INTERCROPPING OF MEDICINAL PLANTS IN RUBBER PLANTATIONS–LIGHT REQUIREMENTS AND PHYSIOLOGY OF SHADE ADAPTATION

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(Botany)

by

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APRIL 1998

. . . to my parents & my husband

भारतीय रबड़ गवेषण संस्थान

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Certificate

This is to certify that the thesis entitled 'Intercropping of medicinal plants in rubber plantations–Light requirements and physiology of shade adaptation' is an authentic record of original research work carried out by Ms. I'ma Neerakkal (Lecturer in Botany, Assumption College, Changanacherry) at the Rubber Research Institute of India, Kottayam under my supervision and guidance during the period December 1990–April 1998, in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Faculty of Science, Mahatma Gandhi University. The work presented in this thesis has not been submitted for the award of any other degree or diploma earlier.

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Declaration

I, I'ma Neerakkal, hereby declare that the thesis entitled 'Intercropping of medicinal plants in rubber plantations–Light requirements and physiology of shade adaptation' is a bona fide record of the research work carried out by me at Rubber Research Institute of India, Kottayam and that no part thereof has been presented earlier for any degree or diploma of any other University.

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Abbreviations

CD	-	Critical difference
CGR	-	Crop growth rate
C_i	-	Leaf internal CO_2 concentration
C_S	-	Conductance
Chl a	-	Chlorophyll a
Chl b	-	Chlorophyll b
E	-	Transpiration
g	-	gram
h	-	hour
HI	-	Harvest index
IR	-	infra red
IRGA	-	infra red gas analyzer
K	-	Kilo (as a prefix), 10^3
l	-	litre
LAGR	-	Leaf area growth rate
LAR	-	Lear area ratio
LAD	-	Leaf area duration
ln	-	Napierian log to the base e (where e = 2.71828)
LSD	-	Least significant difference
LWR	-	Leaf weight ratio
m	-	metre
m	-	milli (as a prefix), 10^{-3}
min	-	minute
mol	-	mole, contains Avogadro's number of molecules
n	-	nano (as a prefix), 10^{-9}
NAR	-	Net assimilation rate
PAR	-	Photosynthetic active radiation
PFD	-	Photon flux density (400-700 nm)
P_n	-	Photosynthetic rate
PS I	-	Photosystem I
PS II	-	Photosystem II
RGR	-	Relative growth rate
RH	-	Relative humidity
rpm	-	rotations per minute
Rubisco	-	Ribulose-1,5-biphosphate carboxylase/oxygenase
SE	-	Standard error
SLA	-	Specific leaf area
SLW	-	Specific leaf weight
TDM	-	Total dry matter
VPD	-	Vapour pressure deficit
µ	-	micro (as a prefix), 10^{-6}

Chapter 1

INTRODUCTION

The tropical rain forests have been the natural abode of most of the medicinal plants used all over the world. The dense canopy of such forests provide dense shade under which these plants could flourish. With the rapid explosion in human population and consequent pressure on cultivable land, denudation of forest has become widespread posing serious ecological imbalances. One of the prime victims of such deforestation is the medicinal plants.

On the other hand, there has been a new global interest in medicinal plants due to their pharmaceutical potentialities. There has been a shift in the consumption of medicines from synthetic to natural as the latter is regarded as harmless. A large percentage of medicines now available in the western market has herbal origin. Tropical countries can exploit this market demand if they can cultivate the medicinal plants on commercial scale and export them (Joseph *et al.*, 1995).

Commercial cultivation of any plant species requires development of appropriate agrotechnology. It therefore becomes imperative to study the optimum conditions which favour growth and yield of marketable parts of medicinal plants. An understanding of the ecophysiology of these plant species is a primary requirement in this direction. Studies in this area are scanty as evidenced by scarcity of literature on these aspects.

In India, one of the potential areas for growing these plants is the west coast of peninsular India as intercrops in tropical plantation crops. The major plantation crop of

south India is coconut. The feasibility of cultivating medicinal plants as intercrop in coconut gardens have been investigated (Nair *et al.*, 1991). Although some of the medicinal plants could be successfully cultivated in coconut gardens, the higher light penetration under the coconut canopy permits cultivation of easily marketable agricultural crops and as such they may get farmers' preference.

Rubber (*Hevea brasiliensis*) is the second most widely cultivated plantation crop in the west coast, occupying more than five lakh hectares. The rubber plantations have a long gestation period of seven years before any returns could be obtained. Cultivation of agricultural crops as intercrops is possible in the first three years of growth of rubber (Mathew *et al.*, 1978). But by the fourth year, the canopy of the trees closes and light penetration is restricted to the extent that agricultural crops cannot be cultivated. The cultivation of shade loving medicinal plants appears a viable proposal from the fourth year onwards. If found viable, it will serve as source of income especially for the small farmers who have to wait further to get returns from the rubber trees. It is in this context that the medicinal plants which are adapted to shade need be evaluated for cultivation as intercrop in rubber plantations.

Several rubber clones are under cultivation in different regions. The architecture of the canopy of individual clones vary. Consequently, the pattern and intensity of light penetration under each clone also varies (Satheesan *et al.*, 1982, 1984). Identification of medicinal plants which are ideally suited for cultivation under different light regimes will help in clone wise recommendation of medicinal plants for intercropping.

Preliminary studies at the Rubber Research Institute of India (RRII) have identified a few commercially important medicinal plants suitable for cultivation under rubber canopy (Rubber Research Institute of India, 1990; Sathik *et al.*, 1995). These

include *Plumbago rosea*, *Adhatoda beddomei*, *Adhatoda vasica*, *Alpinia galanga* and *Strobilanthes heyneanus*. These medicinal plants are important ingredients in many ayurvedic medicines. Species of *Adhatoda* are known for their bronchodilatory and antispasmodic properties. The rhizome of *Alpinia galanga* has diuretic, carminative and expectorant properties. *Plumbago rosea* is widely used for the cure of leprosy, anemia, diabetes, diarrhoea, dyspepsia and leucoderma. *Strobilanthes heyneamus* is used against neurological disorders, gandular swellings, skin diseases etc. (Asolkar *et al.*, 1992; Chopra *et al*, 1992; Kirtiker and Basu, 1984; Sivarajan and Indira, 1995).

The present study envisages investigation on the light requirements of the selected medicinal plants, aimed at elucidating the physiology of adaptation to shade at different phases of its phenology. Growth and yield of these plants under different light regimes, photosynthesis and other related physiological phenomena, differentiation and light and nutrient interaction are the major aspects covered under this study.

Chapter 2

REVIEW OF LITERATURE

The quality, intensity and duration of radiation that impinges on plants have profound effects on many physiological processes. Light is amongst the most important requirements for plant life at every stage, being the driving force of the fundamental assimilatory process viz. photosynthesis and the chief source of biochemical energy. It is also important in many ways in growth and development as an overall determinant of the plant habitat (Noggle and Fritz, 1986). Light influences the plant growth mainly through photosynthesis and light induced growth processes. Seasonal, diurnal and spatial (such as within a canopy of a given plant stand) variations both in light intensity and spectral composition are known (Bjorkman, 1981).

Shade plants have been found to thrive well under low light habitats; for instance, under the canopy of a given plant stand or in the lower strata of multistoreyed plant communities. The shade plants are mostly of the obligate type whose leaves suffer damage and the growth gets drastically affected upon exposure to high light regimes (Hariri and Prioul, 1978). Even within the same species, sun and shade ecotypes are common (Bjorkman and Holmgren, 1963). Facultative responses are more common in the sun plants. Whether of obligate or facultative nature, the growth of sun plants in shade results in photosynthetic light dependence characteristics tending towards those of obligate shade plants (Bjorkman *et al.*, 1972a, b). Thus a classification of plants into sun and shade species cannot be

made on the basis of light saturation curves or light compensation points alone. Plants are classified into sun and shade plants depending on their adaptability to a selected light intensity (Bjorkman, 1968a, b). This adaptability is inherited and it is determined by the genotype and results from genetic adaptation to the light environment prevailing in the native habitat (Boardman, 1977). Extreme shade species can survive at much lower light intensities than sun species.

2.1 Growth

2.1.1 Morphology

2.1.1.1 Plant height

Shading generally increase the height of plants (Aminuddin, 1986; Begonia *et al.*, 1988; de Castro *et al.*, 1962; Guiscafre and Gomez, 1942; Huxley, 1967; Kohyama and Hotta, 1990; Kjelgren, 1994; Lakshmamma and Rao, 1996; McClelland, 1934; Orlando, 1963; Venketaramanan and Govindappa, 1988). In shade tolerant species shading increases growth in height for future exploitation of better lit conditions at higher levels in the canopy. Sturdy (1935) observed an increase in internodal length under shade in coffee.

2.1.1.2 Stem diameter

Shading increased stem diameter growth (Guiscafre and Gomez, 1942; Aminuddin, 1986). In coffee, stem diameter increase in intermediate shades was significantly higher than heaviest shades and open grown plants (de Castro *et al.*, 1962). However, Aminuddin (1986), Kjelgren (1994), Orlando (1963) and Sylvain (1952) observed an inverse relation of stem diameter to the degree of shade.

2.1.1.3 Branches

Shaded plants have a more horizontal branch orientation. Plants grown in 100% sunlight had a more vertical branch orientation (Marler *et al.*, 1994) The most conspicuous developmental response to low R:FR is a marked increase in stem elongation rate (Holmes and Smith, 1977a, b, c; Morgan and Smith, 1978, 1981) and a concomitant reduction in branching. Regnier and Harrison (1993) found a decrease in branch length under shade.

Axillary bud growth (branching) decreased considerably with increasing amounts of shade (Begonia *et al.*, 1988 and Sylvain, 1952) and utilization of assimilates in shade to increase stem extension led to a marked reduction in development of axillary buds into branches. However, in coffee, number of pairs of primary branches increases under shade. There was a highly significant difference in number of pairs of lateral between the trees in full sunlight on one hand and the trees in shade on the other, in favour of these latter ones (de Castro *et al.*, 1962; Guiscafre and Gomez, 1942; Huxley, 1967; Venketaramanan and Govindappa, 1988). .Lower axillary buds were not inhibited under shade (Regnier and Stoller, 1989). However Ducrey (1992) found that occurrence of branching depended more on species type than on light conditions.

2.1.1.4 Number of leaves

Regnier and Harrissons (1993), Sturdy (1935) and Sylvain (1952) found that plants had fewer leaves under shade. But increase in the number of leaves under shade is also reported by many others (Alvin, 1960; Castillo, 1961; Huerta, 1954; Huxley, 1967; Maestri and Gomez, 1961 and Venkataramanan and Govindappa,

1988). Ducrey (1992) also found that for all canopy species the maximum number of leaves was obtained in partial shade.

2.1.1.5 Leaf thickness

Leaf thickness decreases under shade (Adams *et al.*, 1987; Marler *et al.*, 1994; Messier *et al.*, 1989; Regnier *et al.*, 1988; Shiraishi *et al.*, 1996; Utsunomiya and Higuchi, 1996). Thicker leaves in plants grown in full sunlight have been attributed primarily to increases in the thickness of the palisade mesophyll layer (Chabot *et al.*, 1979; Fails *et al.*, 1982; Nobel, 1976; Patterson *et al.*, 1977). Photosynthetic tissue per unit leaf area is therefore increased. Patterson *et al.* (1978) suggested that the greater mesophyll thickness in high irradiance grown plants may lead to chloroplast shading one another within the leaf, causing photosynthesis to become saturated at higher light intensities than in plants grown under shade.

2.1.2 Classical growth parameters

2.1.2.1 Total dry matter (TDM)

Literature pertaining to the effect of shade on TDM are mostly restricted to heliophytes, as such studies in shade adapted plants are relatively few. Of the species studied, coffee respond adversely to exposure to full sunlight (de Castro *et al.*, 1962; Maestri and Gomez, 1961). According to Huxley (1967) and Venketaramanan and Govindappa (1987), TDM decreased under full day light as higher levels of solar radiation appeared to decrease the net photosynthetic capacity. High TDM under moderate shade might be due to high stem (Liu *et al.*, 1997), leaf and root weight (de Castro *et al.*, 1962), high NAR (Huxley, 1967) and large leaf area; which undoubtedly increases the total photosynthetic capacity of the

seedlings (Venketaramanan *et al.*, 1983). However, higher levels of shade treatments (73-88%) where, in general, less favourable for growth (de Castro *et al.*, 1961; Huxley, 1967 and Maestri and Gomez, 1961).

In many studies, reduced solar irradiance resulted in a decrease in dry weight increment, as well as root, stem, leaf and shoot dry weight (Mc Carthy and Dawson, 1990). Similarly, when two shade tolerant species, pacific silverfir and subalpine fir, were sampled along a light gradient ranging from open areas to levels inside a forest stand, it was found that both were equally well adapted to survive under high shade by reducing growth (Klinka *et al.*, 1992). Similar manifestation of shade adaptation was also observed in seedlings of certain rain forest tree species, when they were grown under heavy artificial shades (i.e. 63%, 90%, 97.5%), roughly corresponding to light environments in large gaps, small gaps and forest understorey respectively (Osunkoya *et al.*, 1994).

2.1.2.2 Root dry weight

In coffee, moderate shade treatments produced plants with the heaviest roots as compared to plants grown under full solar explosure (de Castro *et al.*, 1962). But Huxley (1967) and Mc Carthy and Dawson (1990) found that an increase in shade decreased the proportion of dry matter in roots. 'Dense' shade. was however, more detrimental.

2.1.2.3 Leaf weight ratio

Most studies seem to indicate that although shading tends to increase the proportion of the total dry matter which is distributed to the leaves (leaf weight ratio, WL/Wp), generally this influence is small, especially in comparison with the effect of specific leaf area (Begonia *et al.*, 1988; Blackman and Black, 1959;

Cooper, 1967; Doley, 1978; Hughes and Cockshull, 1971; Huxley, 1967; Ledig *et al.*, 1970; Loach, 1970 and Regnier *et al.*, 1988). However, this behaviour does not extend to all species. For example, Loach (1970) showed that in shade tolerant *Acer rubrum* and the moderately shade tolerant *Quercus rubra*, there was a substantial increase in leaf weight ratio with decreased light level. Whitehead (1973) also reported that in shade tolerant species such as *Filipendula ulmaria* and *Iris pseudacorus*, a proportionately greater amount of photosynthate was devoted to the formation of leaf material, when the levels of light was decreased.

2.1.2.4 Root weight ratio

Apparently, increased allocation to leaf growth in response to shading may largely be at the expense of root growth. A reduced root weight ratio may not be harmful in shaded locations with adequate nutrient levels and favourable water relations but is likely to have serious consequences where this is not the case (Bongers *et al.*, 1988). In the study with the shade tolerant species, *Filipendula ulmaria*, the increased allocation to leaf growth in response to shading was accompanied by a corresponding decrease in allocation to root growth (Whitehead, 1973) and shading of *Chamaenerion angustifolium* reduced the root weight ratio to less than half that of unshaded plants (Myerscough and Whitehead, 1966). In the studies with *Impatients parviflora*, a shade tolerant species (facultative shade species), root weight ratio showed a consistent decrease with shading, ranging from 0.44 in full daylight to 0.31 in 5% daylight. However, only a part of this saving was allocated to leaf growth, for shading caused an increase in stem weight ratio from 0.15 in full daylight to 0.24 in 5% daylight. It should also be emphasized that the response of root weight ratio to shading is likely to be strongly influenced by nutrient and water relations.

2.1.2.5 Ratio of shoot to root

The ratio of shoot to root or ratio of above ground dry matter to below ground dry matter increases under shade in shorea seedlings (Aminuddin, 1986), Oak (Mc Carthy and Dawson, 1990), carambola trees (Marler *et al.*, 1994) and in certain other rain forest tree species (Osonkoya *et al.*, 1994). This indicates that they have proportionately less root tissue to maintain in shade (Stoller and Myers, 1989). Popma and Bongers (1988) studied the growth of rain forest species under three environmental conditions: the shaded forest understorey, a small canopy gap and a large canopy gap. Growth was enhanced with increase in light intensity. Plants grown in small gaps or forest understorey showed a shade plant morphology with low ratio of root to shoot, whereas those under large gaps showed a sun plant morphology, with a high ratio of root to shoot.

2.1.2.6 Ratio of photosynthetic tissue to support tissue

In order to utilise available photosynthetic photon flux density (PPFD) efficiently, shade adaptable plants also maximise the photosynthetically active tissue of the total plant biomas by redistributing dry matter. This redistribution maximises efficiency of light interception by increasing the proportion of total dry matter in leaf tissue (Regnier *et al.*, 1988). Stoller and Myers (1989) computed the ratio of support tissue to leaf as a refinement of the leaf area index because the additional support type tissue, stems and petioles also require maintenance energy while contributing very little photosynthate to help the plant to maintain a positive carbon balance, especially when grown in shaded environment. A decrease in the ratio of support tissue to leaves reflect greater partioning of plant biomass in to leaf tissues that harvest the available PPFD, with less biomass diverted to tissues that

deplete photosynthate. Certain weeds which survive under soybean canopy (which permits only less than 5% of the total sunlight) are found to utilise a sizable amount of its biomass in order to harvest the available light.

2.1.2.7 Total leaf area per plant

The response of the leaf area under shade is primarily observed to be related to the foliar anatomy of the species concerned. For instance, the extend to the leaf expansion observed in the case of coffee with thick ever green type leafs was lesser in comparison to uplant cotton plants with thinner leafs, when subjected to similar growth conditions (Huxley, 1962, 1967). Thicker leaf shows a lesser capability to alter the total surface area or specific leaf area. However an increase in leaf area under shade has invariably been reported by several others (Alvim, 1960; Castillo, 1961; Ducrey, 1992; Hampson *et al.*, 1996; Huang and Kuo, 1996; Huerta, 1954; Huxley, 1067; Machado, 1946, Maestri and Gomez, 1961; Marler *et al.*, 1994; Messier *et al.*, 1989 and Venketaramanan and Govindappa, 1987). Sturdy (1935) found that in coffee, shade plants had fewer leaves but more total leaf area than in full sun. On the contrary in white pine, a species classified as intermediate in shade tolerance, total leaf area was greater in open grown saplings than in understorey saplings (O'Conner and Kelty, 1994).

2.1.2.8 Specific leaf weight (SLW)

SLW, the ratio of blade mass to blade area, is in general an indicator of leaf thickness. Leaves in shady environments typically have lower SLW than leaves grown in sunny conditions (Begonia *et al.*, 1988; Beurlein and Pendleton, 1971; Bjorkman *et al.*, 1972a, b; Blackman, 1960; Bongers *et al.*, 1988; Bowes *et al.*, 1972; Evans and Hughes, 1961; Hampson *et al.*, 1996; Jurik, 1986; Mahmoud and

Grime, 1974; Messier *et al.*, 1989; Osonkoya *et al.*, 1994; Popma and Bongers, 1988; Regnier *et al.*, 1988; Singh *et al.*, 1974 and Utsunomiya and Higuchi, 1996). Low SLW represents a complement of leaf characteristics including decreased leaf thickness, decreased palisade cell developments, lesser photosynthesising cells per unit leaf area, decreased assimilatory apparatus per unit area, lower maximum rate of photosynthesis per unit leaf area, lower light saturation point and decreased respiration rate (Boardman, 1977 and Chabot and Chabot, 1977). Even though maximum photosynthetic rate per unit leaf area is low under shade, total photosynthetic rate per plant is higher due to increased leaf area per plant. This in turn may cause increased TDM under low irradiants levels. Therefore SLW is a good indicator of photosynthetic capacity, growth and the relative ability to shade adaptation. SLW is further influenced by genetic differences between species (Jurik, 1986), although the magnitude of such differences are generally much less than differences due to environmental effects.

