 1.1 Cerrados of the State of São Paulo: Itirapina and Fazenda Campininha

Two periods of field work were conducted in Brazil to consider environmental limitations to seedling establishment under field conditions. These were completed at two Cerrado sites within the peripheral area of Cerrado in the State of São Paulo (see Map 1.1), the Reserva Biológica de Mogi-Guaçú (which forms part of the Fazenda Campininha), and the Estação Ecológica de Itirapina. The extent of Cerrados within the State of São Paulo was established in the early nineteen sixties when Cerrado, Cerradão, and grasslands were estimated to cover 10.8%, 2.9% and 1.7% of the area of the state respectively (Borgonovi and Chiarini, 1965). Descriptions of the Reserva Biológica de Mogi-Guaçú are provided by Eiten (1963), Vuono *et al.* (1982), Gibbs *et al.* (1983), Mantovani (1983), and Mantovani and Martins (1988). Descriptions of the Cerrados of the State of São Paulo, including the Estação Ecológica de Itirapina, are provided by Eiten (1970), Pinheiro *et al.* (1976), and Giannotti and Filho (1992).

In the Köppen climate scheme most of the region that includes Cerrado is classified as C_{wa}. Mean annual temperatures are 20°C-21°C, and average annual rainfall levels are between 1100 mm and 1300 mm (-1500) mm, with 10-30 mm in the driest months, and an annual potential evapotranspiration of >900 mm (Eiten, 1970). Frosts are a regular although infrequent phenomena, and some 26 frosts had been recorded up to 1975 (Anon, 1975). Different Cerrado woody species are known to have differing frost sensitivities (Silberbauer-Gottsberger *et al.*, 1977). *K. coriacea* is reported to be both frost sensitive (Gibbs *et al.*, 1983) and frost insensitive (Silberbauer-Gottsberger *et al.*, 1977).

Table A1.1/1 Soil analysis of the campo cerrado site at the Reserva Biológica de Mogi-Guaçú, São Paulo State, Brazil (from Gibbs *et al.*, 1983).

Soil character	campo cerrado
Organic Material	2.17%
pH	4.96
Al^{3+}	1.01 meq/100ml
Ca^{2+}	0.14 meq/100ml
Mg^{2+}	0.1 meq/100ml
K^{+}	19.83 µg/ml
P	1.0 µg/ml

Appendix 2.1 Weather Conditions at the Reserva Biológica de Mogi-Guaçú

Weather conditions at the Reserva Biológica de Mogi-Guaçú, São Paulo State, Brazil, during the period September 1990 to March 1991.

Table A2.1/1 Weather data for each day of September 1990, including: maximum, minimum and mean air temperatures (°C); millimetres of rainfall; mean percentage relative humidity; and hours:minutes of sunshine.

Day	T_{Max}	T_{Min}	T_{Mean}	Rainfall	$\%RH_{Mean}$	Sunshine
1	26.7	15.7	19.58	10.1	90.25	2:25
2	23.5	14.5	21.20	0.0	83.00	2:54
3	25.7	11.6	17.32	0.0	77.75	9:56
4	27.3	11.7	19.06	0.0	74.00	10:24
5	27.3	12.6	18.64	0.0	76.75	7:06
6	28.5	13.1	20.30	0.0	65.75	6:42
7	28.9	14.9	19.42	10.7	81.50	1:00
8	22.7	16.3	19.66	0.0	94.00	0:12
9	27.0	14.7	17.80	0.0	73.25	9:12
10	28.5	7.8	17.68	0.0	62.75	10:06
11	32.5	8.7	19.98	0.0	61.25	10:06
12	33.5	12.2	21.34	0.0	64.50	7:00
13	23.5	12.0	15.88	4.1	92.50	0:24
14	14.8	10.1	11.74	11.7	88.25	0:00
15	18.7	8.5	12.44	0.0	75.25	6:00
16	24.9	4.5	12.58	0.0	76.75	10:12
17	27.9	5.4	15.84	0.0	70.75	7:54
18	31.3	9.5	19.30	0.0	67.75	10:06
19	32.7	11.2	21.44	0.0	58.25	10:06
20	33.1	12.4	22.62	0.0	64.50	9:30
21	32.3	16.8	23.44	0.0	63.00	9:30
22	32.1	16.5	23.78	0.0	66.00	4:48
23	23.9	17.3	19.70	25.5	88.00	1:06
24	21.0	11.7	14.78	0.7	73.75	6:36
25	21.5	9.7	13.98	0.0	72.00	9:48
26	24.9	6.9	15.66	0.0	69.00	10:42
27	27.5	8.4	18.32	0.0	65.25	10:42
28	28.9	9.8	19.96	0.0	57.50	10:42
29	23.7	16.1	18.86	0.7	72.00	0:00
30	20.3	16.1	17.34	4.0	88.75	0:00
Mean/Total	26.50	11.89	18.32	67.5	73.80	195:08

Table A2.1/2 Weather data for each day of October 1990, including: maximum, minimum and mean air temperatures (°C); millimetres of rainfall; mean percentage relative humidity; and hours:minutes of sunshine.