The thin shade grown leaves with low SLW are also reported to maximize the explosure of the radiation harvesting apparatus to the limited number of usable photons (Bjorkman *et al.*, 1972a, b; Blackman, 1960; Goodchild *et al.*, 1972; Mahmoud and Grime, 1974; Myerscough and Whitehead, 1966; Patterson, 1979).

2.1.2.9 Specific leaf area (SLA)

Numerous studies show that increase in SLA under shade is almost universal among both sun and shade species (Ducrey, 1992, 1994; Groninger *et al.*, 1996; Huang and Kuo, 1996; Huxley, 1967; Jurik *et al.*, 1979; McKendrick, 1996 and Regnier and Harrison, 1983), although the extent of such changes may show marked species differences. Shade plants do not necessarily have particularly high

specific leaf areas. It seems probable that the major factor contributing to an increased specific leaf area in response to shading is a reduction in several components of the photosynthetic system which govern the capacity at high quantum flux densities. However, it should be emphasized that changes in specific leaf area are also likely to involve changes in the proportion of photosynthetically inactive to photosynthetically active leaf material. Some studies indicate that a reduction in the pool of photosynthate, mainly sugars and starch, could perhaps account for up to a 20% increase in specific leaf area. A reduction in other photosynthetically inactive components such as epidermal tissue, cell walls, and vascular tissue could perhaps cause a similar increase since the energy load, the requirement for mechanical strength, and the rate of water transport are much reduced in shade situations, and such savings are unlikely to impose any significant disadvantageous effects (Bjorkman, 1981).

Begonia *et al.* (1988) found that the distribution of leaf biomass as leaf area was significantly increased by shading. This was evident from proportional increase in SLA with increasing shade. Difference in SLA reflect changes in structure and thickness of leaves. The thinner leaves characteristically produced under shade have greater SLA than leaves produced under high PAR (Boardman, 1977; Patterson, 1980a, b).

2.1.2.10 Leaf area ratio (LAR)

Several shade adapted species exhibit an increase in LAR when grown at low irradiance (Alvim, 1960; Begonia *et al.*, 1988; Blackman and Wilson, 1951a, b; Castillo, 1961; Cooper, 1967; Huerta, 1954; Huxley, 1967; Maestri and Gomez, 1961; Osonkoya *et al.*, 1994; Patterson, 1985; Popma and Bongers, 1988; Stoller

and Myers, 1989; Utsunomiya and Higuchi, 1996; Venketaraman and Govindappa, 1987 and Whitehead, 1973). This response is found less frequent among sun adapted species (Blackman and Wilson, 1951a; Cooper, 1967 and Patterson *et al.*, 1978). This response compensate for reduced irradiance by increasing light interception in proportion to total plant tissue. The increase in LAR with shading represents an adaptation to low PAR because a greater LAR results from a greater allocation of plant material to the photosynthetic light harvesting structures (Patterson, 1979, 1980).

Photosynthate distribution efficiency has also been expressed by LAR (Patterson, 1985). A decrease of LAR with the increase in age of the plant is noted in coffee (Venketaramanan and Govindappa, 1987) and sweet pepper (Nilwik, 1981).

In a low light environment it is obviously imperative that the photosynthetically active area per total plant mass be as high as possible and it can be achieved in several different ways. One such adjustment involves an increased SLA and another involves an increased leaf weight ratio. The relationship between the different growth parameters is given by the following expression.

$$LAR = LWR \times SLA$$

A comparison between the responses to shading by facultative shade species, *Impatiens parviflora* (Evans and Hughes, 1961), with an obligate sun species, *Helianthus annus* (Hiroi and Monsi, 1963), provides a good illustration of the importance of compensating changes in leaf area ratio. Experiments were conducted with young seedlings during a 3-4 week period following expansion of the first foliage leaves, growth in the field under different degrees of shading

imposed by screens. Shading resulted in an increased specific leaf area in both species. In *helianthus*, maximum specific leaf weight (165% of unshaded controls) was reached under the 22% light regime; further shading led to a decline in specific leaf area and under the 5% light regime it was only about one-third higher than under unshaded conditions. By contrast, *Impatiens* continued to increase its specific leaf area with shading so that under the 5% light regime the value was about 2.5 times that of the unshaded controls. In addition to these large species differences in the response to shading with respect to specific leaf area there were also smaller, but important differences in the response of dry matter distribution to the leaves. In *Impatiens*, shading resulted in slight but significant increase in the weight ratio (about 10% greater in dense shade) whereas in *Helianthus*, shading caused a progressive decline in photosynthate allocation to the leaves, so that in dense shade, the leaf weight ratio was only about 75% of that found in the unshaded controls. The combination of these changes in specific leaf area and leaf weight ratio resulted controls. The combination of these changes in specific leaf area and leaf weight ratio resulted in large differences in leaf area ratio. *Impatiens* plants, grown under the 5% light regime, had almost three times as high leaf area ratio as the unshaded control plants, whereas there was no significant difference in leaf area ratio between *Helianthus* plants grown under the 5% and the 100% light regime.

Increased LAR in shaded plants was reported to be primarily due to increases in SLA rather than LWR (Cooper, 1967; Evans and Hughes, 1961 and Regnier *et al.*, 1988). But in coffee this gain in SLA is relatively small when compared to the data from many other species (Blackman and Wilson, 1951b;

Blackman, 1956; Maggs, 1960 and Njoku, 1960). This could be attributed to the relatively thicker leaves in coffee (Huxley, 1967).

2.1.2.11 Net assimilation rate (NAR)

NAR increases linearly with the logarithm of the percentage full day light up to a maximum to the value corresponding to the full daylight has been reported for many species (Blackman and Wilson, 1951a, b; Mc laren and Smith, 1978; Patterson, 1979; Regnier *et al.*, 1988). Soybean plants showed a linear decline in NAR with increasing level of shade and the reduced NAR was a reflection of the decrease in radiant energy available for photosynthesis under shade (Begonia *et al.*, 1988). From the very high values of NAR recorded for certain species grown under high solar radiation intensities, for example, subterranean clover (Black, 1955) and *Helianthes annuus* (Blackman and Black, 1959 and Huxley, 1963) it would appear that in most adapted plants NAR increases with increasing radiation, up to the maximum provided by the environment. This was not observed for seedlings of citrus (Monselise, 1951) and Cacao (Goodall, 1955), but it cannot be assumed that water was not limiting, particularly in the latter case.

Venketaramanan and Govindappa (1987) found that in general, shade increase the NAR in all the cultivers of coffee and 30% shade showed more NAR than in the full daylight. NAR does not increase linearly with the increase in percentage daylight, as coffee reaches photosaturation in lesser light intensity itself. Higher levels of solar radiation appears to decrease the net photosynthetic capacity of coffee leaves. But unshaded plants showing maximum NAR is also reported in coffee (Huerta, 1954; Castillo, 1961; Orlando, 1963).

A comparison between the responses to shading in the woodland, between a facultative shade species, *Impatiens parviflora* (Evans and Hughes, 1961), and obligate sun species, *Helianthus annus* (Hiroi and Monsi, 1963) showed that the net assimilation rates of these two species were rather similar over a wide range of daily irradiance receipts. Only at the heaviest shade was there a pronounced difference in net assimilation rate, presumably attributable to a lower respiration rate in *Impatiens* than in *Helianthus*.

2.1.2.12 Relative growth rate (RGR)

RGR is an overall measure and considered as a summation of cumulative effect of all the processes that finally result in increased dry weight of the plant (Venketaramanan and Govindappa, 1987). NAR is one of the important component which determine RGR and a high RGR may also probably be due to a large leaf area which undoubtedly increases the total photosynthetic capacity of the seedlings. Regnier *et al.* (1988) found that Soybean and three broad leaf weeds grown at reduced irradiance exhibited an increase in LAR and the increased LAR fully compensated for the decreased NAR in field grown plants, which in turn resulted in a constant RGR over irradiance levels whereas an increase in LAR of the growth chamber plants did not fully compensate for the reduced NAR which resulted in the reduction in RGR of plants grown at low irradiance.

Osunkoya *et al.* (1994) found that in seedlings of certain rain forest tree species, when they were grown under heavy artificial shades, roughly corresponding to the light environments in large gaps (63%), small gaps (90%) and forest understorey (97.5%), 63% and 90% shade plants had high RGR and NAR than the 97.5% shade plants. Similar effect of shade was also observed in

seedlings of certain tropical deciduous trees; when grown under high and low light conditions in a growth chamber. In high light treatment, they achieved highest RGR and NAR than when grown at low light intensity (Rincon and Huante, 1993).

In coffee RGR usually increases under shade. Huxley (1967) found that values of RGR was highest in moderate shade whereas Venketaramanan and Govindappa (1987) found that RGR was higher in plants kept at 75% shade as against other light intensities tried. Generally, higher RGR was associated with higher NAR (Huxley, 1967 and Venketaramanan *et al.*, 1983) and significant correlation between RGR and NAR is reported in coffee (Venketaramanan *et al.*, 1983) and in Lolium (Wilson and Cooper, 1969a, b). In coffee, the values of RGR was less because of low NAR and LAR (Huxley, 1967; Venketaramanan and Govindappa, 1987). Mori *et al.* (1990) found that RGR and NAR for shade tolerant Malaysian tree species tended to be lower than those for light demanding species.

The comparison between the responses to shading by facultative shade species, *Impatiens parviflora* (Evans and Hughes, 1961), with the obligate sun species, *Helianthus annuus* (Hiroi and Monsi, 1963) showed that in *Impatiens*, the relative growth rate under the 10% light regime was as high as 80% of that under the 100% regime even though the corresponding net assimilation rate was only 33% of the unshaded control. In *Helianthus*, the effect of shading on relative growth rate was nearly the same as the effect on net assimilation.

The shade intolerance of *Helianthus annuus* becomes increasingly pronounced with advancing plant age (Hiroi and Monsi, 1964). During the fourth and fifth week, the relative growth rate fell sharply under the lower light treatments and under the 22% light regime it fell to about 28% of that of the unshaded plants

and became negative under the 10% and 5% regimes. This time-dependent decline in relative growth rate was associated with a decreased allocation of photosynthate to new leaf growth (expressed as WL/WP), ultimately leading to premature senescence of the leaves. By comparis. n, the moderately tolerant *Phaseolus aureus* maintained relatively high growth rates and allocation to new leaf growth under the 22% light regime and these parameters were still positive under the 10% light regime. In the highly shade-tolerant *Impatiens parviflora*, there was little time-dependent decline in relative growth rate even under the 10% light regime and allocation of photosynthate to new leaf growth remained at a high level.

2.2 Anatomy

2.2.1 Foliar anatomy

It has long been recognised that leaf anatomy may be strongly influenced by the light level during growth (Bjorkman *et al.*, 1972a, b; Crookston *et al.*, 1975; Easu, 1965; Grahi and Wild, 1973; Hesselman, 1904; Kramer and Kozlowski, 1979; Ludlow and Wilson, 1971; Nobel *et al.*, 1975; Stahl, 1983; Turrell, 1936; Wylie, 1951). Low light causes a weaker development of the mesophyll regions, resulting in thinner leaves (Abrams, 1987; Abrams and Kubiske, 1990; Adams *et al.*, 1987; Boardman, 1977; Fahl *et al.*, 1994; Marler *et al.*, 1994; Messier *et al.*, 1989; Regnier *et al.*, 1988; Shiraishi *et al.*, 1996 and Utsunomiya and Higuchi, 1996). Shade plants in their native habitats often have thin leaves with a lower fresh weight per leaf area (Bjorkman, 1968a, b; Goodchild *et al.*, 1972; Rabinowitch, 1945). However, thin leaves are not always a characteristic of shade plants; many rain forest species such as *Cordyline rubra* and *Lomandra longifolia* have thick leaves (Goodchild *et al.*, 1972). These variations in shade plants probably reflect species variation in leaf structure.

Thicker leaves in plants grown at high irradiance have been attributed primarily to increase in the thickness of the palisade mesophyll layer (Chabot *et al.*, 1979; Fails *et al.*, 1982; Huang and Kuo, 1996; Nobel, 1976; Patterson *et al.*, 1977). Reduction in spongy cell number in the shade plants was also noted. Leaves were thicker in unshaded plants than in shaded ones, because of the increased size of the palisade and spongy parenchyma tissues (Fahl *et al.*, 1994).

In a typical shade leaf, the mesophyll cells tend to be round or highly irregular in shape unlike the long columnar palisade parenchyma cells of sun plants (Huang and Kuo, 1996), and the total number of cells across a leaf section is often smaller than that in the sun leaf (Bjorkman, 1981). The epidermis and cell walls are thin, the vascular system less developed and there are large intercellular spaces (Anderson *et al.*, 1973 and Huang and Kuo, 1996).

Several workers have discussed in detail the relationship of internal leaf structure and photosynthetic rate (Mansfied and Jones, 1976; Boardman, 1977; Bothar-nordenkampf, 1982). The palisade cells account for major part of the photosynthetic machinery. They contain at least twice or even three to five times chlorophyll corpuscles, than the spongy cells in which CO_2 exchange is only a subsidiary function (Haberlandt, 1914). Moreover the elongated palisade cells expose 1.6 to 3.5 times free surface area than the spongy parenchyma (Turrel, 1936) facilitating a higher ratio of internal to external surface area resulting in efficient gas exchange. In alfalfa leaves, Delaney and Dobrenz (1974a, b) obtained significant positive correlation between apparent photosynthesis and thickness of palisade tissue.

2.2.2 Chloroplast structure

Studies on leaves of shade species, *Alocasia, Cordyline* and *Lomandra* indicated that in comparison with sun species, greater number of chloroplasts are in the mesophyll cells adjacent to the upper leaf surface, and the cells in the lower part of the mesophyll contain relatively few chloroplasts (Boardman, 1977).

It is generally stated that the leaves of shade plants have large chloroplasts (Kirk and Tilney Basset, 1967; Rabinowitch, 1945). A striking feature of shade plant chloroplasts is their large grana stacks which may contain as many as 100 thylakoids per granum (Anderson *et al.*, 1973; Goodchild *et al.*, 1972; Lichtenthaler *et al.*, 1981). The grana are irregularly arranged within a chloroplast and not oriented in one place as they are in the sun plant chloroplasts. The irregular orientation in the shade plant chloroplast might be expected to increase their efficiency for the collection of the weak diffuse radiation on the forest floor.

The proportion of lamellae-forming grana and the ratio of thylakoid membranes to stroma is greater in shade plants than in sun plants (Boardman *et al.*, 1975; Goodchild *et al.*, 1972). According to Sukenik *et al.* (1989), the cells grown under low light condition were characterised by large relative volume of chloroplast and high surface density of thylacoid membranes. However, Poulson and Delucia (1993) found that the shade acclimation of *Silphium* is accomplished without adjustment to thylakoid membrane structure.

2.3 Respiration

Shade plants have a very low rate of dark respiration, a characteristic which is of paramount importance in the maintenance of a positive carbon balance in shaded habitats. The shade plants exhibited low dark respiration rates (0.06-0.16

mole CO_2 evolved dm ^{2}min ^{1}) compared with the sun species which showed dark respiration rates of 0.4-0.8 mole CO_2 dm $^{-2}$min ^{1}. Although such low respiratory rates could be caused by regulation of respiration (primarily determined by the demand for ATP required for heterotrophic biosynthesis), it seems likely that, at least in part, it is associated with a lower content of respiratory machinery than in sun plants. If the latter situation exists, then the shade plants would presumably incur a significantly lower cost in the production and maintenance of the respiratory system (Bjorkman, 1981).

2.4 Photosynthesis

2.4.1 Light response characteristics

In general, at low light intensities, photosynthesis has been found to be linearly dependent on light intensity and efficiency of light utilization. At higher light intensity, on the other hand, photosynthesis is less proportional to light, due to partial light saturation. Photosynthesis fails to respond to increased light when it reaches complete saturation point (Bjorkman, 1981). Great differences exist in the light dependence of photosynthesis between sun and shade plants.

The sun plants are capable of high photosynthetic rates at saturating light intensity (16-20 mg CO_2 $dm^{-2}hr^{-1}$) whereas shade plants are not so (2-5 mg CO_2 $dm^{-2}hr^{-1}$). In the latter, photosynthesis reaches saturation levels at relatively low light intensity of 300-1000 fc or at about 100 E $m^{-2}s^{-1}$ (equivalent to about 5% of maximum daylight) whereas in sun plants it continues up to 2000-3000 fc (Bjorkman *et al.*, 1972a; Bjorkman, 1973; Bohning and Burnside, 1956; Ehleringer and Bjorkman, 1978; Ludlow, 1968). The light compensation point is always higher in sun plants (100-150 fc) compared to shade plants (approximately 50 fc)

(Bjorkman *et al.*, 1972a; Bohning and Burnside, 1956; Ludlow, 1968). This is so because of very low levels of dark respiration in shade plants (Bjorkman, 1968a, b). Therefore their performance at low light intensity is efficient and high in contrast to the sun plants which cannot perform efficiently at low light intensity.

According to Bjorkman (1981), it is possible to identify a plant in terms of its adaptation to shade based on light response curves. The plants are clearly adaptive, if the plants functions efficiently under low quantum flux densities that prevail in its habitat.

2.4.2 Maximum photosynthetic rate

Many reports are available on the effect of shade on different photosynthetic characteristics (Kitajima, 1994; Marler *et al.*, 1994; Ducrey, 1994; Madsen *et al.*, 1991; Mulkey *et al.*, 1991; Mori *et al.*, 1990; Mckiernan and Baker, 1991; Sondergaard and Bonde, 1988; Carter and Teramura, 1988; Agata *et al.*, 1985; Masarovicova and Elias, 1985). A decrease in photosynthetic rate on a leaf area basis, under shade was reported by Ducrey (1994), Fukuoka *et al.* (1996), Madsen *et al.*, (1991), Mori *et al.* (1990) and Agata *et al.* (1985). Numerous shade and sun adapted plants are known to develop thin leaves when grown at low irradiance (Chabot and Chabot, 1977; Marler *et al.*, 1994; Abrams and Kubiske, 1990; Messier *et al.*, 1989; Regnier *et al.*, 1988; Abrams, 1987 and Adams *et al.*, 1987). Considering the difference in the leaf thickness in plants grown under open and shaded condition, Regnier *et al.* (1988) measured the maximum photosynthetic rate per unit leaf volume basis and observed an increase in maximum photosynthetic rate per unit leaf volume under shade. Traditionally photosynthetic rate is expressed on a leaf area basis, due to the ease of the measurement.

Reduced irradiance during growth results in decrease in leaf thickness in all species (I'ma *et al.*, 1993). Thinner leaves in plants grown at low irradiance have been attributed primarily to decreases in the thickness of the palisade mesophyll layer (Paulson and Delucia, 1993; Chabot *et al.*, 1979 and Fails *et al.*, 1982; Nobel, 1976 and Patterson *et al.*, 1977). Photosynthetic tissue per unit leaf area is therefore decreased resulting in low photosynthetic rate at low light intensities.

Maintenance of a high leaf surface area support tissue ratio may also be as important as photosynthesis per unit leaf area to survive under shade. However, according to Boardman (1977), the efficiency of photosynthesis is expected to be independent of the efficiency of light absorption and primary photochemical reaction. It will be influenced by some steps of dark reaction: stomatal resistance for CO_2, activity of RuDP carboxylase and the rate of photosynthetic electron transport. Plants grown under low irradiance show high stomatal resistance, high mesophyll resistance, low stomatal conductances, low RuDP carboxylase activity and low rate of photosynthetic electron transport (Boardman, 1977). These can be probably some of the intrinsic factors that give low maximum photosynthetic rate in shade plants.