Day	T_{Max}	T_{Min}	T_{Mean}	Rainfall	$\%RH_{Mean}$	Sunshine
1	20.7	15.3	18.02	4.2	89.75	0:00
2	26.7	14.7	19.34	4.6	85.00	4:06
3	30.5	14.1	21.92	0.7	80.00	9:36
4	31.3	16.9	23.98	14.8	67.50	8:48
5	30.5	15.3	26.22	2.3	54.25	9:24
6	31.1	15.3	23.06	0.0	64.75	9:42
7	30.9	11.7	21.64	0.0	69.25	9:24
8	31.7	15.3	23.34	0.0	65.00	6:36
9	33.7	16.3	24.74	0.0	60.25	9:06
10	34.9	16.8	26.84	0.0	54.75	10:24
11	35.5	19.1	27.66	0.0	58.25	8:00
12	34.5	19.5	24.46	7.3	72.50	6:36
13	30.3	18.9	23.76	0.6	76.50	8:06
14	33.5	18.2	25.74	0.0	69.25	9:30
15	24.7	19.5	21.22	0.0	80.00	0:30
16	19.7	15.3	16.94	23.4	84.50	0:00
17	23.9	14.9	19.54	5.7	90.50	1:00
18	26.7	18.3	22.34	0.0	83.75	2:06
19	27.5	19.8	22.00	37.7	88.50	0:36
20	29.3	19.5	23.46	5.8	83.75	5:36
21	28.7	15.3	21.48	0.0	78.50	10:42
22	26.3	13.8	19.44	0.0	62.75	11:54
23	30.00	11.6	20.48	0.0	74.00	11:30
24	30.7	15.8	22.28	0.0	74.00	9:48
25	28.5	17.3	21.86	0.0	72.50	11:06
26	30.5	13.4	22.60	0.0	62.25	10:08
27	30.1	15.3	22.54	0.0	64.00	9:24
28	29.6	14.7	19.76	0.0	78.00	11:48
29	33.5	14.1	24.62	0.0	65.75	10:18
30	33.9	17.9	25.40	0.0	63.50	8:18
31	32.7	19.8	25.86	0.0	65.50	3:30
Mean/Total	29.74	16.25	22.66	107.1	72.31	227:32

Table A2.1/3 Weather data for each day of November 1990, including: maximum, minimum and mean air temperatures (°C); millimetres of rainfall; mean percentage relative humidity; and hours:minutes of sunshine.

Day	T_{Max}	T_{Min}	T_{Mean}	Rainfall	$\%RH_{Mean}$	Sunshine
1	33.7	18.9	24.54	0.0	73.25	3:24
2	32.5	19.1	23.10	20.8	79.5	7:30
3	33.1	20.1	24.78	0.0	73.55	9:30
4	31.3	21.3	24.24	6.1	88.50	3:00
5	26.1	19.3	21.34	1.8	88.55	0:24
6	25.3	17.4	21.14	0.4	84.00	0:12
7	30.0	18.4	24.22	0.0	83.75	4:00
8	29.1	19.7	22.58	8.7	88.75	0:42
9	32.5	19.3	25.58	1.4	76.75	7:06
10	32.1	20.4	25.85	0.4	82.25	7:48
11	36.1	18.5	25.3	0.3	71.75	11:01
12	32.9	19.2	25.66	0.0	78.75	7:54
13	35.7	19.1	27.04	0.0	71.00	9:50
14	35.3	20.1	27.38	0.0	69.5	10:18
15	35.8	20.1	27.68	0.0	67.25	10:36
16	35.1	21.3	26.48	0.9	68.00	8:42
17	32.5	19.5	24.14	1.6	74.75	7:06
18	32.1	19.5	23.74	7.8	78.00	5:36
19	33.7	18.7	25.38	0.0	68.75	8:54
20	34.5	18.9	25.22	0.0	67.25	8:54
21	32.3	18.9	24.70	0.0	72.75	9:06
22	31.7	20.1	24.86	4.5	72.50	9:12
23	30.4	18.9	22.42	2.9	84.50	6:00
24	27.5	18.7	22.46	1.6	85.75	0:36
25	30.3	16.8	23.90	0.0	76.00	7:54
26	32.0	16.3	24.08	0.0	72.75	10:00
27	29.7	18.9	23.50	2.0	76.00	5:02
28	30.3	17.6	23.02	0.0	65.75	12:12
29	31.5	14.3	22.54	0.0	65.25	10:30
30	34.0	14.8	23.30	0.4	68.50	10:24
Mean/Total	31.97	18.8	24.37	61.6	75.69	213:23

Table A2.1/4 Weather data for each day of December 1990, including: maximum, minimum and mean air temperatures (°C); millimetres of rainfall; mean percentage relative humidity; and hours:minutes of sunshine.

Day	T_{Max}	T_{Min}	T_{Mean}	Rainfall	$\%RH_{Mean}$	Sunshine
1	34.4	18.3	26.28	0.0	67.00	9:30
2	34.7	18.7	26.44	0.0	58.75	10:12
3	34.7	18.5	27.08	0.0	58.75	10:30
4	31.4	19.8	23.82	0.5	74.25	6:00
5	32.9	18.3	23.56	0.4	78.25	5:30
6	33.1	17.8	26.36	0.0	61.00	8:28
7	28.5	19.8	22.44	0.0	80.00	0:06
8	27.7	19.7	20.06	0.0	84.25	2:12
9	27.6	16.3	23.16	0.0	71.00	3:42
10	30.1	19.8	23.22	0.0	82.00	2:06
11	30.3	20.1	24.90	0.9	82.50	2:36
12	29.5	21.2	25.08	37.5	81.00	6:12
13	30.7	21.8	24.48	5.0	80.75	3:24
14	26.3	20.3	21.98	19.9	94.75	0:00
15	29.7	18.1	21.50	31.0	87.50	3:24
16	31.4	18.7	24.96	0.2	78.25	9:24
17	33.1	16.3	24.74	0.0	68.00	12:30
18	33.1	18.8	23.90	0.0	76.25	11:00
19	32.9	19.1	24.10	0.8	75.00	11:00
20	29.5	18.7	23.30	32.7	83.00	8:30
21	31.3	18.9	24.66	0.0	74.75	12:06
22	32.9	17.7	24.82	0.0	68.50	12:24
23	34.1	16.7	25.66	0.0	72.00	10:00
24	31.7	19.1	23.48	0.0	82.25	6:00
25	31.5	18.5	24.10	0.0	78.25	7:12
26	29.2	16.8	23.06	0.0	71.50	10:00
27	31.3	15.8	24.16	0.0	70.00	11:48
28	32.0	16.6	23.80	0.0	65.00	12:12
29	24.9	16.8	19.12	0.0	76.00	2:30
30	28.5	10.5	19.42	0.0	66.25	12:36
31	28.5	12.1	19.80	0.0	77.00	11:42
Mean/Total	30.88	18.05	23.66	128.9	74.97	234:46

Table A2.1/5 Weather data for each day of January 1991, including: maximum, minimum and mean air temperatures (°C); millimetres of rainfall; mean percentage relative humidity; and hours of sunshine.

Day	T_{Max}	T_{Min}	T_{Mean}	Rainfall	$\%RH_{Mean}$	Sunshine
1	30.9	15.5	22.94	0.0	67.00	8.9
2	31.3	18.3	24.74	0.0	65.00	8.4
3	30.7	16.3	22.36	10.9	76.00	4.8
4	26.3	19.1	22.02	4.3	93.00	0.2
5	28.7	16.5	22.30	0.0	76.00	7.9
6	30.2	15.5	22.88	0.0	74.00	12.6
7	30.9	16.2	24.32	0.0	70.00	10.5
8	31.7	16.9	24.26	0.0	76.00	8.9
9	32.3	20.1	24.54	8.4	80.00	4.7
10	30.3	20.1	23.98	3.8	84.00	6.4
11	28.0	19.9	23.40	19.4	87.00	1.8
12	27.3	20.3	23.16	0.9	82.00	3.2
13	31.8	16.5	24.28	0.2	81.00	8.3
14	28.5	21.4	23.80	4.0	88.00	0.5
15	26.9	21.3	23.58	6.3	91.00	0.0
16	28.3	20.5	23.66	58.5	93.00	2.1
17	28.0	20.5	22.68	1.1	84.00	9.0
18	29.3	16.1	22.34	0.0	73.00	11.1
19	28.9	16.4	22.64	0.0	78.00	7.9
20	32.0	17.3	23.72	2.2	81.00	8.1
21	32.5	17.4	24.84	1.4	79.00	10.7
22	33.3	19.7	26.02	5.5	77.00	11.2
23	33.6	20.3	26.08	0.0	75.00	9.4
24	31.1	18.7	24.50	0.0	75.00	5.3
25	29.0	19.1	23.60	0.0	79.00	0.1
26	26.9	17.7	20.32	15.5	89.00	0.8
27	24.7	12.3	19.84	30.9	89.00	0.0
28	27.3	17.8	22.32	7.5	90.00	3.5
29	31.3	17.5	23.06	0.4	79.00	11.0
30	28.6	21.9	24.46	5.7	82.00	5.7
31	29.5	20.1	23.38	0.8	82.00	3.5
Mean/Total	29.69	18.29	23.41	187.7	80.48	186.5

Table A2.1/6 Weather data for each day of February 1991, including: maximum, minimum and mean air temperatures (°C); millimetres of rainfall; mean percentage relative humidity; and hours of sunshine.

Day	T_{Max}	T_{Min}	T_{Mean}	Rainfall	$\%RH_{Mean}$	Sunshine
1	27.3	20.7	22.72	10.9	90.50	1.1
2	27.5	19.3	21.94	13.2	89.00	0.5
3	30.8	18.5	23.48	0.0	82.50	4.2
4	32.9	17.4	24.66	0.0	73.25	10.5
5	30.3	18.7	22.06	45.8	84.00	3.0
6	30.5	19.3	22.46	30.9	86.50	5.8
7	31.5	19.2	23.08	8.4	87.50	4.7
8	28.1	20.3	23.74	17.1	84.50	5.9
9	29.8	19.2	22.70	15.8	87.75	5.2
10	29.5	20.3	23.94	28.3	88.75	2.3
11	27.5	18.9	22.82	11.2	83.75	2.7
12	27.3	19.5	23.42	7.7	87.75	6.2
13	29.3	21.5	24.26	0.0	85.25	7.0
14	31.3	17.8	23.24	0.6	85.75	8.2
15	28.7	19.7	23.26	4.2	88.25	1.9
16	29.9	18.7	23.06	0.0	80.25	3.2
17	31.1	18.3	23.58	0.0	81.75	7.0
18	30.3	19.6	22.72	13.5	90.25	3.8
19	28.9	16.9	22.14	0.0	82.25	6.5
20	30.3	14.8	21.90	0.0	74.50	11.4
21	31.5	15.6	23.60	0.0	79.25	10.8
22	32.7	17.3	24.82	0.0	74.50	11.5
23	29.5	19.0	22.84	0.0	77.75	6.2
24	28.3	13.9	20.70	0.0	66.50	11.7
25	31.5	13.8	22.66	0.0	74.25	11.4
26	29.9	15.4	22.34	0.0	83.00	7.2
27	31.3	17.4	24.24	0.0	70.50	9.9
28	31.5	17.6	23.04	0.0	75.50	7.7
Mean/Total	29.93	18.16	23.05	207.6	82.33	177.5

Table A2.1/7 Weather data for each day of March 1991, including: maximum, minimum and mean air temperatures (°C); millimetres of rainfall; mean percentage relative humidity; and hours of sunshine.