Maximum photosynthetic rate, light saturated rate of carbon dioxide assimilation, light saturation point, light compensation point and dark respiration were lower in shade grown plants than in sun grown plants (Agata *et al.*, 1985; Ducrey, 1994; Fahl *et al.*, 1994; Friend, 1984; Kitagima, 1994; Marlet *et al.*, 1994; Mckiernan and Baker, 1991). On the basis of the low photosynthetic light saturation, low light compensation point and low dark respiration rate under shaded condition coffee qualifies well as a shade adapted species (Fahl *et al.*, 1994 and Friend, 1984).

When young carambola trees were exposed to 25%, 50% and 100% sunlight, shading reduced dark respiration and light compensation and saturation points (Marler *et al.*, 1994). In *Rhus lucida* maximum photosynthetic rate remained unchanged under shade (Midgley *et al.*, 1992) whereas *Chenopodium*, when grown under low light had high maximum photosynthetic rate (Sehaefer and Schmidt, 1991). Most shade tolerant species had low photosynthetic rate (Carter and Teramura, 1988; Madsen *et al.*, 1991; Mori *et al.*, 1990; Mulkey *et al.*, 1991) low light saturation point (Carter and Teramura, 1988; Newell *et al.*, 1993) low light compensation point (Carter and Teramura, 1988) and low stomatal conductance (Mori *et al.*, 1990; Mulkey *et al.*, 1991) than others. But Kjelgrel (1994) observed a high stomatal conductance under shade.

Photosynthetic carbondioxide efficiency is defined as the rate of increase in net photosynthesis with increase in ambient carbondioxide concentration. Shade grown shade tolerant species have high photosynthetic carbondioxide efficiency. High photosynthetic carbondioxide efficiency may be advantageous for maintaining a positive carbon balance in low light environment under a forest canopy (Teskey and Shrestha, 1985).

Curves relating net photosynthetic rate to irradiance (P(I) curve) were estimated in a perennial herb, *Mercurialis* from different light regime conditions and the analysis of P(I) curve characterised the species as shade tolerant (Masarovicova and Elias, 1985).

2.4.3 Photosynthetic pigments

2.4.3.1 Chlorophyll contents

Shade plants having larger chloroplasts are reported to be rich in chlorophyll compared to sun plants (Kirk and Tilney-Bassett, 1967; Rabinowitch, 1945) and contain a high proportion of chlorophyll *b*/chlorophyll *a* ratio (Egle, 1960). These distinctions have been readily observed in sun and shade leaves of many species, as well as when a single species is grown under different light intensities. Shade plants in their native habitats often have thin leaves with a lower fresh weight per leaf area and a higher content of total chlorophyll expressed on a weight basis (Adams *et al.*, 1987, 1988; Andrew *et al.*, 1984; Bjorkman, 1968a, b, 1981; Bjorkman and Holmgren, 1963; Goodchild *et al.*, 1972; Hampson *et al.*, 1996; Lakshmamma and Rao, 1996; Lichtenthaler *et al.*, 1981; Rabinowitch, 1945; Sandergaard and Bonde, 1988 and Shiraishi *et al.*, 1996). Total chlorophyll per leaf increased in shade plants. However, total chlorophyll per unit leaf area decreased due to increase in leaf area and chlorophyll gets diluted (Bjorkman, 1981). On the contrary, total chlorophyll on a unit leaf weight basis increased because of a decrease in leaf thickness (Adams *et al.*, 1988). However, Abrams (1987)'s findings, contradict the established ideas of high total chlorophyll for shade tolerant species.

Increase in chlorophyll content under shade condition is generally attributed to

(a) chloroplast with large grana stacks which may contain as many as hundred thylakoids per granum (Anderson *et al.*, 1973; Goodchild *et al.*, 1972; Lichtenthaler *et al.*, 1981) and

(b) high proportion of lamellae forming grana and the ratio of thylakoid membranes to stroma (Boardman *et al.*, 1975; Goodchild *et al.*, 1972). Greater chlorophyll content per unit leaf weight may be a factor in the higher photosynthetic rates on a leaf weight basis exhibited by shade plants when exposed to low light intensities enhanced light capture capacity per unit leaf volume. According to the calculations by Bjorkman (1981), however, a 50% increase in chlorophyll content results in only a 3% increase in absorption of photosynthetically active radiation. Increased chlorophyll content on a leaf weight or volume basis in response to reduced irradiance has been reported for shade and sun adapted species (Bjorkman and Holmgren, 1963; Patterson *et al.*, 1978).

Reduced irradiance during growth induces an increase in chlorophyll *a* (Sukenik *et al.*, 1989; Goldborough and Kemp, 1988; Berner *et al.*, 1987 and Geider *et al.*, 1985). An asymptotic increase in light absorption with increasing chlorophyll *a* density across the plant kingdom from single celled cynobacteria to trees has been confirmed (Augusti *et al.*, 1994). Chlorophyll *a* concentration of photosynthetic tissue decreased as the tissues become thicker. This resulted in low chlorophyll *a* density, inefficient light absorption and finally low growth rate. It is well known that growth under low light levels tends to result in an enrichment in chlorophyll *b* relative to chlorophyll *a* (Sartoni *et al.*, 1993 and Sondergaard and Bondi, 1988) as chlorophyll *b* can harvest light prevailing in shaded habitats more efficiently than chlorophyll *a*. Shade plants grown in deep shade tend to have a markedly lower chl *a*/chl *b* ratio compared to sun plants grown under a high light level (Egle, 1960). More recent reports have confirmed these earlier findings (Adams *et al.*, 1988; Andrew *et al.*, 1984; Lichtenthaler *et al.*, 1981; Mckiernan and Baker, 1991; Osunkoya *et al.*, 1994; Schaefer and Schmidt, 1991; Sondergaard

and Bonde, 1988 and Wejnar and Gundermann, 1987). However, Paulson and Delucia (1993) reported that shade acclimation of Silphium is accomplished without adjustment to the chlorophyll *a*/*b* ratio.

Chlorophyll *b* belongs to light harvesting chl *a b* protein complex, LHchl (Thornber, 1975) which is primarily associated with photosystem (PS) II (Butler, 1977). High chlorophyll *b* or low chlorophyll *a*/*b* ratio reflects a difference in the proportion of the LHchl complex in the total chlorophyll (Lichtenthaler *et al.*, 1981). In general, the shade plants have a higher ratio of PS II to PS I reaction centres than sun plants (Mckiernan and Baker, 1991). A possible function of an increased PS II/PS I ratio in shade plants is to provide a more balanced energy distribution between the two photosystems in shaded habitats such as forest floors which, because of the filtering effect of the forest canopy, have a very high proportion of far-red light, effective only in excitation of PS I (Bjorkman, 1981). Such changes in PS II/PS I ratio could also explain the tendency of shade plants to have a slightly higher ratio of total chlorophyll to p-700 (Patterson *et al.*, 1978).

2.4.3.2 Carotenoid contents

Carotenoid content increases in plants when grown at reduced irradiance (Sukenik *et al.*, 1989). Carotenoids function in the photosynthetic tissues of higher plants in two major ways (Cegdell, 1988; Young, 1992). They act as accessory pigments harvesting light for photosynthesis, and as photoprotective agents limiting the damaging effects of high irradiance. The absorption spectra of carotenoids are distinct from those of chlorophylls, enabling plants to harvest light over a wider wavelength range. Carotenoids of leaves are highly conserved, forming major components of the photosynthetic apparatus. Carotenoids are generally divided in

to two classes; those which contain oxygen (xanthophylls) and those which do not (carotenes). Carotenes contain alpha and beta carotene whereas xanthophylls contain lutein and xanthophyll cycle intermediates like zeaxanthin, antheraxanthin and violaxanthin. Johnson *et al.* (1993a, b) found that lutein and xanthophyll cycle intermediates are correlated with ability to grow in shade, with lutein content being high in shade species and xanthophyll cycle intermediates low. The ratio of lutein to xanthophyll cycle carotenoids was strongly correlated to an index of shade tolerance (Johnson *et al.*, 1993a, b). It has previously been observed (Thayer and Bjorkman, 1990) that leaves of shade plants often contain significant amounts of alpha carotene. An increase in carotenoid contents may be due to an increased lutein and alpha carotene.

Chapter 3

MATERIALS AND METHODS

This study was conducted in Rubber Research Institute of India (RRII) at Kottayam. Five species of medicinal plants selected for this studies were grown in the research gardens of RRII and the laboratory experiments were carried out in the division of Plant Physiology. Their morphological, physiological, anatomical and biochemical parameters were studied periodically. Detailed methodology are given below.

3.1 Location

All the pot culture experiments were conducted at the Rubber Research Institute of India at Kottayam district in Kerala.

3.2 Physiography and climatology

Kottayam is situated in southern India (9° 32'N, longitude of 76° 36' E) at an altitude of 73 meters above mean sea level. The warm tropical climate prevails with high humidity during most parts of the year (Table 1).

3.2.1 Soil

The soil belongs to clay loam texture with organic carbon 2.1 per cent, total nitrogen 0.21 per cent, available phosphorus 0.25 mg/100 gm soil, available potassium 0.75 mg/100 gm soil, available magnesium 1.15 mg/100 gm soil and pH 4.9.

Season

1. Monsoon(South West) : June - September
2. Post monsoon : October-November
3. Winter : December-February
4. Summer (premonsoon) : March-May

3.3 Meteorological observations

Meteorological data on minimum and maximum temperature, relative humidity, rainfall and bright sunshine hours (Table 1) were recorded from the weather chart maintained by the Institute observatory during the most part of the study.

Table 1 **Meteorological data during the period under study (1991)**

	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Photosynthetically active radiation cal/cm^2/d	236.3	271.9	275.5	281.5	261.6	168.7	180.6	187.6	247.4	205.2	223.5	230.7
Max. temp. (°C)	32.7	34.0	34.4	34.1	33.6	29.3	30.2	29.2	31.1	30.7	31.7	32.2
Min. temp. (°C)	23.6	23.8	25.0	23.8	24.9	23.3	22.5	22.8	23.4	22.8	22.6	21.2
Relative humidity (%)	65	64	71	74	76	90	85	86	81	87	79	73
Sunshine hrs. (hrs./day)	8.6	9.9	9.2	9.4	8.5	3.7	4.3	3.6	7.4	5.1	7.3	8.6
Rainfall (mm)	2.0	7.2	58.5	215.1	171.9	1373.4	648.6	438.4	38.3	416.4	171.9	22.9

Unfortunately radiation was not measured at RRII meteorological sites. It was necessary to estimate solar or net radiation from other measurements, such as the duration of bright sunshine (n),. The conversion from sunshine duration to total solar or net radiation depends on site, type of cloud and time of year (Jones, 1983).

To a reasonable approximation, the average value of Is over periods of weeks or longer may be obtained from the Angstrom equation :

$$Is = IA\ (a + (bn/N)) \text{ where}$$

a and b are constants depending on time of year ($\simeq$ 0.29 & 0.42 for Humid tropical zones), n is the actual sunshine hours, N is the astronomically possible sunshine hours and IA is the extra terrestrial irradiance on a horizontal surface appropriate for the time of the year and latitude (See Frere and Popov (1979) for the calculation of N and IA). For average sun + sky light, IPAR $\simeq$ 0.5 Is.

3.4 Cultural practices and management

3.4.1 Materials:

Adhatoda beddomei C.B. Clarke, *Adhatoda vasica* Nees, *Alpinia galanga* Sw, *Plumbago rosea* Linn and *Strobilanthes heyneanus* Nees were selected for this study. Preliminary studies at RRII have identified that the above five commercially important species of medicinal plants (Plate I) are suitable for cultivation under *Hevea brasiliensis* (Sathik *et al* 1995).

i) *Adhatoda beddomei* C.B. Clarke

A large shrub with entire leaves and small flowers in short heads.

ii) *Adhatoda vasica* Nees

A dense shrub with a foetid scent having entire leaves and white flowers with the throat barred with yellow.

te I. Medicinal plants grown as intercrops in rubber plantations

(1) *Strobilanthes heyneanus* (2) *Plumbago rosea*

(3) *Adhatoda vasica* (4) *Adhatoda beddomei*

(5) *Alpinia galanga*

iii) *Alpinia galanga* Sw

A perennial herb with fleshy rhizome and greenish white flowers with lip veined with red.

iv) *Plumbago rosea* Linn

A perennial undershrub with alternate, ovate leaves and petiole often auricled at the base, with bright red flowers.

v) *Strobilanthes heyneanus* Nees

A small perennial shrub reaching 3 ft in height with opposite, lineolate leaves with serrate margin and pale blue flowers.

Vegetative cuttings and rhizome for the experimental studies were obtained from Central Experimental Station, Chethackal, which were already growing under rubber plantations.

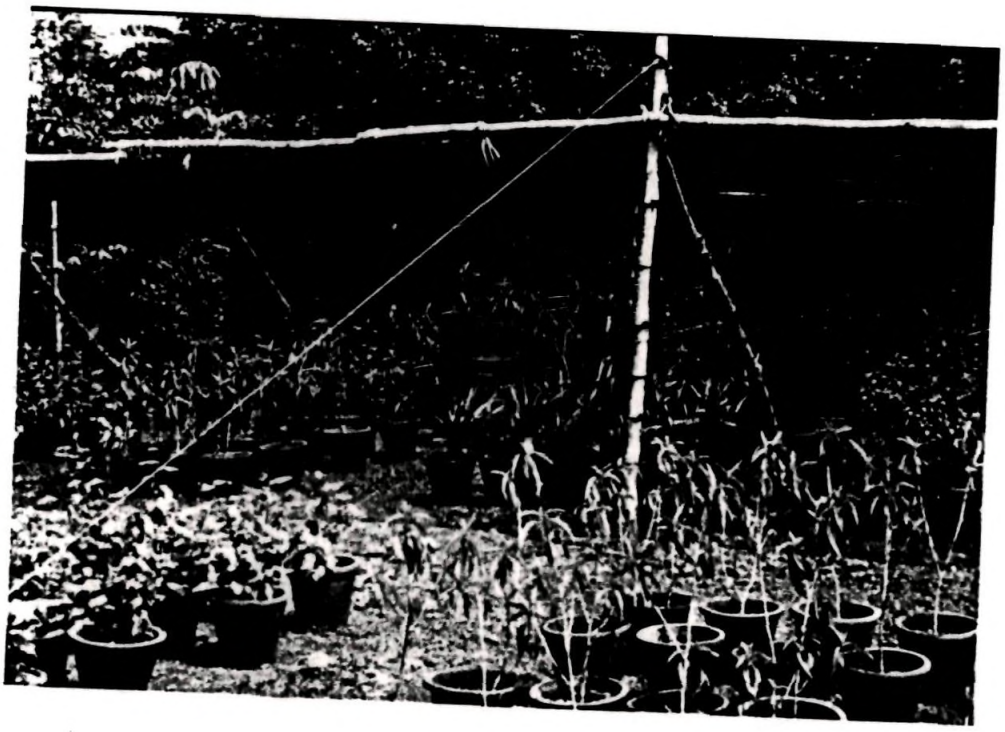
3.4.2 Planting

Tender vegetative cuttings of *Adhatoda vasica*, *Adhatoda beddomei* and *Strobilanthes heyneanus;* stem cuttings with at least three nodes of P*lumbago rosea* and rhizome with bud of *Alpinia galanga* were grown under field condition employing pot culture technique. Uniform earthenware pots (1' x 1') were used to raise the plants. Six kilogram soil (see section 3.2.1) and half a kilogram cowdung were taken in each pot.

Four healthy planting materials were grown in each pot. All pots were kept under 70% shade (heaviest shade strength tildenet) so as to ensure optimum germination. Experimental materials were planted by the last week of November 1990.

Pots were arranged according to completely randomized design. They were kept in rows 10cm apart aligned east west. Plants were thinned down to one in

Plate II. View of the experimental plots



II

It is designed to filter a specific degree of sunlight. Tildenet is available in a complete range of grades ranging from 25% to 85%. The grades which were selected for the study were 30%, 40%, 50%, 60% and 70%. 30% means it cuts 30% of the sunlight and allows only 70% to pass through it and so on. Some quantum sensor readings were made inside each plot, and the acceptable accuracy of the different percentages of shade was tested. At the time of treatment, the plants were with many well developed leaves.

3.6 Sampling

Sampling for physiological, anatomical and biochemical investigation were carried out on the day of treatment (zero day) and on the 92nd, 148th, 211th & 274th day after treatment, ie. 90th, 182nd, 238th, 301st and 364th days of growth respectively as per the details given below.

Date of planting: 30th November, 1990.

Date of treatment: 28th February, 1991.

Sample No.	Date of sampling	Period represented	Days after treatment	Days of growth
I	February 28	December-February (Winter)	0	90
II	May 31	March-May (Pre-monsoon)	92	182
III	July 26	July-July (Monsoon)	148	238
IV	September 27	August-September (Monsoon)	211	301
V	November 29	October-November (Post monsoon)	274	364

The sampling were done at random and in four replicates. The physiologically mature leaves were taken for all photosynthetic measurements and biochemical analyses.

The main objective of the study is to identify the optimal light requirement and physiology of shade adaptation of these five medicinal plants at different stages of their growth.

Their optimal and comparative performance is assessed in terms of growth, differentiation, production, photosynthesis and other related physiological phenomena in varying light regimes, with the ultimate objective of selecting medicinal plant species to be introduced as intercrops under the canopy of rubber plantations.

3.7 Parameters studied

For periodic observations during the crop growth period, destructive growth analysis was followed.

Plants were harvested in four replicates for the measurements of plant height, internode length, internode diameter, shoot number (primary and secondary branches), leaf number, leaf area and dry weights of plant parts.

To estimate the dry weight of plant parts, plants were separated into component parts (leaf, stem, root, rhizome) which were oven-dried at 80°C to constant weight and dry weights recorded.

The techniques adopted in recording the observations on different characters are briefly indicated below:

Plant height

Plant height was measured with a metallic tape to the nearest cm, from the base to the tip. The height per replicate was measured and average calculated.

Internode length

The length of three consecutive fully matured internode from the top was measured to the nearest cm. and average calculated. This measurement is extended to the replications too.

Internode diameter

This was measured at the middle portion of the internode selected for length measurement with vernier calipers.

Shoot number

Shoot number, both primary and secondary branches (including branches with 1-2 nodes) per plant was counted.

No. of leaves

The number of leaves at the time of harvest was recorded.

Leaf area

Leaf area of all plants except *Strobilanthes* was recorded on a leaf area meter (model LI 3000). Leaf area of Strobilanthes was measured on a weight to area basis. A sub sample of about 50 leaves from different positions at random was taken and the leaf area recorded on a leaf area meter. The sub sample was oven-dried and weighed. The area of the rest of the leaves was computed on the basis of area to weight ratio of sub sample for each replicate.

Single leaf area

It was computed from the values of total leaf area and total number of leaves using the formula:

Single leaf area = Total leaf area / Total number of leaves

Number of tubers

The number of tubers of *Alpinia galanga* from each pot was counted and recorded.

Tuber yield

Fresh and dry weight of tubers of *Alpinia galanga* from each pot was recorded.

Total dry matter (Total biomass production, TDM)

Above ground drymatter

For *Adhatoda beddomei*, *Adhatoda vasica*, *Plumbago rosea* and *Strobilanthes heyneanus* the above ground drymatter includes leaves and stem whereas for *Alpinia galanga* it includes only leaves.