Day	T_{Max}	T_{Min}	T_{Mean}	Rainfall	$\%RH_{Mean}$	Sunshine
1	30.3	18.1	23.72	7.9	82.25	8.3
2	25.9	19.7	21.50	50.6	93.25	0.0
3	29.4	19.3	23.68	0.0	84.00	1.2
4	27.3	18.4	22.04	31.9	89.75	1.2
5	25.2	20.1	22.24	0.6	90.75	0.0
6	26.5	19.8	22.36	11.5	89.25	1.4
7	27.5	19.4	22.18	31.8	87.50	1.3
8	28.6	19.2	23.46	0.0	77.75	5.7
9	32.1	16.7	22.54	0.0	80.00	11.1
10	31.6	16.5	24.64	0.0	76.00	8.6
11	32.7	17.6	23.08	9.1	75.75	9.6
12	31.3	17.4	24.40	4.2	79.50	10.6
13	29.9	19.6	22.94	21.1	85.25	5.5
14	29.0	19.3	23.00	71.6	82.00	6.3
15	29.0	17.4	22.40	0.0	69.25	11.8
16	28.7	15.9	21.56	0.0	67.35	10.2
17	29.9	15.3	22.02	0.0	77.00	7.2
18	29.0	15.6	22.18	0.0	79.25	5.3
19	31.4	19.8	23.94	0.0	82.00	4.1
20	30.3	19.3	24.54	0.0	83.50	4.8
21	30.4	20.2	23.50	0.0	91.25	5.9
22	27.6	19.5	22.48	0.0	85.75	2.4
23	28.7	18.3	22.80	0.0	73.00	9.5
24	29.1	16.8	22.78	0.0	78.75	2.3
25	27.4	19.6	22.80	3.5	87.50	0.6
26	22.7	16.3	18.90	21.7	96.00	0.0
27	18.3	16.3	17.02	44.4	96.25	0.0
28	18.7	16.2	17.44	60.0	96.25	0.0
29	20.3	16.5	18.34	22.5	96.25	0.0
30	22.7	17.7	20.06	35.1	95.25	0.6
31	21.9	18.3	20.72	32.0	94.00	4.2
Mean/Total	27.53	18.06	22.10	459.5	84.58	139.7

Appendix 2.2 Calculation Formulae for the LCA-2 Field Analytical System

Photosynthetic and transpirational values for the LCA-2 field analytical system are calculated by the DL2 data-logger from keyboard and sensor inputs according to von Caemmerer and Farquhar (1981):

The mass flow of air through the cuvette (F_M) is:

$$F_M = ((F_V \cdot P)/((273+\theta_a)A_c)) \cdot 20.311 \text{ (mol m}^{-2}\text{ s}^{-1}\text{)}$$

Assuming dry air enters the cuvette, the leafs transpiration rate (E) is:

$$E = (e_o/(P-e_o)) \cdot F_M \text{ (mol m}^{-2}\text{ s}^{-1}\text{)}$$

where $e_o = e_s \cdot \%RH_o/100$

—

The radiation absorbed by the leaf (H) is:

$$H = (Q \cdot 698/3190) \cdot ((0.8 \cdot 0.85)+(0.2 \cdot 0.6))$$

$$\text{that is } H = Q \cdot 0.175 \text{ (W m}^{-2}\text{)}$$

where:
(i) 698/3190 converts the incident photon flux density on the cuvette from μmol m^{-2} s^{-1} to W m^{-2}
(ii) 0.8 and 0.2 are the proportions of visible and infra-red light absorbed by the leaves respectively
(iii) 0.85 and 0.6 are the proportions of visible and infra-red light transmitted through the cuvette windows respectively.

The difference between leaf and cuvette air temperature ($\delta\theta$) is:

$$\delta\theta = (H - l_v \cdot E)/(0.93 \cdot M_a \cdot (c_p/r_b) + 4 \cdot \sigma(\theta_a + 273)^3)$$

In the program $4 \cdot \sigma(\theta_a+273)^3$ is approximated to $(4.5+\theta_a/16)$

$$\text{then } \theta_L = \theta_a + \delta\theta$$

—

The stomatal resistance to water vapour transfer (r_s) is:

$$r_s = (e_i/e_o - 1)/F_M - r_b$$

$$\text{and } g_s = 1/r_s$$

—

The analyser reading of the 'analysis' line [CO_2] (C_A) must be corrected for the analyser cross-sensitivity to water vapour:

$$C_C = C_A - f_n \cdot C_A \cdot E_{max} \cdot (1 - e^{(-0.07 \cdot e_o \cdot 1000)})$$

where $f_n \cdot C_A = (1+7.87E\text{-}4 \cdot C_A)$, and compensates for the background [CO_2].

To determine the net CO_2-assimilation rate (P_n) and sub-stomatal [CO_2] (c_i) adjustment for the diluting effect of water vapour must be made:

$$P_n = (C_R - (C_C/(P - e_o))) \cdot F_M$$

$$c_i = ((g_c - E/2) \cdot C_C - P_n)/(g_c + E/2)$$

where $1/g_c = 1.6/g_s + 1.37/g_b$

—

Appendix 2.3 Calibration of the LCA-2 Field Analytical System

Certain of the LCA-2 Field Analytical System sensors require regular re-adjustment, and were calibrated as follows:

A2.3.1 LCA2 CO_2-Analyser

The LCA2 CO_2-analyser requires regular calibration of its settings (A.D.C.™, 1986[a]):

Zero Adjustment: This was adjusted before use and at regular intervals (1 hr) during LCA-2 operation. Drift was minimal, often within a 2-3 p.p.m. range. Adjustment was achieved by switching the LCA2 to the 'zero' mode, which circulates a volume of air through the external soda-lime column. The display setting was then adjusted to '000' on the front panel potentiometer.