Below ground dry matter

For *Adhatoda beddomei*, *Adhatoda vasica*, *Plumbago rosea* and *Strobilanthes heyneanus* the below ground dry matter includes only roots whereas for *Alpinia galanga* it includes both rhizome (stem tuber) and roots.

Above ground dry matter : Below ground dry matter

Roots : Shoot ratio

Photosynthetic tissue : Support tissue

Harvest index

For crops, the economic yield is the amount of net productivity or net biomass gain which is partitioned into the useful portion of the crop. The proportion of total biomass production which is invested into the harvested parts of the plant is termed the harvest index. The harvest index (HI) was computed as per cent ratio of harvestable component to total dry weight.

HI = (Economical yield / TDM) x 100

In *Adhatoda beddomei*, *Adhatoda vasica* and *Strobilanthes heyneanus*, the bulk of the plant, forms the harvestable component whereas in *Alpinia galanga* it is the rhizome and in *Plumbago rosea*, it is the roots which forms the harvestable component.

The data obtained on leaf area, dry weight of plant parts and total dry matter were expressed on a unit plant basis. The above parameters were used to calculate the followmg physiological growth parameters using the formulae given by Watson (1952), Friend *et al* (1962), Radford (1967) and Hunt (1982).

1. Relative Growth Rate (RGR)

The basic component of growth analysis, which arose from the work of Blackman (1919) referred to above, is the relative growth rate of the plant. This is defined at any instant in time t, as the increase of material per unit of material present. Thus RGR represents increase in dry weight in time $t_2 - t_1$, over dry weight at time t_1, i.e.,.

$$RGR = (\ln W_2 - \ln W_1)/(t_2 - t_1)\ g\ g^{-1}\ day^{-1}$$

where, W_1 and W_2 refer to total dry weight of the plant of two consecutive samples at time t_1 and t_2 (in days) respectively.

2. Crop Growth Rate (CGR)

It represents the dry weight gained by unit plant of a crop in unit time, i.e.

$$CGR = (W_2 - W_1)/(t_2 - t_1)\ g\ plant^{-1}\ day^{-1}$$

where, W_1 and W_2 refer to total dry weight of the plant of two consecutive samples at time t_1 and t_2 (in days) respectively.

3. Net Assimilation Rate (NAR)

Net assimilation rate of a plant or crop at any instant in time t is defined as the increase of plant material per unit of assimilatory material per unit of time. Thus NAR represents dry weight gained in time $t_2 - t_1$ over the average leaf area during $t_2 - t_1$.

$$NAR = (W_2 - W_1) \times (\ln A_2 - \ln A_1) / (t_2 - t_1) \times (A_2 - A_1) \text{ g cm}^{-2} \text{ leaf area day}^{-1}$$

where W_1 and W_2 refer to total dry weight of the plant, A_1 and A_2 are cumulative leaf areas of the plant, of two consecutive samples at time t_1 and t_2 (in days) respectively.

4. Leaf Area Ratio (LAR)

The Leaf area ratio of a plant or crop at any instant in time, is the ratio of the assimilatory material per unit of plant material present.

$$LAR = (A_2 - A_1) \times (\ln W_2 - \ln W_1) / (W_2 - W_1) \times (\ln A_2 - \ln A_1)$$

5. Leaf Weight Ratio (LWR)

Leaf weight divided by plant weight i.e., LW/W is called leaf weight ratio. LWR is a measure of the leafiness of the plant on a weight basis.

6. Specific Leaf Area (SLA)

A/LW is called specific leaf area. SLA defines leaf area ratio in terms of leaf density (i.e., m^2/g). A refer to cumilative leaf area and LW refer to dry weight of leaves of the plant.

7. Specific Leaf Weight (SLW)

LW/W (i.e.) leaf weight divided by leaf area is called specific leaf weight.

8. Stem Weight Ratio (SWR)

Stem weight divided by plant weight (i.e.) SW/W is called Stem Weight Ratio.

9. Root Weight Ratio (RWR)

Root weight divided by plant weight (i.e.) RW/W is called Root Weight Ratio.

10. Leaf Area Growth Rate (LAGR)

This refers to the change in leaf area per unit time.

$$LAGR = (A_2 - A_2) / (t_2 - t_1)\ cm^2\ day^{-1}$$

where, A_1 and A_2 are cumilative leaf areas of the plant, of two consecutive samples at time t_1 and t_2 (in days) respectively.

11. Leaf Area Duration (LAD)

It is a measure of the persistence of the assimilatory surface. LAD is computed from planting to harvest by multiplying mean leaf area with number of days under each growth period, i..e.,

$$LAD = [(A_1+A_2) \times (t_2 - t_1)]/2 + \ldots\ldots + [(A_4+A_5) \times (t_5 - t_4)]/2$$

12. Photosynthetic Potential

Total dry weight per unit leaf area is called photosynthetic potential. i.e.,

Photosynthetic Potential = Total plant dry wt. / Cumulative leaf area of the plant

Measurement of Photosynthetic Rate

Gas exchange measurements were made using portable photosynthesis system (LI 6200 LICOR, USA), based on the principle of infrared gas analyser

(IRGA). Heteratomic molecules absorbs infrared radiation at specific wave bands. Each heteratomic gas molecule have a characteristic absorption spectrum The major absorption band of CO_2 is at λ = 4.25 μm with secondary peaks at λ = 2.66, 2.77 and 14.99 μm.

In IRGA, the IR source is typically a spiral of Nichrome alloy or tungsten, heated to about 600-800°C through a low voltage circuit. Mostly IRGAs used for photosynthetic measurements are dual beam, passing equal amounts of radiation into two parellel cells ie. the analysis and the reference cells. The detector commonly used is Luft type which operates on the principle of positive filtration ie., it absorbs IR in the CO_2 absorption bands (Wolfe and Zissis 1978).

The LICOR LI - 6200 photosynthesis system is a closed system. In a closed system air is pumped from the chamber enclosing the leaf into an IRGA which continuously records the CO_2 concentration of the system. The air is then recycled back to the chamber. No air leaves the system nor enters it from outside. If the leaf enclosed in the chamber is photosynthesising, the CO_2 concentration in the system will decline. The rate of CO_2 assimilation is equal to the change in the amount of CO_2 in the system per unit time.

Measurements were taken on single intact youngest mature leaves. The following parameters were estimated for each measurement period:

Photosynthetic rate Pn (μ mol m^{-2} s^{-1}), Stomatal conductance Cs (mol m^{-2} s^{-1}), Intercellular CO_2 concentration Ci (ppm), Photosynthetically active radiation PAR (μ mol m^{-2} s^{-1}), humidity (%) and air and leaf temperature (°C). All observations were taken above saturated light interisity, which was determined earlier, at the peak hour of the day for each species. The values reported are means of measurements made on three leaves of same age in each replication.

Diurnal changes in photosynthetic rate

The variation in photosynthetic rate during the course of the day of open as well as 70% shade treated leaves was assessed. The multiple measurements on diurnal changes in photosynthetic rate Pn (μ mol m^{-2} s^{-1}), Cs (mol m^{-2} s^{-1}), E (mmol m^{-2} s^{-1}), Ci (ppm), PAR (μ mol m^{-2} s^{-1}), humidity and air and leaf temperature (^{o}C) on intact physiologically mature leaves were conducted at 1 hour intervals during the day from 7 to 18 hrs in five medicinal plants with a portable photosynthesis system (LI-6200).

Biochemical Analysis

In the case of chlorophyll and carotenoid estimations, four samplings were carried out corresponding to 92nd, 148th, 211th and 274th day after treatment, i.e., 182nd, 238th, 301st and 364th days of growth respectively.

1. Chlorophyll contents

Leaf pigments were extracted with ice cold 80% acetone (Harbone, 1973) and the chlorophylls were estimated as per the method of Arnon (1949). Fresh leaves weighing 200 mg were ground in a mortar using glass power and extracted with cold 80% acetone until the tissue became colourless. The extract was filtered and the filtrate was made upto a known volume with the same acetone.

The concentration of chlorophylls was estimated by measuring the absorbance at 663 and 645 mm in the shimadzu spectrophotometer (UV 240) using the following formula and results were expressed in mg g^{-1} dry weight.

Chlorophyll a = (12.7 x D663) - (2.69 x D645) x V/W

Chlorophyll b = (22.9 x D645) - (4.68 x D663) x V/W

Total Chlorophyll = (20.2 x D645) + (8.02 x D663) x V/W

$$\text{Chlorophyll a/b ratio} = \frac{\text{Chlorophyll a}}{\text{Chlorophyll b}}$$

D = The absorbance at respective wavelength

V = The volume of extract (ml) and

W = The dry weight of the material (mg)

2. Carotenoid contents

The pigments are extracted with 80% acetone. The homogenate was kept for 10 minutes in darkness and then centrifuged. The clear supernatant was measured at 480 nm using shimadzu UV visible recording spectrophotometer (UV 240). The content of carotenoid was calculated according to Kirk and Allen's (1965) formula.

Foliar anatomical traits (Foliar anatomy)

Youngest mature leaves were sampled for the purpose. Approximately 1 sq.cm. of leaf tissue was removed from the mid-laminar region of youngest mature leaves of open as well as 70% shade grown plants and preserved in FAA solution (70% ethanol : glacial acetic acid : formaldehyde 90:5:5). Transverse sections were prepared according to the conventional techniques (Johansen, 1940), stained in 1 per cent aqueous safranin and mounted in DPX. Ten random observations were recorded from four leaf samples per plant, on total leaf thickness, palisade thickness, thickness of spongy mesophyll and epidermal thickness by means of an ocular micrometer. Measurements on leaf blade thickness was made at equal distance from either side of the midrib.

For stomatal observations, upper and lower epidermal peels were obtained by Jeffrey's method (Purvis *et al.*, 1966). The following measurements were made from 20 randomly selected guard cells of each species for both the treatments.

1. Length of the guard cell

2. Frequency of stomata per unit area.

Trichome length and frequency were also measured as above, for both the treatments.

3.8 Statistical techniques

All the data were analysed statistically as per the design of the experiment. Treatment differences were worked out by Dunken's Multiple Range Test (Panse and Sukhatme 1967). Values followed by same letters are not significantly different from each other.

3.9 Photography

Photomicrographs were taken employing a Leitz orthopan microscope.

Chapter 4

RESULTS

4.1 Impact of Shade on Growth

4.1.1 Morphology

The effect of shade on discernible morphological characteristics in 5 species of medicinal plants: *Adhatoda beddomei*, *Adhatoda vasica*, *Alpinia galanga*, *Plumbago rosea* and *Strobilanthes heyneanus* at different light intensities (open, 30%, 40%, 50%, 60% and 70% shade) was studied by measuring the following parameters: Plant height, no. of branches internodal length and diameter.

In general, plant height of all the 5 species increased with shade and the lowest height was observed in plants grown under open sunlight. *Adhatoda beddomei*, *Adhatoda vasica* and *Plumbago rosea* attained the maximum height under 70% shade (Table 2, Plate III and IV). Plant height also increased with age, irrespective of the species.

In the case of *Adhatoda beddomei*, *Adhatoda vasica* and *Plumbago rosea*, the highest internodal length was observed in plants under 70% shade and the lowest internodal length in plants under open condition. In *Strobilanthes heyneanus*, the best shade level in this regard was 60%. Internodal length also increased with age. In general, increase in internodal diameter in intermediate shades was higher than heaviest shades and open grown plants.

te III & IV Effect of different levels of shade on the growth of five species of medicinal plants

(1) *Adhatoda beddomei* (2) *Adhatoda vasica*

(3) *Alpinia galanga* (4) *Plumbago rosea*

(5) *Strobilanthes heyneanus*

Number of branches increased with shade in *Plumbago rosea* and *Adhatoda vasica* with the total number of branches, maximum at 50% shade level in the former and under 70% in the latter. In the case of *Strobilanthes heyneanus*, even though the number of primary branches increased, a decrease in the number of secondary branches and the total number of branches was observed under shades.

4.1.2 Classical growth parameters

Effect of different levels of shade on growth was assessed in five species of medicinal plants *Adhatoda beddomei, Adhatoda vasica, Alpinia galanga, Plumbago rosea* and *Strobilanthes heyneanus* by measuring the following parameters: total dry matter (TDM), leaf dry weight, stem dry weight, root dry weight, leaf number, total leaf area per plant, the ratio of above ground dry matter to below ground dry matter, the ratio of photosynthetic tissue to support tissue, single leaf area, specific leaf weight (SLW), specific leaf area (SLA), leaf weight ratio (LWR), crop growth rate (CGR), net assimilation rate (NAR), leaf area ratio (LAR) and leaf area growth rate (LAGR).

4.1.2.1 Total dry weight

In all the five species studied, the total dry matter (TDM) under various shade levels were found to record significant increase as compared to the open plants (Table 3, Figure 1). The highest shade level of 70% was found to be the best suited in the case of *Adhatoda vasica* and *Plumbago rosea*, whereas it was 50% for *Alpinia galanga and Strobilanthes heyneamus* particularly towards the later period of sampling. The best treatment level for *Adhatoda beddomei* was 60% shade. TDM also showed an increase with age in all the species.

4.1.2.2 Leaf dry weight

As regards leaf weight all the species showed an increase in weight under shade compared to open condition (Table 4, Figure 2). 70% shade level was found best suited for *Adhatoda vasica* and *Plumbago rosea* whereas in the case of *Strobilanthes heyneanus* leaf dry weight was highest under 80% shade and for *Adhatoda beddomei* it was highest under 60% shade. In the case of *Alpinia galanga*, lamina dry weight as well as leaf dry weight was found to be optimum under 60% shade.

4.1.2.3 Stem dry weight

An increase in stem weight was observed for all the species, both under different shade levels as well as with increase in age. The results are presented in Table 5, Figure 3.

4.1.2.4 Root dry weight

Root dry weights of plants grown under different levels of shades did not show any significant difference between treatments in *Adhatoda beddomei* and *Adhatoda vasica* (Table 6, Figure 4).

4.1.2.5 Total leaf number

The effect of shade on leaf number is illustrated in Table 7 (Figure 5). It was non-significant in the case of *Adhatoda beddomei*. In the rest of the species however leaf number generally increased with higher levels of shade; the best suited levels being 70% for *Adhatoda vasica* and *Plumbago rosea* and 60 and 50% for *Alpinia galanga* and *Strobilanthes heyneanus* respectively.

4.1.2.6 Total leaf area per plant

The total leaf area per plant for the 5 species are given in Table 8, Figure 6. In general, the total leaf area per plant increased with shade. In the case *Adhatoda vasica* and *Plumbago rosea* this increase was maximum at 70% shade whereas the optimum was 50% shade for *Alpinia galanga* and *Strobilanthes heyneanus* and 60% shade for *Adhatoda beddomei.*

4.1.2.7 Ratio of above ground dry weight to underground dry weight

Above ground dry weight (Table 9, Figure 7) and the ratio of above ground dry weight to underground dry weight increased with increasing shade levels in all the five species (Table 10, Figure 8). These parameters were highest at 70% shade for *Adhatoda vasica* and *Plumbago rosea. Adhatoda beddomei* produced highest above ground dry matter at 60% shade whereas *Strobilanthes heyneanus* recorded the highest value at 50% shade.

4.1.2.8 Ratio of photosynthetic tissue to support tissue

The ratio of photosynthetic tissue to support tissue generally increased with higher levels of shade, *Adhatoda vasica* recorded the highest values at the level of 70% shade whereas for *Adhatoda beddomei* and *Alpinia galanga* 60% shade was the optimum. The ratio of photosynthetic to support tissue in general showed a decreasing trend with age (Table 11, Figure 9).

4.1.2.9 Single leaf area

Single leaf area increased with shade (Table 12, Figure 10), the optimum levels for different species were as follows: *Adhatoda beddomei* - 60% shade, *Strobilanthes heyneanus* - 60% shade, *Adhatoda vasica* - 70% shade, *Alpinia galanga* - 70% shade and *Plumbago rosea* - 70% shade.

4.1.2.10 Specific leaf weight (SLW)

Specific leaf weight (SLW) of all the species decreased with shade except in the case of *Alpinia galanga*. The lowest values were observed with the highest shade treatment in *Plumbago rosea* and *Strobilanthes heyneanus* (Table 13, Figure 11).

4.1.2.11 Specific leaf area (SLA)

Specific leaf area (SLA) of plants increased under shade in all species, except in *Adhatoda vasica*, where the increase was not significant. However, irrespective of the species, SLA decreases with age (Table 14, Figure 12).

4.1.2.12 Leaf weight ratio (LWR)

Leaf weight ratio (LWR) was also found to increase with shade. LWR was highest (Table 15, Figure 13) under 70% shade in the case of *Adhatoda vasica*, *Alpinia galanga* and *Plumbago rosea* (Table 15, Figure 13).

4.1.2.13 Crop growth rate (CGR)

The effect of shade on crop growth rate (CGR) was found to increase with shade intensity only during the initial sampling. CGR either remained the same or showed a decline in comparison with the open plants during the final phases of growth (Table 16, Figure 14).

4.1.2.14 Relative growth rate (RGR)

Relative growth rate (RGR) also followed a similar trend as that of CGR. With increase in age RGR decreased (Table 17, Figure 15).

4.1.2.15 Net assimilation rate (NAR)

The effect of shade on net assimilation rate (NAR) was not significant in the case of *Adhatoda beddomei*, *Adhatoda vasica* and *Plumbago rosea*. NAR decreased during the fourth sampling corresponding to 301st day of growth, in *Alpinia galanga*. In *Strobilanthes heyneanus*, NAR decreased in the first and fourth sampling periods. The unshaded control plants exhibited maximum NAR in *Alpinia galanga* whereas the plants under 30% showed more NAR that in the unshaded plants in *Strobilanthes heyneanus* (Table 18, Figure 16).

4.1.2.16 Leaf area ratio (LAR)

Leaf area ratio (LAR) invariably increased with shade, the maximum being attained at 70% shade for all the species except *Adhatoda beddomei* in which the optimum level was 60%. Unshaded plants registered minimum LAR in all the five species. With advancing age the LAR was found to decrease as evidenced by the data at different periods of sampling (Table 19, Figure 17).

4.1.2.17 Leaf area growth rate (LAGR)

Leaf area growth rate (LAGR) showed significant increase under shade in all the species studied during initial sampling. However, the rate decreased during the 3rd and 4th sampling corresponding to 238th and 301st days of growth in *Adhatoda vasica* and *Adhatoda beddomei* respectively (Table 20, Figure 18).

4.1.2.18 Leaf Area Duration (LAD)

Leaf area duration (LAD) increased with shade in *Adhatoda vasica* and *Adhatoda beddomei* and decreased in *Plumbago rosea* and *Strobilanthes heyneanus* (Table 21, Figure 19).