Span Calibration: This was adjusted at 14 day intervals and generally showed little if any drift. Calibration against an air source of known [CO_2], was made in the 'reference' mode. In Edinburgh this was provided by a Wostoff Pump System mixing sources of pure CO_2 and CO_2-free air to produce a constant [CO_2] of 350 p.p.m.. In the field it was provided by an aerosol canister of air of a specific [CO_2], (400 p.p.m.) obtained from A.D.C.™.

Differential Calibration: This was adjusted at the same time as the CO_2 Span Calibration and again showed little drift. A common air source of constant [CO_2] was connected to both 'analysis' and 'reference' gas lines of the LCA-2, and the analyser adjusted in the 'differential' mode.

A2.3.2 PLC2-B Parkinson Leaf Chamber

The humidity sensor of the PLC2-B Parkinson Leaf Chamber requires regular calibration (A.D.C.™, 1985[b]). This was generally completed every 14 days.

Zero Adjustment: This was achieved by passing silica-gel dried air from the ASU(MF) through the chamber unit in the normal manner. The PLC2-B was adjusted to zero at 45 s after chamber closure, *i.e.* the time usually required to achieve 'equilibrium' when operating the LCA-2 system.

Span Calibration: This was achieved by passing air of known water vapour concentration through the chamber unit via the exhaust line, *i.e.* 'analysis' gas line, to obtain a faster response. Air of known water vapour content was generated by passing air (<150 $cm^3\ min^{-1}$) through a column (30 cm × 5 cm) of fresh $FeSO_4.7H_2O$, and establishing the emergent %RH depending on the ambient temperature (A.D.C.™, 1985[b]). According to:

$$\%RH \text{ above } FeSO_4.7H_2O = a + b \cdot \text{Ambient Temperature.}$$

where: $a = 41.44$; $b = 0.7406$.

Appendix 3.1 Parameters for Growth Indice Calculation

The growth indices, specific growth rate (**R**), unit leaf rate (**E**) and leaf area ratio (**F**) were calculated from polynomials of the natural-logarithmic transformed plant dry weight and leaf-area data, as described in section 2.2.10. Controlled environment (*C.C.*1 and *C.C.*2) and field (*F.C.*) data, along with best-fit polynomials, are plotted in Figures A3.1/1, A3.1/2, A3.1/3 and A3.1/4. Function parameter values for these polynomials are displayed in Table A3.1/1.

Table A3.1/1 Function parameter values from which **R**, **E** and **F** were calculated for *C.C.*1, *C.C.*2 and *F.C.* seedlings.

Experiment		Parameters				
	y	*a*	*b*	*c*	*d*	*e*
*C.C.*1						
	ln W	-2.24	-0.0536	0.00262	-2.56E-5	7.74E-8
	ln L_A	-8.01	0.0171	0.00128	-1.61E-5	5.29E-8
*C.C.*2						
	ln W	-2.09	-0.0160	0.00133	-1.00E-5	
	ln L_A	-8.05	0.0240	0.00131	-1.50E-5	
F.C.						
	ln W	-2.01	-0.0260	9.33E-4	-5.56E-6	
	ln L_A	-7.71	-0.0517	0.00612	-1.39E-4	9.89E-7

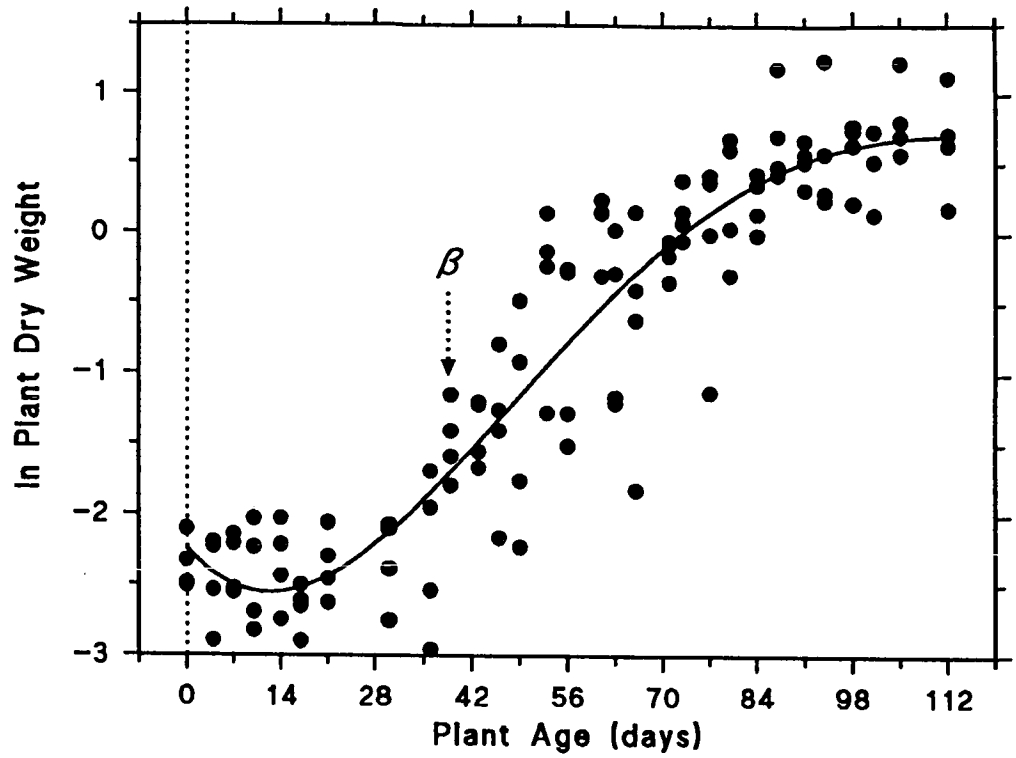


Figure A3.1/1 The relationship between ln (plant dry weight) and plant age, for *K. coriacea* seedlings grown under controlled conditions (*C.C.*1). The line is the best-fit 4th-order polynomial of the *C.C.*1 data (see Table A3.1/1 for parameter values). "β" indicates the point of initial significant ($p<0.05$) dry weight increase.

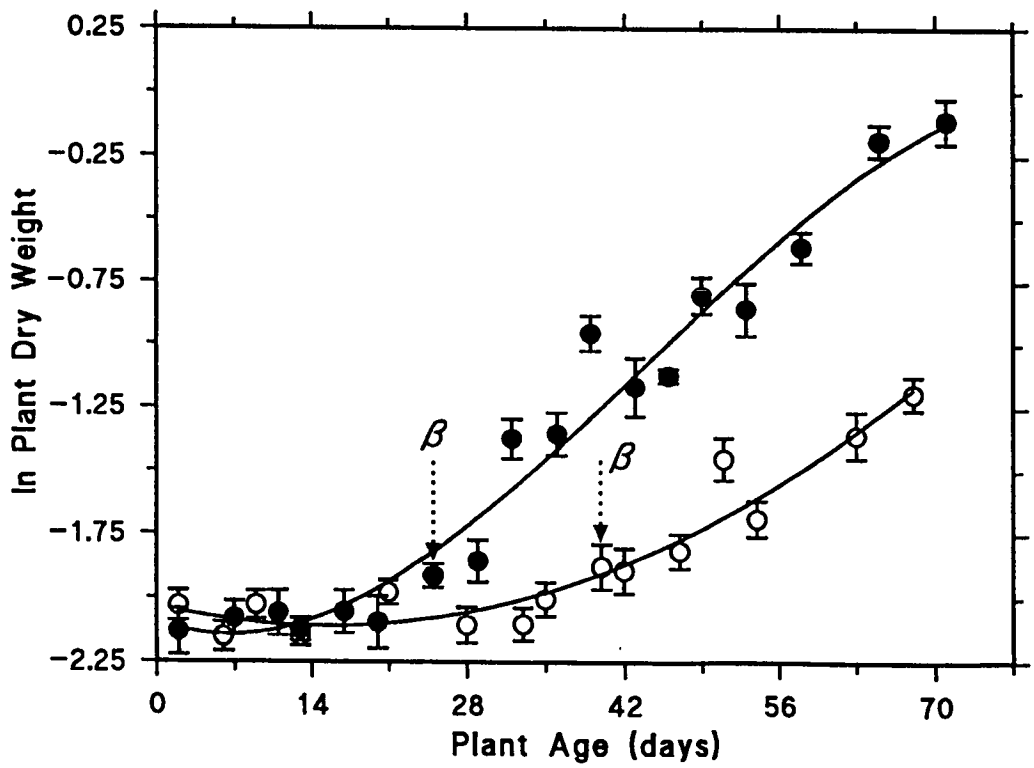


Figure A3.1/2 The relationship between ln (plant dry weight) and plant age, for *K. coriacea* seedlings grown under controlled (●; *C.C.*2), and field (○; *F.C.*) conditions. Each point is the mean of 7 and 10 replicates respectively, with error bars representing standard errors of the mean. Lines are best-fit 3rd-order polynomials for the *C.C.*2 and *F.C.* data (see Table A3.1/1 for parameter values).