Table 2 **Height (cm) in shade treated medicinal plants at different periods of analysis**

a. *Adhatoda beddomei*

Shade treatments	I	II	III	
	Sampling periods			
Open	–	63.4 D	67.0 C	66.4 C
30%	–	68.3 D	71.6 BC	72.0 C
40%	–	74.0 CD	76.1 BC	87.8 B
50%	–	84.6 BC	82.3 B	91.3 AB
60%	–	96.5 AB	97.5 A	97 8 AB
70%	–	98.8 A	101.5 A	102.8 A
SE±		4.06	4.35	4.49
CD(P=0.05)		12.07	12.93	13.35

b. *Adhatoda vasica*

Open	–	45.5 D	49.4 D	51.6 C
30%	–	51.8 CD	54.0 D	69.4 B
40%	–	63.3 BC	63.9 C	69.0 B
50%	–	64.5 B	67.5 BC	71.7 B
60%	–	62.8 BC	73.8 B	77.8 AB
70%	–	82.5 A	82.6 A	83.8 A
SE±		3.92	2.49	2.91
CD(P=0.05)		11.63	7.39	8.64

c. *Alpinia galanga*

Open	–	28.0 B	–	29.3 C
30%	–	28.9 B	–	36 8 BC
40%	–	38.8 A	–	42.4 AB
50%	–	40.5 A	–	46.0 AB
60%	–	43.9 A	–	52.1 A
70%	–	39.0 A	–	48.5 A
SE±		2.96		3.62
CD(P=0.05)		8.784		10.75

d. *Plumbago rosea*

Open	–	43.6 D	44.4 D	57.2 C
30%	–	52.0 D	69.3 C	94.0 B
40%	–	87.0 C	92.3 B	103.5 B
50%	–	96.8 BC	101.8 B	106.1 B
60%	–	102.8 AB	117.8 A	124.3 A
70%	–	111.5 A	126.5 A	129.8 A
SE±		4.73	5.06	5.37
CD(P=0.05)		14.06	15.03	15.96

e. *Strobilanthes Heyneanus*

Open	–	57 D	59 D	80.1 C
30%	–	64 CD	66 D	82.5 C
40%	–	77 C	79.6 C	90.5 C
50%	–	104 AB	108.75 B	141.0 A
60%	–	116 A	127 A	129.5 B
70%	–	100.8 B	115.8 B	127.3 B
SE±		4.63	3.49	3.82

Table 3 **Total dry matter (g/plant) in shade treated medicinal plants at different periods of analysis**

a. *Adhatoda beddomei*

Shade treatments	Sampling periods I	II	III	IV	V
Open	5.73	24.7 C	25.3 D	25.8 C	30.1 C
30%	5.73	28.8 BC	29.5 CD	29.9 BC	33.5 BC
40%	5.73	30.8 B	31.3 BCD	31.7 B	36.9 AB
50%	5.73	35.7 A	36.5 AB	39.3 A	38.5 AB
60%	5.73	36.8 A	38.1 A	40.7 A	42.5 A
70%	5.73	37.1	32.5 ABC	38.4 A	29.0 C
SE±	0.82	1.54	1.94	1.46	1.89
CD(P=0.05)	NS	4.58	5.77	4.35	5.6

b. *Adhatoda vasica*

Open	3.50	20.7 C	19.6 C	21.0 C	22.6 C
30%	3.35	25.0 B	27.3 B	28.2 B	29.9 B
40%	3.35	25.4 B	27.4 B	30.1 B	32.6 B
50%	3.35	27.9 AB	32.4 AB	32.4 V	35.3 B
60%	3.35	32.1 A	33.2 AB	34.0 B	36.5 B
70%	3.35	31.0 A	36.9 A	44.1 A	44.2 A
SE±	0.26	1.39	1.88	2	2.08
CD(P=0.05)	NS	4.12	5.58	5.94	6.18

c. *Alpinia galanga*

Open	4.6	18.4	38.9 C	57.4 D	81.9 D
30%	4.6	21.2	46.5 AB	72.9 BC	85.8 CD
40%	4.6	22.7	48.3 AB	77.4 BC	97.9 B
50%	4.6	26.1	54.0 A	86.7 A	107.0 A
60%	4.6	23.6	52.3 A	80.6 AB	99.4 AB
70%	4.6	22.5	41.2 BC	70.8 C	93.1 BC
SE±	0.38	1.6	2.4	2.5	2.7
CD(P=0.05)	NS	NS	7.1	7.6	7.9

d. *Plumbago rosea*

Open	0.83	26.1 B	48.0 C	52.3 C	47.3 C
30%	0.83	38.9 A	58.6 BC	61.5 BC	62.1 B
40%	0.83	43.8 A	59.7 BC	67.7 BC	87.5 A
50%	0.83	45.2 A	72.1 AB	76.1 AB	90.0 A
60%	0.83	43.4 A	74.4 AB	85.7 A	91.6 A
70%	0.83	45.0 A	77.9 A	87.6 A	96.0 A
SE±	0.10	3.67	5.15	5.1	4.72
CD(P=0.05)	NS	10.9	15.3	15.1	14

e. *Strobilanthes heyneanus*

Open	11.4	53.5	74 C	92 C	106 D
30%	11.4	58.7	80 C	104 C	142 CD
40%	11.4	59.0	84 C	125 C	165 C
50%	11.4	72.5	140 A	264 A	375 A
60%	11.4	60.5	138 A	237 A	305 B
70%	11.4	61.0	113 B	197 B	288 B
SE±	1.03	4.99	7.34	11.7	15
CD(P=0.05)	NS	NS	21.8	34.9	44.5

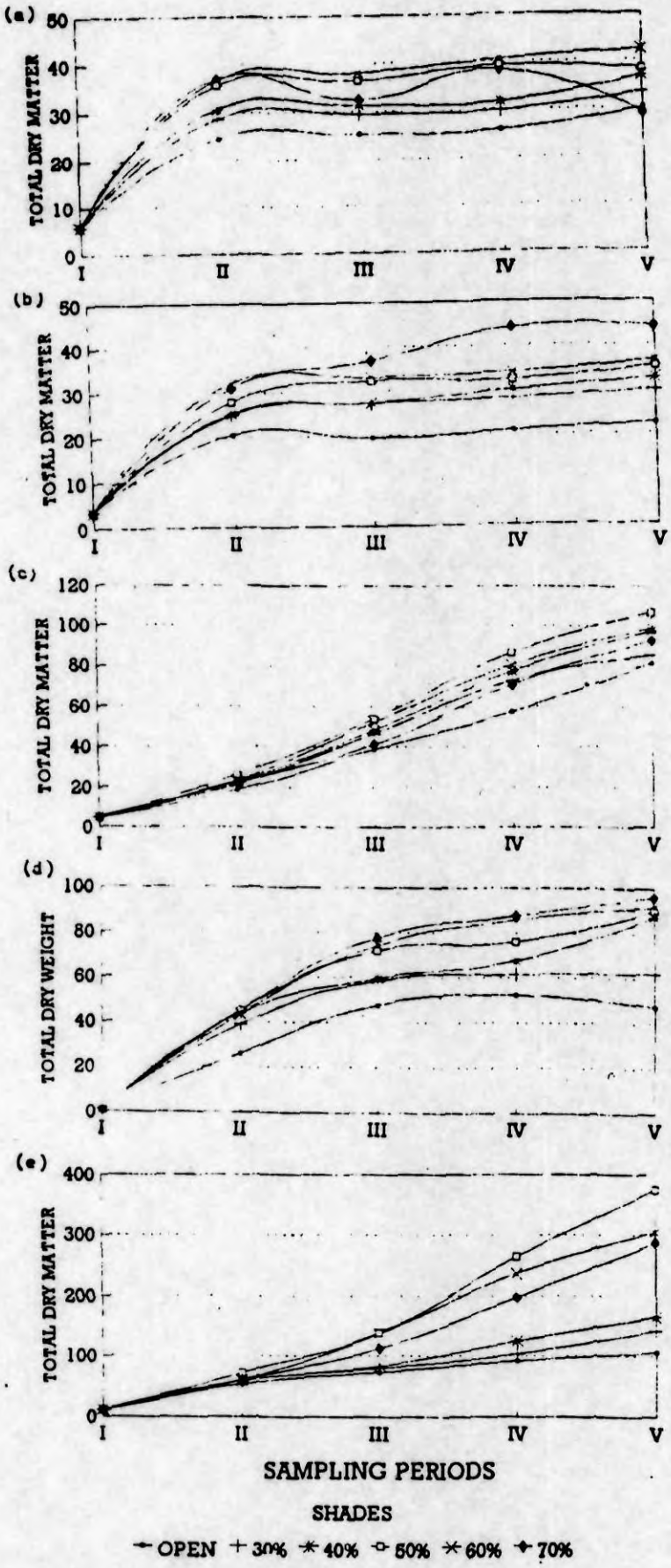


Figure 1. Total dry matter (g/plant) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 4 **Total leaf dry weight (g/plant) in shade treated medicinal plants at different periods of analysis**

	Shade treatemnts	Sampling periods I	II	III	IV	V
a. *Adhatoda beddomei*	Open	2.7	7.93 B	4.93 C	2.28 C	3.6 B
	30%	2.7	9.18 AB	7.63 AB	3.65 B	4.03 B
	40%	2.7	9.45 AB	7.80 AB	4.03 B	4.23 B
	50%	2.7	11.80 A	8.48 AB	5.45 A	4.38 B
	60%	2.7	11.70 A	9.08 A	6.13 A	6.05 A
	70%	2.7	11.40 A	6.20 BC	4.35 B	3.08 B
	SE±	0.36	0.82	0.73	0.35	0.43
	CD(P=0.05)	NS	2.43	2.17	1.05	1.27
b. *Adhatoda vasica*	Open	1.58	6.18 D	3.90 C	3.88 C	3.2 C
	30%	1.58	8.30 C	7.98 B	4.48 BC	4.4 C
	40%	1.58	9.13 BC	7.43 B	4.49 BC	4.6 C
	50%	1.58	9.88 B	9.55 AB	5.15 BC	7.4 AB
	60%	1.58	11.30 A	8.23 B	6.00 B	6.8 B
	70%	1.58	12.00 A	11.30 A	9.93 A	9.3 A
	SE±	0.19	0.46	0.69	0.53	0.72
	CD(P=0.05)	NS	1.38	2.06	1.59	2.13
c. *Alpinia galanga* (i)	Open	1.23	6.73 B	15.8 C	11.4 D	17.9 E
	30%	1.23	8.98 AB	16.0 C	16.8 C	25.7 D
	40%	1.23	9.08 AB	19.7 AB	19.8 C	30.0 C
	50%	1.23	11.30 A	22.5 A	25.2 B	40.3 A
	60%	1.23	11.40 A	20.7 AB	30.7 A	37.8 AB
	70%	1.23	10.70 A	17.9 BC	25.0 B	34.5 B
	SE±	0.17	0.81	0.91	1.6	1.3
	CD(P=0.05)	NS	2.39	2.7	4.8	3.8
	(ii) Total lamina dry weight (g./plant)					
	Open	0.93	4.65 C	10.7	7.5 E	10.6 D
	30%	0.93	6.05 BC	11.0	11.0 D	16.0 C
	40%	0.93	6.40 AB	12.7	12.2 CD	17.0 C
	50%	0.93	7.68 AB	14.5	16.1 B	23.0 A
	60%	0.93	7.83 A	13.4	19.4 A	20.9 AB
	70%	0.93	7.00 AB	12.3	14.9 BC	19.2 B
	SE±	0.14	0.54	0.88	1.05	0.71
	CD(P=0.05)	NS	1.6	NS	3.13	2.11
d. *Plumbago rosea*	Open	0.23	10.1 C	12.3 C	8.4 B	4.38 C
	30%	0.23	12.2 BC	16 BC	9.5 B	6.03 C
	40%	0.23	14.1 AB	15.3 BC	10.6 B	6.90 BC
	50%	0.23	14.1 AB	18.9 AB	12.7 B	8.83 B
	60%	0.23	14.9 AB	22.7 A	20.3 A	12.00 A
	70%	0.23	16.2 A	21.4 A	20.5 A	12.10 A
	SE±	0.05	1.2	1.6	1.63	0.87
	CD(P=0.05)	NS	3.56	4.74	4.86	2.58
e. *Strobilanthes heyneanus*	Open	3.88	16	18.3 B	20.1 C	18.6 D
	30%	3.88	16.5	19.0 B	21 C	21.5 D
	40%	3.88	16.7	20.2 B	27.7 C	34.9 C
	50%	3.88	21	35.4 A	67.7 A	85.0 A
	60%	3.88	19	38.9 A	53.9 B	67.8 B
	70%	3.88	17.9	31.9 A	50 B	61.8 B
	SE±	0.45	1.8	2.62	3.76	4.01
	CD(P=0.05)	NS	NS	7.79	11.2	11.9

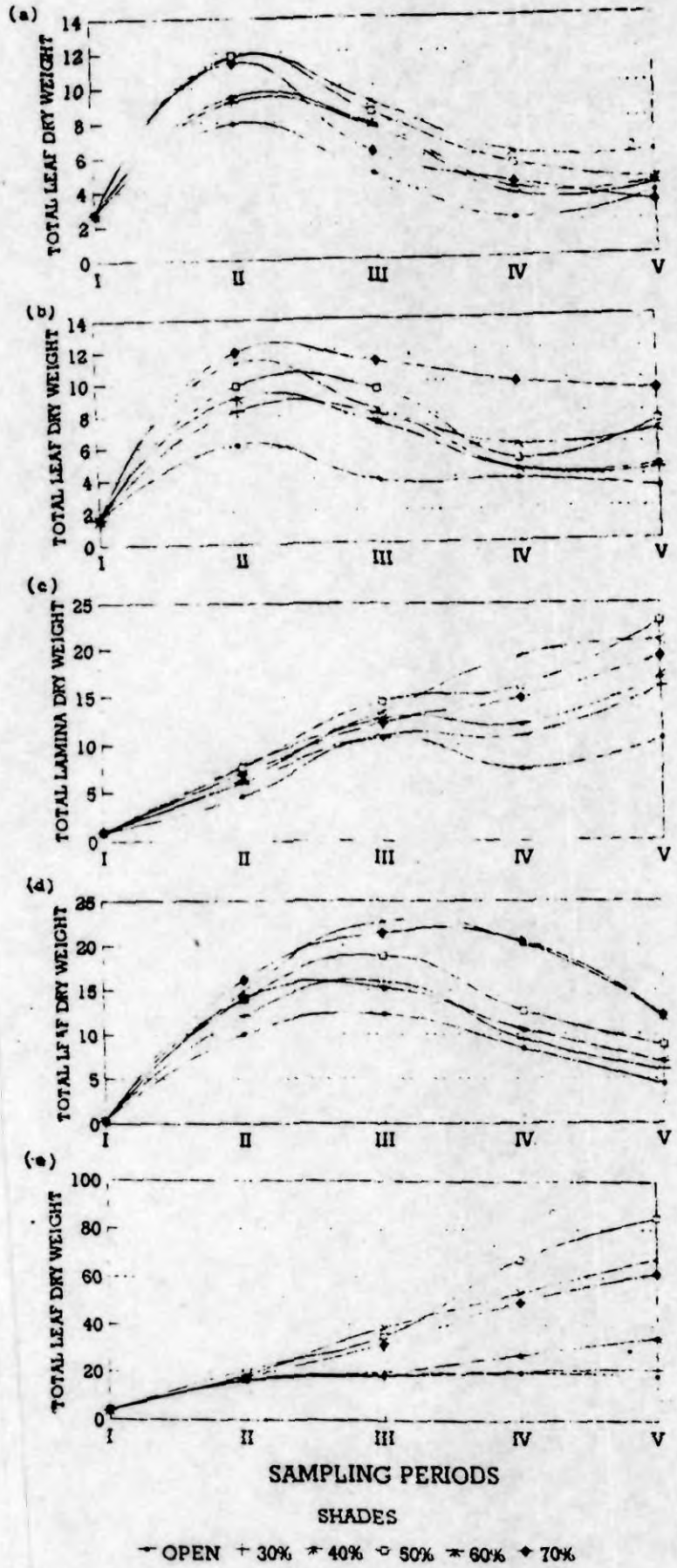


Figure 2. Total leaf dry weight (g/plant) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 5 **Total stem dry weight (g/plant) in shade treated medicinal plants at different periods of analysis**

a. *Adhatoda beddomei*

Shade treatments	Sampling periods I	II	III	IV	V
Open	1.8	9.2 C	12.3 D	13.3 C	15.9 B
30%	1.8	12.0 B	14.0 CD	15.2 BC	18.3 B
40%	1.8	12.8 B	16.2 BC	17.0 B	22.8 A
50%	1.8	15.4 A	18.9 AB	22.0 A	24.6 A
60%	1.8	15.5 A	20.0 A	22.1 D	25.3 A
70%	1.8	15.3 A	17.7 AB	22.1 A	17.5 B
SE±	0.36	0.82	1.1	0.97	1.18
CD(P=0.05)	NS	2.44	3.26	2.89	3.52

b. *Adhatoda vasica*

Open	0.93	6.78 C	7.2 C	8.1 C	9.9 C
30%	0.93	7.9 BC	9.8 BC	11.1 BC	14.0 B
40%	0.93	8.5 BC	11.0 B	13.5 B	15.9 B
50%	0.93	9.3 B	13.0 AB	14.2 B	16.1 B
60%	0.93	12.0 A	15.8 A	13.7 B	15.1 B
70%	0.93	11.5 A	16.7 A	20.5 A	22.1 A
SE±	0.06	0.67	1.19	1.15	1.18
CD(P=0.05)	NS	1.99	3.54	3.42	3.5

c. *Alpinia galanga* (Rhizome dry weight)

Open	2.9	5.9	12.8	19.2 C	28.8 BC
30%	2.9	6.0	13.1	23.1 B	30.7 ABC
40%	2.9	6.8	13.2	26.9 A	32.6 AB
50%	2.9	6.7	12.4	28.7 A	35.0 A
60%	2.9	6.0	12.3	23.5 B	27.7 C
70%	2.9	5.9	10.9	22.6 B	26.0 C
SE±	0.23	0.47	0.84	0.94	1.5
CD(P=0.05)	NS	NS	NS	2.8	4.5

d. *Plumbago rosea*

Open	0.33	3.6 C	10.1 D	11.2 D	14.6 C
30%	0.33	7.6 B	16.9 CD	15.8 CD	22.5 C
40%	0.33	9.9 AB	18.7 BC	16.2 CD	32.2 B
50%	0.33	11.5 A	25.3 AB	22.7 BC	40.9 AB
60%	0.33	11.8 A	25.9 AB	29.6 AB	41.. AB
70%	0.33	13.6 A	30.8 A	34.4 A	44.4 A
SE±	0.06	1.15	2.47	2.44	3.08
CD(P=0.05)	NS	3.43	7.35	7.26	9.14

e. *Strobilanthes heyneanus*

Open	4.28	27	36.4 C	47.8 C	63.48 C
30%	4.28	27.5	38.2 C	52.1 C	86.78 C
40%	4.28	27.7	42.7 C	63.9 C	95.90 C
50%	4.28	36.6	82.7 A	165.0 A	252.3 A
60%	4.28	30.9	84.5 A	147.0 A	206.2 B
70%	4.28	30.8	65.7 B	118.0 B	194.4 B
SE±	0.34	3.07	4.89	8.03	11.35
CD(P=0.05)	NS	NS	14.5	23.8	33.74