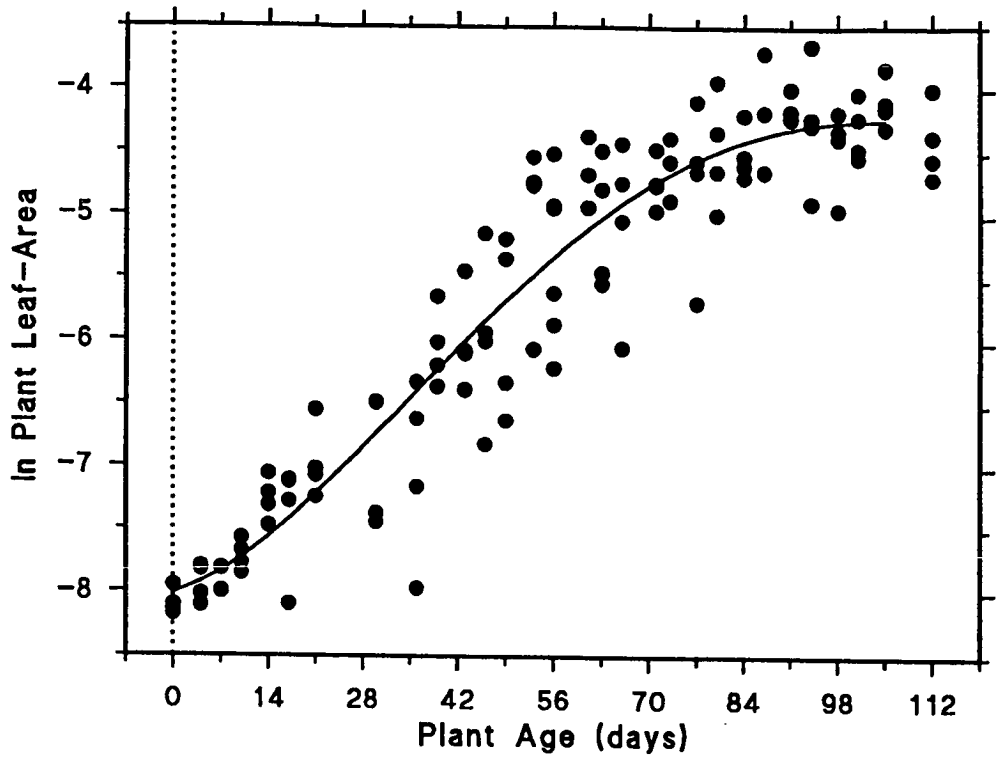


Figure A3.1/3 The relationship between ln (plant leaf area) and plant age, for *K. coriacea* seedlings grown under controlled conditions (*C.C.*1). The line is the best-fit 4th-order polynomial for the *C.C.*1 data (see Table A3.1/1 for parameter values).

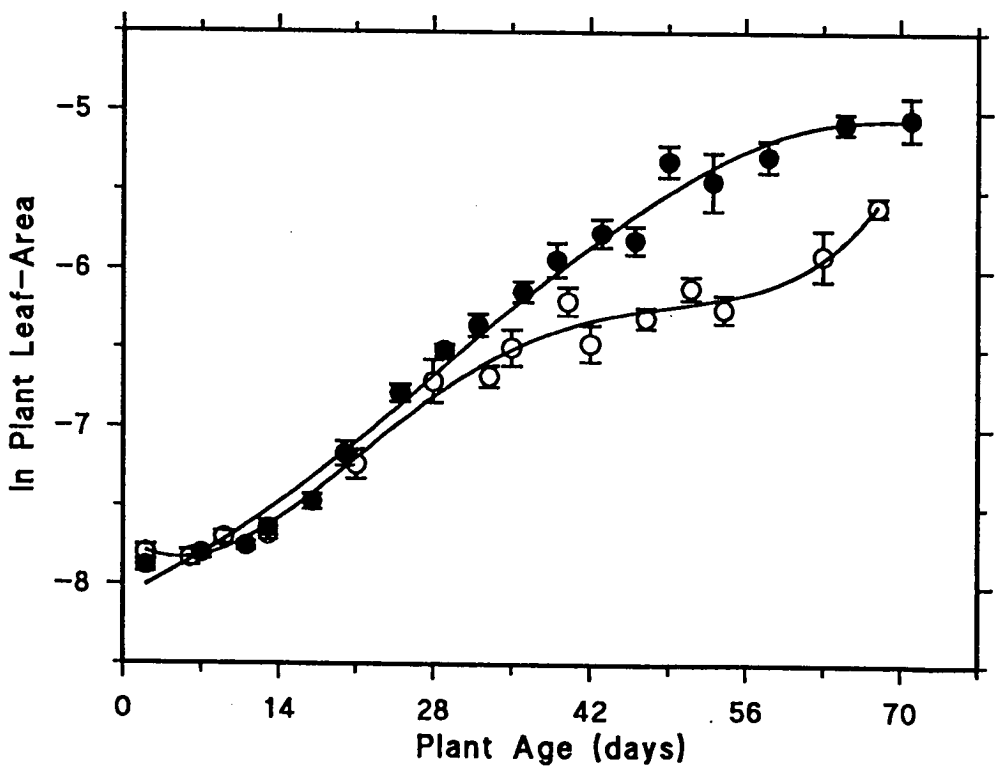


Figure A3.1/4 The relationship between ln (plant leaf area) and plant age, for *K. coriacea* seedlings grown under controlled (●; *C.C.*2), and field (○; *F.C.*) conditions. Each point is the mean of 7 and 10 replicates respectively, with error bars representing standard errors of the mean. Lines are 3rd and 4th-order polynomials for the *C.C.*2 and *F.C.* data (see Table A3.1/1 for parameter values).

Appendix 3.2 Calculation of Maximum Specific Growth Rates from Other Studies

Many plants exhibit a characteristic pattern of early development whereby specific growth rate (**R**) rapidly increases from zero (or some negative value) to some maximum value, and slowly decreases thereafter (Hunt and Lloyd, 1987). Maximum **R** values provide a convenient means of growth rate comparison, and have previously been used in ecological studies (Grime and Hunt, 1990). Calculation of **R** from other studies involved, plotting dry weight data, and after natural-logarithmic transformation, specific growth rate calculation (see section 2.2.10). Figure A3.2/1 shows **R** calculation from data for the growth of *Qualea grandiflora* Mart. under semi-natural greenhouse conditions (Paulilo, 1991).

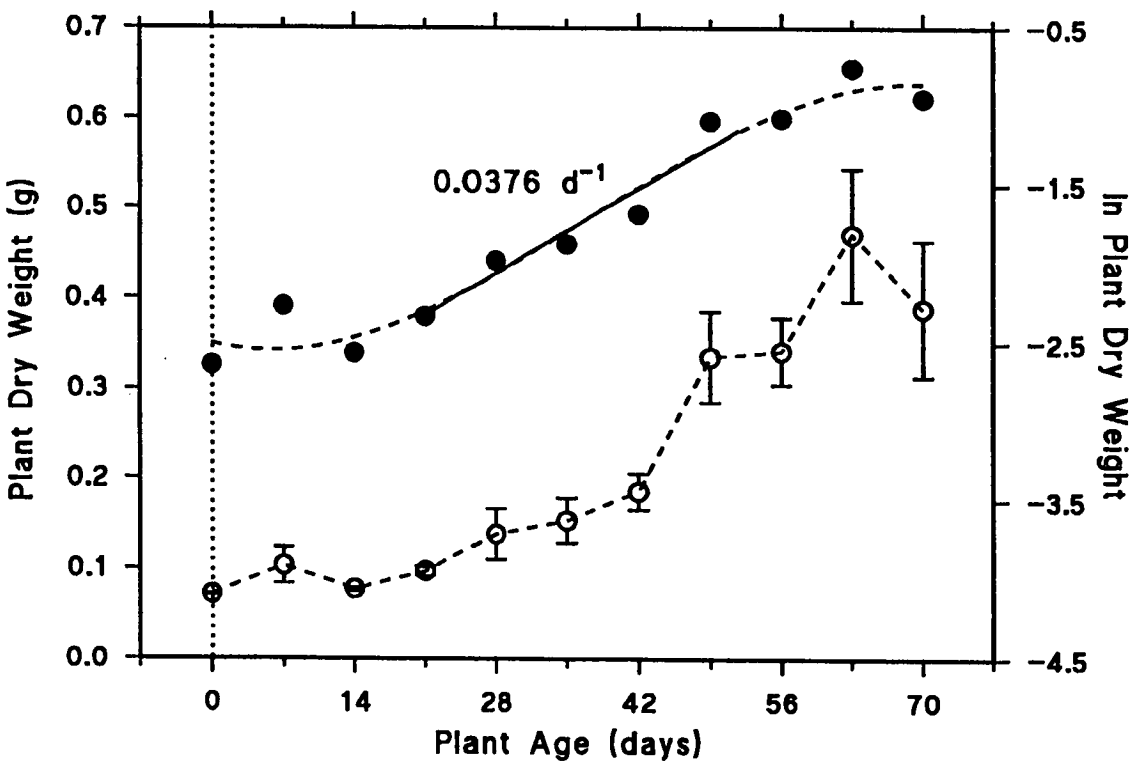


Figure A3.2/1 Changes in dry weight (○) and ln (dry weight) (●) with plant age, for *Qualea grandiflora* seedlings grown under greenhouse conditions (data from Paulilo, 1991). Maximum **R** is the maximum $\delta \ln(\text{dry weight})/\delta T$, in this case 0.0376 d^{-1}.

Table A3.2/1 Estimated maximum specific growth rates (**R**) for seedlings of Cerrado woody species. Columns also indicate culture conditions (Irradiance-I, Growing-medium-M, Temperature-T), and plant age at which maximum **R** occurred. Species referred to are, *Dalbergia miscolobium* Benth., *Dimorphandra mollis* Benth., *Kielmeyera coriacea* Mart., *Qualea cordata* (Spreng.), *Qualea grandiflora* Mart., *Stryphenodendron adstringens* (Mart.) Coville, and *Sweetia pseudelegans* Mohlenbr..

Species	Culture Conditions I	M	T	**R** (d^{-1})	Age (d)
Da. miscolobium[a]	N	N	N	0.035	35-50
Da. miscolobium[a]	N	N	G	0.038	30-45
Da. miscolobium[b]	N	N	N	0.026	28
Di. mollis[c]	N	N	N	0.031	27-39
K. coriacea[d]	N	N	N	0.014	20-40
K. coriacea[e]	N	N	N	0.024	30-60
K. coriacea[e]	N	N	N	0.027	30-60
K. coriacea	N	N	N	0.026	56
K. coriacea[f]	N	N	G	0.043	42-63
K. coriacea[d]	C^{300}_{12}	P/S+	$C^{20/30}$	0.038	30-50
K. coriacea	C^{300}_{12}	P/S+	$C^{20/30}$	0.054	48
Q. cordata[g]	N	N	N	0.035	31-52
Q. cordata[g]	N	N	G	0.076	32-42
Q. grandiflora[h]	N	N	N	0.031	35-91
Q. grandiflora[h]	N	N	G	0.038	21-63
Q. grandiflora[h]	C^{300}_{12}	S+	$C^{20/30}$	0.036	20-65
Q. grandiflora[i]	C^{350}_{12}	S+	$C^{20/30}$	0.036	29-50
St. adstringens[j]	N	N	N	0.043	25-54
Sw. pseudelegans[j]	N	N	N	0.050	33-54

[a] calculated from Sassaki (1991)
[b] Arasaki unpublished
[c] calculated from Poggiani (1973)
[d] Self (1990)
[e] calculated from Arasaki and Felippe (1990)
[f] calculated from Arasaki (1992)
[g] calculated from Godoy (1991)
[h] calculated from Paulilo (1991)
[i] Felippe and Dale (1990)
[j] calculated from Poggiani (1971)

Culture Conditions

Irradiance (I):
- N-Natural Cerrado PPFD
- C-Controlled Artificial Lighting; $^{PPFD}_{Photoperiod}$

Growing-medium (M):
- N-Cerrado Soil
- P-Peat
- S-Sand
- +-Plus nutrient feeding.

Temperature (T):
- N-Natural Cerrado temperatures
- G-Glasshouse (unheated) temperatures
- C-Controlled temperatures; $^{\text{Night Temperature}}_{\text{Day Temperature}}$.

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