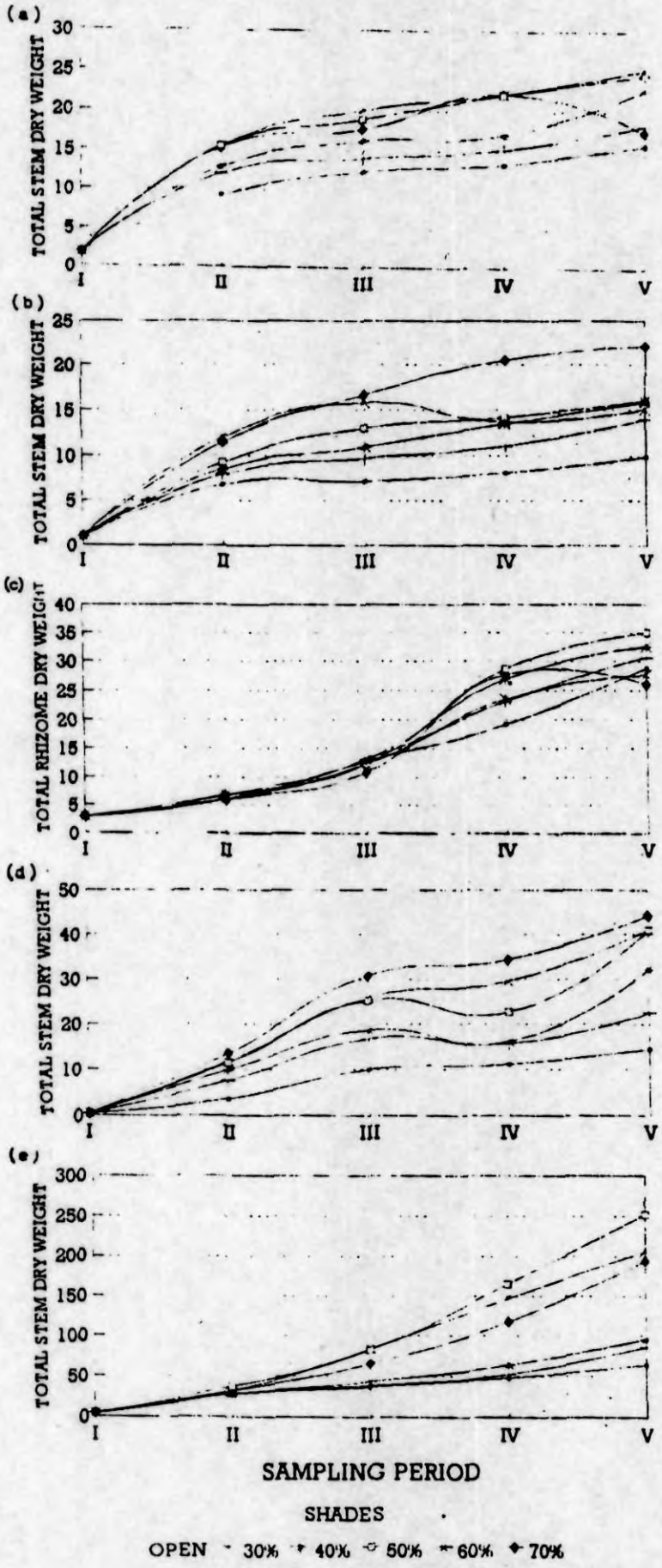


Figure 3. Total stem dry weight (g/plant) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 6 **Total root dry weight (g/plant) in shade treated medicinal plants at different periods of analysis**

	Sampling periods				
Shade treatments	I	II	III	IV	V
a. *Adhatoda beddomei*					
Open	1.23	7.58	8.08	10.2	10.6
30%	1.23	7.63	7.85	11.0	11.2
40%	1.23	8.55	7.38	10.7	9.8
50%	1.23	8.48	9.09	11.8	9.5
60%	1.23	9.65	9.03	12.5	11.2
70%	1.23	10.4	8.6	12.0	8.5
SE±	0.11	0.81	0.77	0.61	0.69
CD(P=0.05)	NS	NS	NS	NS	NS
b. *Adhatoda vasica*					
Open	0.85	7.7	8.5	8.98	9.5
30%	0.85	8.8	9.58	12.7	11.4
40%	0.85	7.8	8.95	12.1	12.1
50%	0.85	8.75	9.83	13.0	11.9
60%	0.85	8.78	9.2	14.3	14.6
70%	0.85	7.43	8.9	13.8	12.8
SE±	0.06	0.7	1.25	1.31	1.07
CD(P=0.05)	NS	NS	NS	NS	NS
c. *Alpinia galanga*					
Open	0.48	5.8	10.3 C	26.8 BC	35.2
30%	0.48	6.25	17.4 A	33.1 A	29.5
40%	0.48	6.78	15.4 AB	30.7 AB	35.3
50%	0.48	8.15	19.1 A	32.9 A	31.9
60%	0.48	6.23	19.4 A	26.4 BC	34.0
70%	0.48	5.85	12.4 BC	23.1 C	32.7
SE±	0.08	0.54	1.3	1.6	2.0
CD(P=0.05)	NS	NS	4.0	4.8	NS
d. *Plumbago rosea*					
Open	0.28	12.4	25.5	32.7	28.3 C
30%	0.28	19.1	25.7	36.2	33.6 BC
40%	0.28	19.8	25.8	41.0	48.4 A
50%	0.28	19.6	27.9	40.8	40.4 A
60%	0.28	16.7	25.8	35.8	38.5 B
70%	0.28	15.3	25.6	32.8	39.5 B
SE±	0.05	2.25	3.04	2.7	2.51
CD(P=0.05)	NS	NS	NS	NS	7.46
e. *Strobilanthes heyneanus*					
Open	3.25	10.5 B	19.3 A	23.7 C	24.4 C
30%	3.25	14.7 A	22.9 A	30.9 B	33.4 AB
40%	3.25	14.6 A	21.0 A	33.0 AB	34.0 AB
50%	3.25	15.0 A	22.3 A	30.6 B	38.2 A
60%	3.25	10.6 B	14.5 B	36.7 A	31.2 B
70%	3.25	12.3 B	15.4 B	29.0 B	32.0 B
SE±	0.38	0.68	1.29	1.76	1.88
CD(P=0.05)	NS	2.03	3.82	5.22	5.59

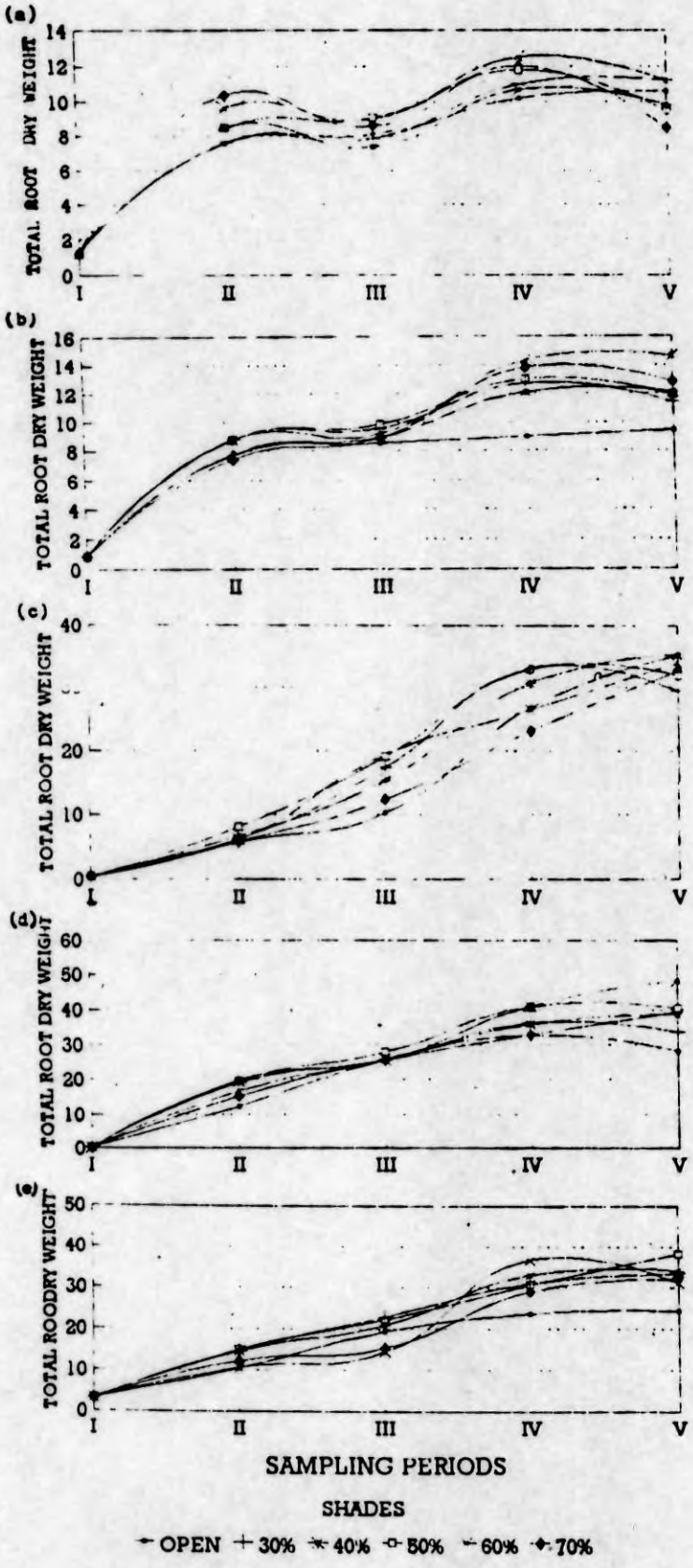


Figure 4. Total root dry weight (g/plant) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 7 **Total leaf number/plant in shade treated medicinal plants at different periods of analysis**

	Shade treatments	Sampling periods I	II	III	IV	V
a. *Adhatoda beddomei*	Open	22	54.3	50.8	54.0	50.5
	30%	22	57.0	60.5	44.8	58.3
	40%	22	57.3	60.5	47.0	60.5
	50%	22	68.0	70.0	64.0	55.8
	60%	22	73.0	67.0	66.3	67.3
	70%	22	59.8	58.5	54.0	40.8
	SE±	3.19	4.60	7.56	7.23	6.82
	CD(P=0.05)	NS	NS	NS	NS	NS
b. *Adhatoda vasica*	Open	12.3	44.8	44.8 C	50.3 C	47 C
	30%	12.3	48.0	65.0 B	52.0 C	74 B
	40%	12.3	48.0	63.6 B	55.5 C	59 C
	50%	12.3	46.3	84.0 A	72.3 B	73.8 B
	60%	12.3	58.3	54.0 BC	56.5 C	80.0 B
	70%	12.3	55.3	86.0 A	87.8 A	109.0 A
	SE±	0.63	3.51	3.94	4.24	4.58
	CD(P=0.05)	NS	NS	11.7	12.6	13.6
c. *Alpinia galanga*	Open	7	23.0 C	40 C	42.8 D	67.8 C
	30%	7	30.3 B	42.3 C	54.5 BC	83.0 B
	40%	7	28.3 BC	48.5 BC	59.3 ABC	74.8 BC
	50%	7	25.0 BC	54.5 B	63.8 AB	99.8 A
	60%	7	36.8 A	68.0 A	69.5 A	89.0 AB
	70%	7	24.5 BC	54.0 B	51.5 CD	79.8 BC
	SE±	0.4	2.0	3.0	3.5	4.7
	CD(P=0.05)	NS	6.1	8.8	10	14
d. *Plumbago rosea*	Open	4.75	57.3	90.0 BC	69.3 B	59
	30%	4.75	55.5	94.5 ABC	76.8 B	78
	40%	4.75	80.5	81.8 C	74.0 B	96
	50%	4.75	76.0	107 AB	109.0 AB	121
	60%	4.75	67.3	110 AB	128.0 A	126
	70%	4.75	60.3	118 A	155.0 A	114
	SE±	0.85	7.37	7.79	15.6	17.6
	CD(P=0.05)	NS	NS	23.1	46.5	NS
e. *Strobilanthes heyneanus*	Open	157	376	386 C	488 C	399 C
	30%	157	358	403 C	460 C	496 C
	40%	157	382	382 C	541 C	637 C
	50%	157	362	731 A	1166 A	1531 A
	60%	157	292	592 B	868 B	1217 B
	70%	157	330	572 B	683 BC	1175 B
	SE±	12.6	40.9	45.4	81.5	93.3
	CD(P=0.05)	NS	NS	135	242	277

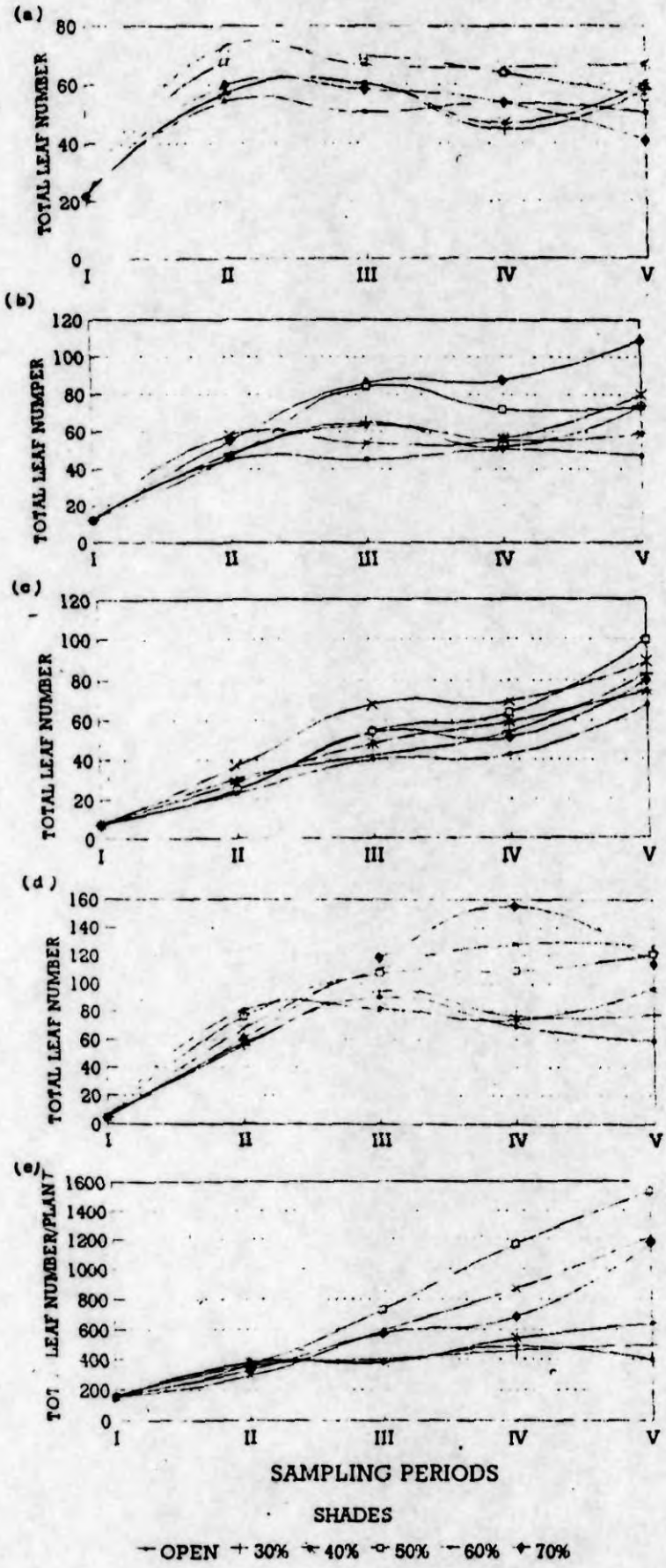


Figure 5. Total leaf number per plant in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 8 Cumulative leaf area/plant (cm^2) in shade treated medicinal plants at different periods of analysis

a. *Adhatoda beddomei*

Shade treatments	Sampling periods I	II	III	IV	V
Open	480	763 C	542 D	273 D	376 C
30%	480	1189 B	800 C	426 CD	533 BC
40%	480	1366 AB	980 BC	499 C	587 B
50%	480	1435 AB	1218 B	718 AB	600 B
60%	480	1619 A	1473 A	824 A	880 A
70%	480	1515 A	1023 BC	610 BC	396 A
SE±	56.2	104	87.8	66.9	54.2
CD(P=0.05)	NS	308	261	199	161

b. *Adhatoda vasica*

Open	235.2	628.71 C	449.45 D	373.01 D	299.55 D
30%	235.2	1097.0 B	884.35 C	401.49 D	493.73 C
40%	235.2	1102.1 B	934.43 C	480.99 CD	508.22 C
50%	235.2	1138.8 B	1218.8 B	675.93 BC	772.31 B
60%	235.2	1521.6 A	1277.1 B	735.77 B	908.50 B
70%	235.2	1449.5 A	1757 A	1340.6 A	1261.6 A
SE±	43.85	66.8	75.7	67.27	46.79
CD(P=0.05)	NS	198.47	224.94	198.89	139.02

c. *Alpinia galanga*

Open	172	730 B	1005 C	1013 C	935 D
30%	172	910 A	1595 B	1633 B	1773 C
40%	172	918 A	1755 AB	1835 AB	1866 C
50%	172	987 A	1842 AB	2096 A	2849 A
60%	172	1045 A	1907 A	2130 A	2666 AB
70%	172	939 A	1804 AB	1962 A	2513 B
SE±	10.5	59.7	87	99.6	89.7
CD(P=0.05)	NS	177	259	296	267

d. *Plumbago rosea*

Open	73.5	1248 C	1545 D	771 C	482 D
30%	73.5	1511 C	2240 C	1041 C	627 D
40%	73.5	2260 B	2270 C	1282 BC	683 CD
50%	73.5	2600 AB	3483 B	1838 B	954 C
60%	73.5	2611 AB	3773 B	2791 A	1456 B
70%	73.5	2808 A	4409 A	3400 A	1831 A
SE±	5.8	147	199	245	97.3
CD(P=0.05)	NS	437	591	729	289

e. *Strobilanthes heyneanus*

Open	636	1909 B	2275	2244 B	1876.1 D
30%	636	2005 B	2967	2690 B	2479.1 D
40%	636	3748 A	3423	3721 B	4836.9 C
50%	636	3930 A	6987	10103 A	12503.0 A
60%	636	3813 A	8843	8944 A	10810.0 AB
70%	636	3512 A	6871	9136 A	9906.4 B
SE±	30.6	347	5186	585.2	732.17
CD(P=0.05)	NS	1032	NS	1739	2175.5

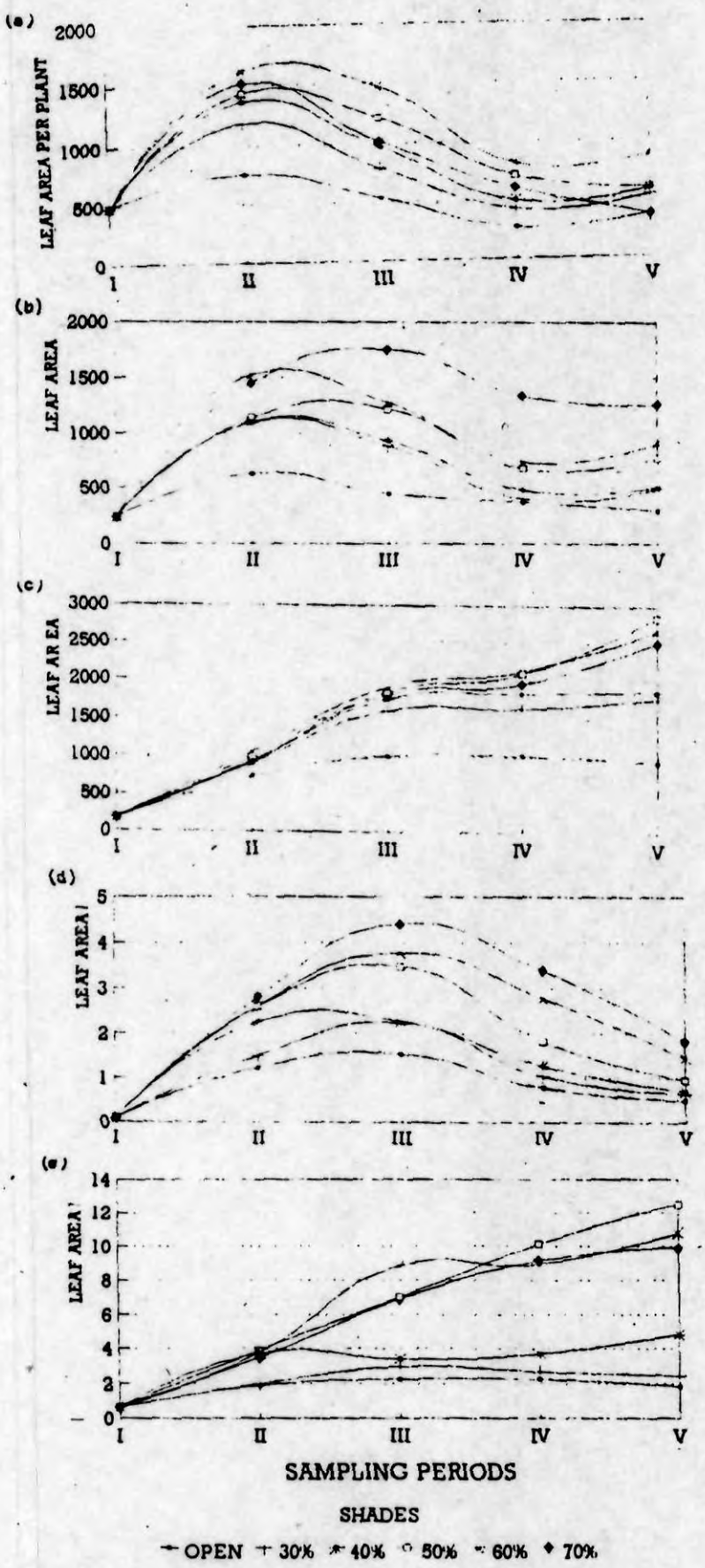


Figure 6. Total leaf area per plant (cm^2) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 9 **Above ground dry matter in shade treated medicinal plants at different periods of analysis**

	Sampling periods					
	Shade treatments	I	II	III	IV	V
a. *Adhatoda beddomei*	Open	4.5	17.2 C	17.3 D	15.6 C	19.5
	30%	4.5	21.1 B	21.6 CD	18.9 BC	22.3
	40%	4.5	22.2 B	24.0 BC	21 0 B	27.0
	50%	4.5	27.2 A	27.4 AB	27.5 A	29.0
	60%	4.5	27.2 A	29.1 A	28.3 A	31.3
	70%	4.5	26.7 A	23.9 BC	26.4 A	20.6
	SE±	0.73	1.21	1.57	1.22	3.09
	CD(P=0.05)	NS	3.58	4.68	3.62	NS
b. *Adhatoda vasica*	Open	2.5	13.0 D	11.1 D	12.0 C	13.2 D
	30%	2.5	16.2 C	17.8 C	15.6 BC	18.4 C
	40%	2.5	17.6 BC	18.4 C	17.9 B	20.5 BC
	50%	2.5	19.2 B	22.5 BC	19.4 B	23.4 B
	60%	2.5	23.3 A	24.0 AB	19.7 B	21.9 BC
	70%	2.5	23.6 A	28.0 A	30.4 A	31.4 A
	SE±	0.23	0.95	1.68	1.44	1.52
	CD(P=0.05)	NS	2.82	4.98	4.29	4.52
c. *Alpinia galanga*	Open	1.23	6.73 B	15.8 C	11.4 D	17.9 E
	30%	1.23	8.98 AB	16.0 C	16.8 C	25.7 D
	40%	1.23	9.08 AB	19.7 AB	19.8 C	30.0 C
	50%	1.23	11.30 A	22.5 A	25.2 B	40.3 A
	60%	1.23	11.40 AB	20.7 AB	30.7 A	37.8 AB
	70%	1.23	10.7 A	17.9 BC	25.0 B	34.5 B
	SE±	0.17	0.81	0.91	1.6	1.3
	CD(P=0.05)	NS	2.39	2.7	4.8	3.8
d. *Plumbago rosea*	Open	0.55	13.7 C	22.5 C	19.6 C	19.0 C
	30%	0.55	19.8 BC	33.0 B	25.3 BC	28.5 C
	40%	0.55	24.1 AB	33.9 B	26.7 BC	39.1 B
	50%	0.55	25.6 AB	44.2 A	35.3 B	49.7 A
	60%	0.55	26.7 A	48.6 A	49.9 A	53.1 A
	70%	0.55	29.8 A	52.3 A	54.8 A	56.5 A
	SE±	0.10	2.06	3.31	3.69	3.35
	CD(P=0.05)	NS	6.13	9.82	10.2	9.97
e. *Strobilanthes heyneanus*	Open	8.15	43.0	54.6 C	67.9 D	82.1 D
	30%	8.15	44.0	57.1 C	73.1 D	108 CD
	40%	8.15	44.4	62.9 C	91.5 D	131 C
	50%	8.15	57.5	118.0 AB	233.0 A	337 A
	60%	8.15	49.9	123.0 A	201.0 B	274 B
	70%	8.15	48.7	97.6 B	168.0 C	256 B
	SE±	0.66	4.76	6.92	10.7	14
	CD(P=0.05)	NS	NS	20.6	31.9	41.5

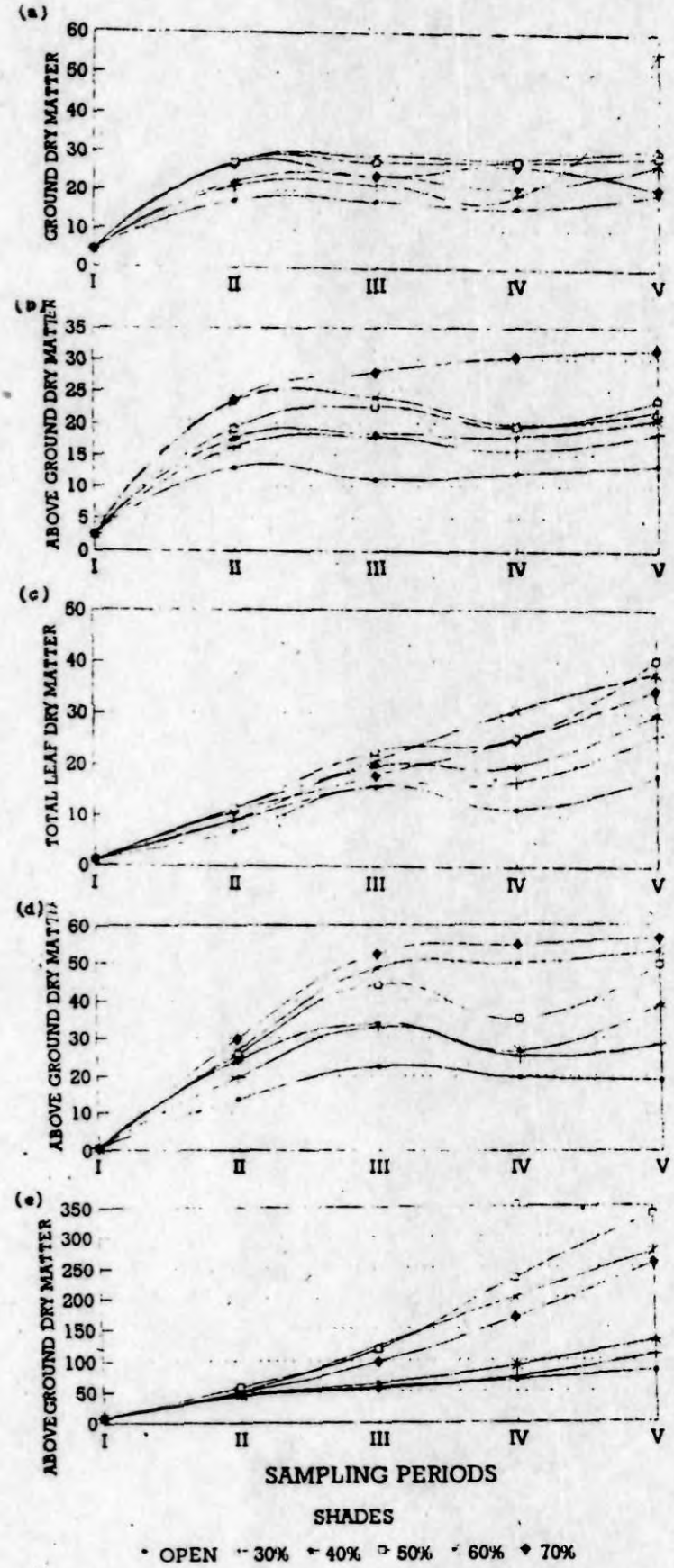


Figure 7. Above ground dry matter (g/plant) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 10 **Ratio of above ground dry matter to below ground dry matter (g/plant) in shade treated medicinal plants at different periods of analysis**

	Sampling periods				
Shade treatments	I	II	III	IV	V
a. *Adhatoda beddomei*					
Open	3.61	2.3	2.15	1.53 C	1.84 D
30%	3.61	2.78	2.8	1.72 BC	2.01 CD
40%	3.61	2.64	3.3	2.03 AB	2.77 AB
50%	3.61	3.39	3.0	2.33 A	3.05 A
60%	3.61	2.89	3.31	2.28 A	2.87 AB
70%	3.61	2.59	2.95	2.19 A	2.43 BC
SE±	0.31	0.26	0.31	0.14	0.14
CD(P=0.05)	NS	NS	NS	0.42	0.43
b. *Adhatoda vasica*					
Open	2.97	1.72 C	1.30 C	1.34 B	1.44 C
30%	2.97	1.83 C	1.91 BC	1.24 B	1.63 BC
40%	2.97	2.34 BC	2.08 BC	1.50 B	1.73 BC
50%	2.97	2.23 BC	2.48 AB	1.52 B	2.06 AB
60%	2.97	2.68 AB	2.62 AB	1.57 B	1.52 BC
70%	2.97	3.26 A	3.18 A	2.20 A	2.47 A
SE±	0.28	0.21	0.28	0.18	0.18
CD(P=0.05)	NS	0.63	0.83	0.54	0.54
c. *Alpinia galanga*					
Open	0.37	0.57 D	0.70	0.25 C	0.28 C
30%	0.37	0.74 C	0.53	0.30 C	0.43 B
40%	0.37	0.67 CD	0.69	0.34 BC	0.44 B
50%	0.37	0.77 BC	0.72	0.41 B	0.60 A
60%	0.37	0.94 A	0.65	0.62 A	0.61 A
70%	0.37	0.90 AB	0.79	0.55 A	0.59 A
SE±	0.05	0.05	0.06	0.03	0.03
CD(P=0.05)	NS	0.14	NS	0.16	0.08
d. *Plumbago rosea*					
Open	2.33	1.11 C	0.88	0.61 B	0.67 B
30%	2.33	1.13 BC	1.3	0.71 B	0.85 B
40%	2.33	1.22 BC	1.32	0.66 B	0.82 B
50%	2.33	1.37 BC	1.61	0.86 B	1.23 A
60%	2.33	1.65 AB	1.92	1.39 A	1.40 A
70%	2.33	2.01 A	2.06	1.71 A	1.46 A
SE±	0.71	0.16	0.82	0.12	0.11
CD(P=0.05)	NS	0.49	NS	0.35	0.32
e. *Strobilanthes heyneanus*					
Open	2.55	4.15 AB	2.95 C	2.84 C	3.38 B
30%	2.55	3.03 B	2.50 C	2.39 C	3.20 B
40%	2.55	3.00 B	3.00 C	2.81 C	3.88 B
50%	2.55	3.82 AB	5.33 B	7.66 A	8.91 A
60%	2.55	4.87 A	8.57 A	5.44 B	8.86 A
70%	2.55	3.95 AB	6.42 B	5.82 B	8.01 A
SE±	0.15	0.43	0.45	0.3	0.47
CD(P=0.05)	NS	1.26	1.34	0.88	1.39

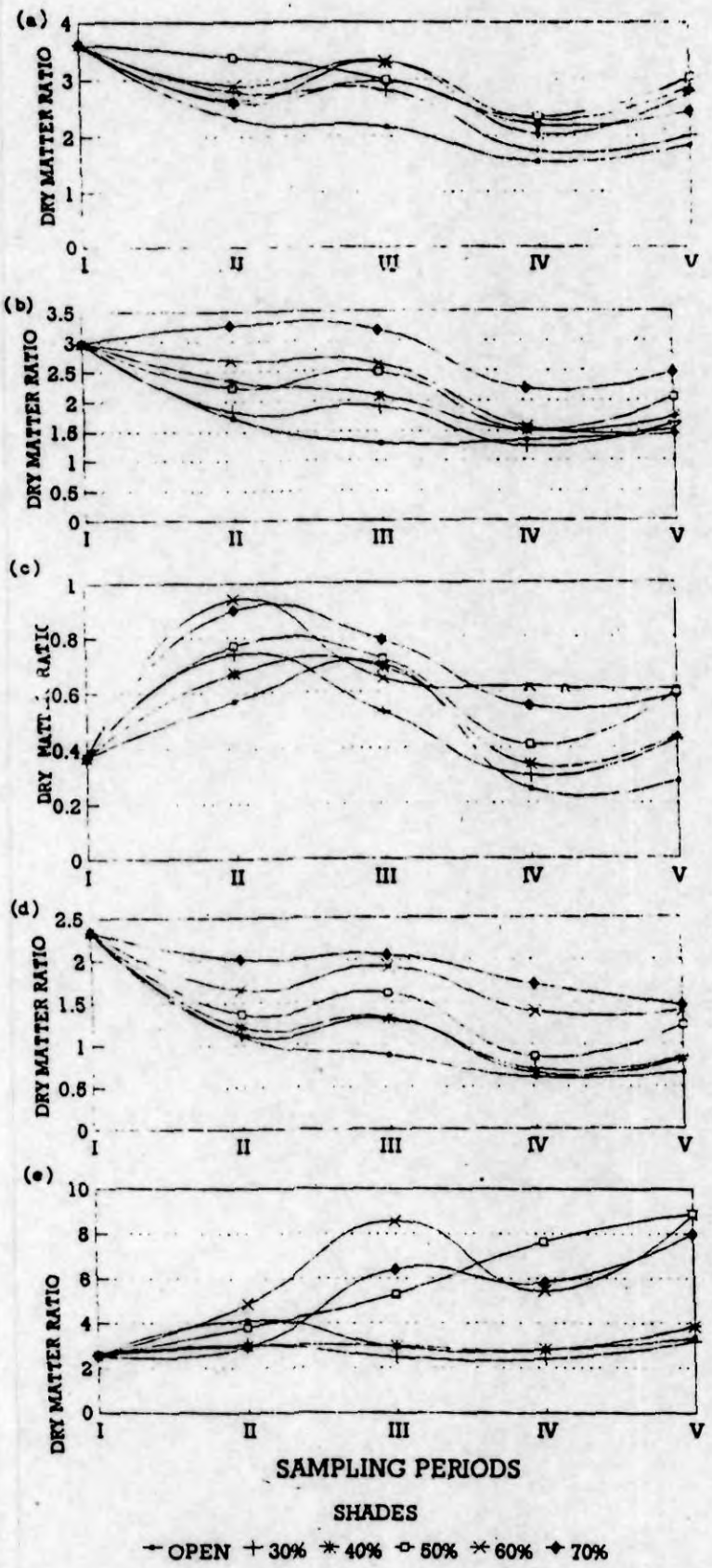


Figure 8. Above ground dry matter to below ground dry matter ratio in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 11 **Ratio of photosynthetic tissue to support tissue in shade treated medicinal plants at different periods of analysis**

	Sampling periods				
Shade treatments	I	II	III	IV	V
a *Adhatoda beddomei*					
Open	0.9	0.49	0.24 B	0.10 C	0.14
30%	0.9	0.47	0.35 A	0.14 B	0.14
40%	0.9	0.45	0.34 A	0.15 AB	0.13
50%	0.9	0.50	0.30 AB	0.16 AB	0.13
60%	0.9	0.47	0.32 A	0.18 A	0.17
70%	0.9	0.44	0.23 B	0.13 BC	0.12
SE±	0.01	0.05	0.03	0.01	0.01
CD(P=0.05)	NS	NS	0.07	0.03	NS
b. *Adhatoda vasica*					
Open	0.9	0.43 C	0.25 C	0.23 AB	0.16 B
30%	0.9	0.49 BC	0.41 A	0.19 B	0.17 B
40%	0.9	0.57 AB	0.37 AB	0.18 B	0.17 B
50%	0.9	0.55 AB	0.43 A	0.19 B	0.27 A
60%	0.9	0.55 AB	0.32 BC	0.22 B	0.23 AB
70%	0.9	0.64 A	0.44 A	0.29 A	0.27 A
SE±	0.12	0.03	0.03	0.02	0.03
CD(P=0.05)	NS	0.09	0.09	0.06	0.08
c. *Alpinia galanga*					
Open	0.252	0.337 C	0.386	0.149 D	0.150 D
30%	0.252	0.405 B	0.311	0.179 D	0.228 BC
40%	0.252	0.393 BC	0.358	0.187 CD	0.212 C
50%	0.252	0.418 B	0.370	0.229 BC	0.274 A
60%	0.252	0.497 A	0.344	0.316 A	0.267 A
70%	0.252	0.449 AB	0.423	0.267 B	0.261 AB
SE±	0.03	0.02	0.03	0.02	0.01
CD(P=0.05)	NS	0.06	NS	0.05	0.03
d. *Plumbago rosea*					
Open	0.38	0.63	0.34	0.20 B	0.10 BC
30%	0.38	0.51	0.37	0.18 B	0.11 BC
40%	0.38	0.47	0.35	0.19 B	0.09 C
50%	0.38	0.46	0.36	0.20 B	0.11 BC
60%	0.38	0.53	0.44	0.31 A	0.16 A
70%	0.38	0.58	0.39	0.30 A	0.14 AB
SE±	0.09	0.06	0.11	0.02	0.01
CD(P=0.05)	NS	NS	NS	0.07	0.04
e. *Strobilanthes heyneanus*					
Open	0.52	0.43	0.33 ABC	0.28	0.21 BC
30%	0.52	0.39	0.31 C	0.25	0.19 C
40%	0.52	0.39	0.32 BC	0.28	0.27 AB
50%	0.52	0.41	0.34 ABC	0.35	0.29 A
60%	0.52	0.46	0.40 A	0.30	0.28 AB
70%	0.52	0.41	0.39 AB	0.34	0.27 AB
SE±	0.05	0.02	0.02	0.02	0.02
CD(P=0.05)	NS	NS	0.07	NS	0.07

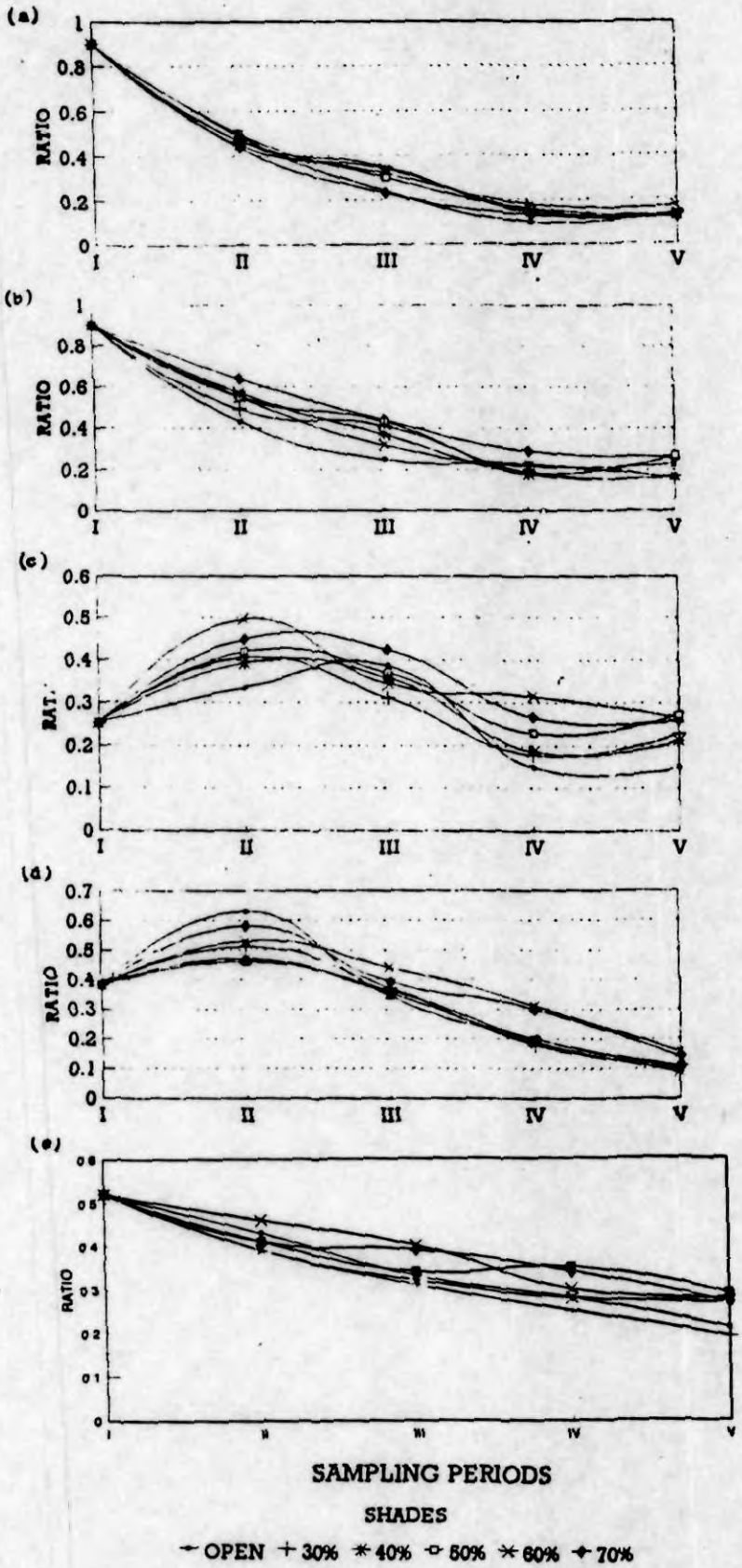


Figure 9. Photosynthetic tissue to support tissue ratio in shade treated medicinal plants at different periods of analysis
(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 12 **Single leaf area (cm^2) in shade treated medicinal plants at different periods of analysis**

	Shade treatments	Sampling periods I	II	III	IV	V
a. *Adhatoda beddomei*	Open	22	14.4 B	12.2 B	5.29 B	7.51 C
	30%	22	20.9 A	13.4 B	9.59 A	9.12 BC
	40%	22	24.9 A	16.4 B	10.90 A	10.10 ABC
	50%	22	21.3 A	17.6 AB	11.80 A	11.7 AB
	60%	22	22.2 A	23.6 A	12.40 A	13.3 A
	70%	22	25.2 A	17.7 AB	11.00 A	9.81 ABC
	SE±	0.66	1.8	2.2	1.16	1.19
	CD(P=0.05)	NS	5.35	6.55	3.44	3.53
b. *Adhatoda vasica*	Open	18.9	14.1 B	10.2 C	7.40 B	6.4 C
	30%	18.9	23.9 A	13.7 B	7.69 B	6.8 BC
	40%	18.9	23.0 A	14.6 B	8.68 B	8.6 B
	50%	18.9	24.7 A	14.6 B	9.58 B	10.5 A
	60%	18.9	26.2 A	23.6 A	13.30 A	11.5 A
	70%	18.9	26.3 A	20.8 A	15.30 A	11.6 A
	SE±	2.86	1.68	1.1	1.14	0.63
	CD(P=0.05)	NS	5.0	3.27	3.38	1.87
c. *Alpinia galanga*	Open	24.8	32.06 AB	25.3 C	23.87 C	14.0 D
	30%	24.8	30.107 B	37.9 A	30.19 BC	21.4 C
	40%	24.8	32.281 AB	36.4 AB	31.83 AB	25.3 BC
	50%	24.8	39.731 A	33.9 AB	33.03 AB	28.6 AB
	60%	24.8	29.531 B	28.9 BC	30.78 BC	30.1 A
	70%	24.8	38.675 A	33.8 AB	38.41 A	31.7 A
	SE±	1.8	2.44	2.64	2.33	1.36
	CD(P=0.05)	NS	7.24	7.84	6.93	4.03
d. *Plumbago rosea*	Open	16.8	22.1 D	17.4 D	11.1 C	8.61 BC
	30%	16.8	27.6 CD	23.8 C	13.9 BC	9.13 BC
	40%	16.8	29.5 BCD	28.1 BC	18.0 AB	7.08 C
	50%	16.8	34.5 BC	33.0 AB	18.2 AB	8.68 BC
	60%	16.8	39.8 AB	34.5 AB	23.0 A	12.70 AB
	70%	16.8	49.1 A	37.8 A	22.2 A	16.20 A
	SE±	3.03	3.73	2.15	2.04	1.52
	CD(P=0.05)	NS	11.1	6.39	6.07	4.53
e. *Strobilanthes heyneanus*	Open	4.11	5.0 C	5.85 E	4.65 E	4.57 C
	30%	4.11	5.6 C	7.41 D	5.99 D	4.96 C
	40%	4.11	10.3 B	8.99 C	6.93 D	7.56 B
	50%	4.11	11.0 AB	9.53 C	8.80 C	8.22 AB
	60%	4.11	13.5 A	14.9 A	10.4 B	8.98 A
	70%	4.11	10.6 B	12.0 B	13.3 A	8.39 AB
	SE±	0.22	0.89	0.36	0.42	0.31
	CD(P=0.05)	NS	2.64	1.07	1.24	0.92

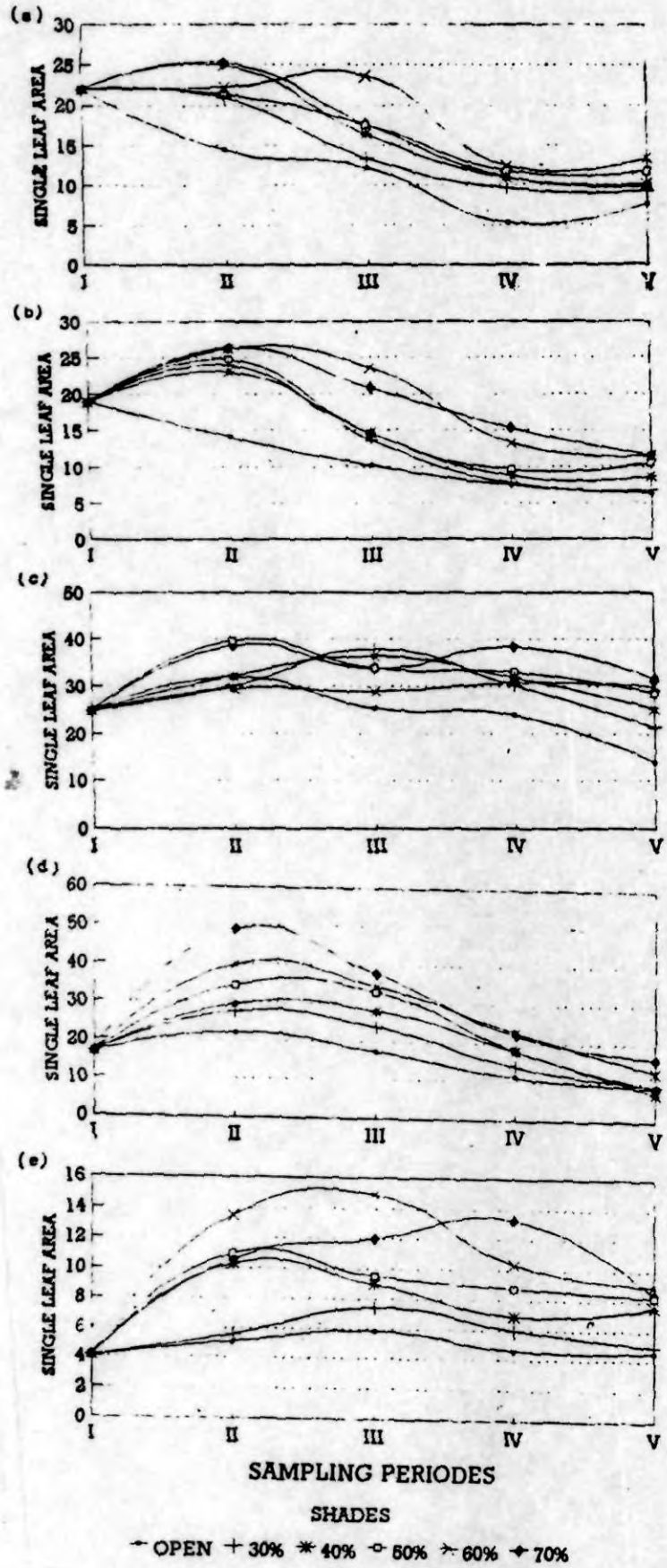


Figure 10. Single leaf area (cm^2) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 13 **Specific leaf weight (g/cm^2) in shade treated medicinal plants at different periods of analysis**

	Sampling periods				
Shade treatments	I	II	III	IV	V
a. *Adhatoda beddomei*					
Open	0.0056	0.0104 A	0.009 AB	0.0084	0.0094
30%	0.0056	0.0078 BC	0.0097 A	0.0087	0.0077
40%	0.0056	0.0069 C	0.0079 BC	0.0080	0.0074
50%	0.0056	0.0083 B	0.0070 CD	0.0076	0.0073
60%	0.0056	0.0072 BC	0.0062 D	0.0076	0.0069
70%	0.0056	0.0076 BC	0.0060 D	0.0081	0.0079
SE±	0.0001	0.0004	0.0005	0.0009	0.0007
CD(P=0.05)	NS	0.0012	0.0014	NS	NS
b. *Adhatoda vasica*					
Open	0.007	0.0100 A	0.0087 A	0.0108 A	0.0106 A
30%	0.007	0.0076 B	0.0091 A	0.0113 A	0.0091 AB
40%	0.007	0.0084 AB	0.0081 AB	0.0101 AB	0.0091 AB
50%	0.007	0.0087 AB	0.0079 AB	0.0075 B	0.0095 AB
60%	0.007	0.0074 B	0.0065 B	0.0082 AB	0.0074 B
70%	0.007	0.0084 AB	0.0064 B	0.0074 B	0.0074 B
SE±	0.001	0.0006	0.0007	0.001	0.0007
CD(P=0.05)	NS	0.0016	0.0019	0.003	0.0022
c. *Alpinia galanga*					
Open	0.007	0.0092	0.016	0.0113 B	0.0192
30%	0.007	0.0099	0.010	0.0103 B	0.0146
40%	0.007	0.0100	0.0113	0.0108 B	0.0160
50%	0.007	0.0115	0.0123	0.0120 B	0.0142
60%	0.007	0.0109	0.0109	0.0145 A	0.0142
70%	0.007	0.0114	0.010	0.0128 AB	0.0137
SE±	0.0006	0.0007	0.0079	0.0008	0.001
CD(P=0.05)	NS	NS	NS	0.0023	NS
d. *Plumbago rosea*					
Open	0.003	0.0081 A	0.0079 A	0.0112	0.0096
30%	0.003	0.0081 A	0.0072 A	0.0092	0.0095
40%	0.003	0.0065 AB	0.0068 AB	0.0083	0.0101
50%	0.003	0.0054 B	0.0054 C	0.0069	0.0093
60%	0.003	0.0057 B	0.0060 BC	0.0074	0.0086
70%	0.003	0.0058 B	0.0049 C	0.0060	0.0066
SE±	0.0005	0.0006	0.0003	0.0096	0.012
CD(P=0.05)	NS	0.0018	0.001	NS	NS
e. *Strobilanthes heyneanus*					
Open	0.006	0.0084 A	0.0081 A	0.0090 A	0.0109 A
30%	0.006	0.0082 A	0.0064 B	0.0079 B	0.0087 B
40%	0.006	0.0045 B	0.0059 C	0.0074 BC	0.0073 BC
50%	0.006	0.0054 B	0.0051 D	0.0067 CD	0.0068 BC
60%	0.006	0.0050 B	0.0044 E	0.006 DE	0.0063 C
70%	0.006	0.0051 B	0.0046 E	0.0055 E	0.0063 C
SE±	0.0005	0.0004	0.0002	0.0003	0.0007
CD(P=0.05)	NS	0.0011	0.0005	0.0008	0.0021

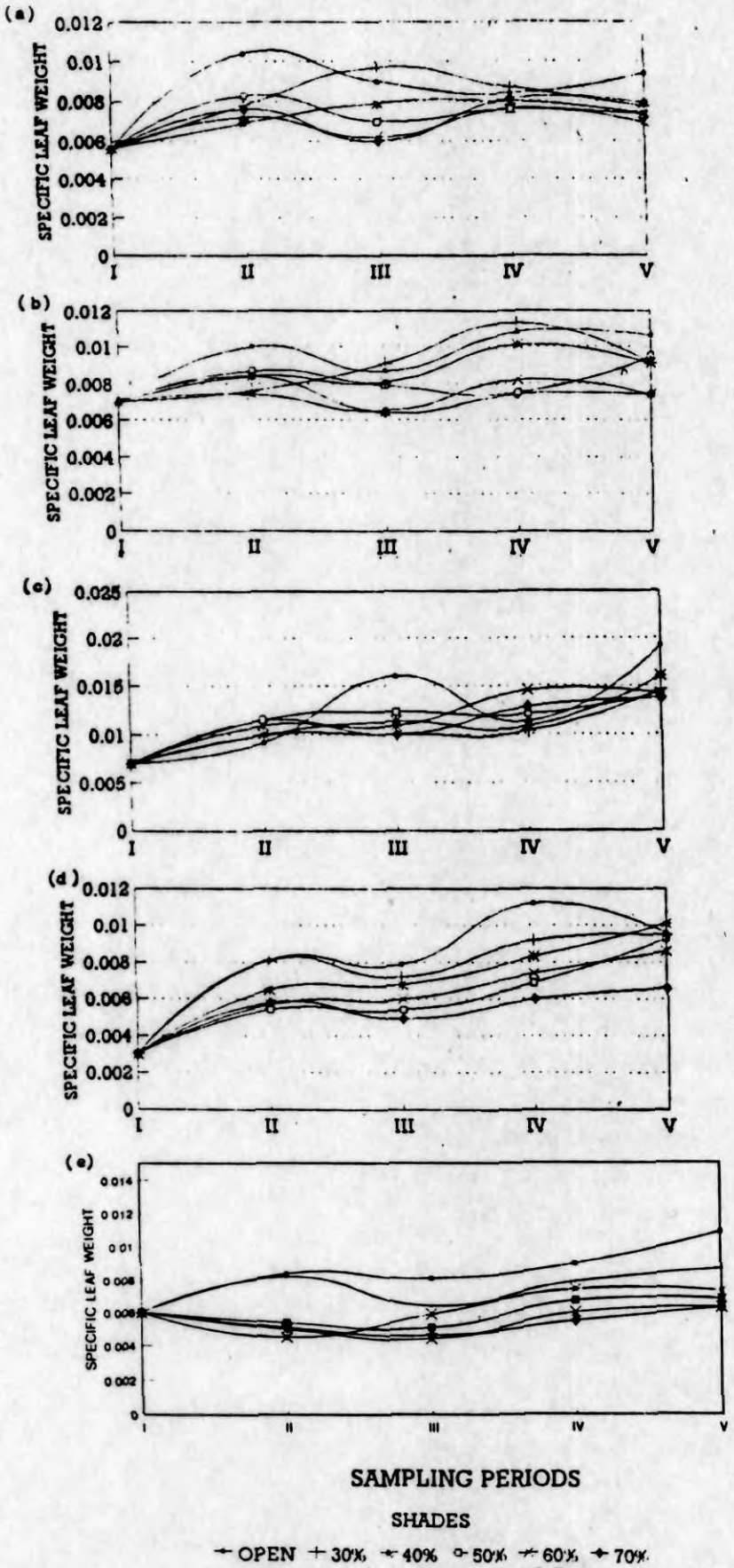


Figure 11. Specific leaf weight (g/cm^2) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 14 **Specific leaf area (cm^2/g) in shade treated medicinal plants at different periods of analysis**

a. *Adhatoda beddomei*

Shade treatments	Sampling periods I	II	III	IV	V
Open	179	96.9 C	111 C	119	107
30%	179	130 AB	105 C	116	134
40%	179	148 A	126 BC	126	139
50%	179	121 B	147 AB	132	141
60%	179	140 AB	163 A	134	146
70%	179	133 AB	169 A	141	132
SE±	3.32	7.51	8.91	10.7	12.2
CD(P=0.05)	NS	22.3	26.5	NS	NS

b. *Adhatoda vasica*

Open	146.5	103.0	115.5	95.1	94.95
30%	146.5	132.8	110 6	90.1	116 6
40%	146.5	122.3	130.7	108.9	110.5
50%	146.5	115.3	127.9	138.3	107.6
60%	146.5	134.7	168 6	123.6	146.6
70%	146.5	120.7	155.9	134.9	137.0
SE±	13.53	7.3	15 4	15.2	13.92
CD(P=.05)	NS	NS	NS	NS	NS

c. *Alpinia galanga*

Open	145	109	64.9 B	89.0 AB	52.5 C
30%	145	104	99 8 A	99 5 A	69 4 AB
40%	145	102	89.0 A	92.8 AB	62.4 B
50%	145	88.1	82.7 A	84.1ABC	71.1 AB
60%	145	92.5	92.8 A	70.4 C	70.8 AB
70%	145	88.7	101.0 A	78.6 BC	73.0 A
SE±	11.4	7.2	5.6	5.4	3.2
CD(P=0.05)	NS	NS	16.7	16.1	9.5

d. *Plumbago rosea*

Open	372	127 B	127 D	96.5 D	114
30%	372	124 B	141 CD	110 CD	108
40%	372	166 AB	148 CD	121 BCD	98.8
50%	372	186 A	189 AB	146 AB	109
60%	372	179 A	168 BC	137 BC	123
70%	372	176 A	206 A	169 A	157
SE±	72.2	14.7	9.51	9.1	13.6
CD(P=0.05)	NS	43.7	28.3	27	NS

e. *Strobilanthes heyneanus*

Open	169	120 C	124 D	111.1 D	97.08 A
30%	169	122 C	157 C	127.7 CD	115.3 A
40%	169	236 A	170 C	136 3 BC	138.2 A
50%	169	186 B	197 B	149.1 B	147.1 AB
60%	169	202 AB	227 A	167.1 A	159.3 BC
70%	169	195 AB	218 A	183.2 A	160.9 C
SE±	12.6	20.7	6.2	5.8	8.0
CD(P=0.05)	NS	61.5	18.5	17.2	23.8

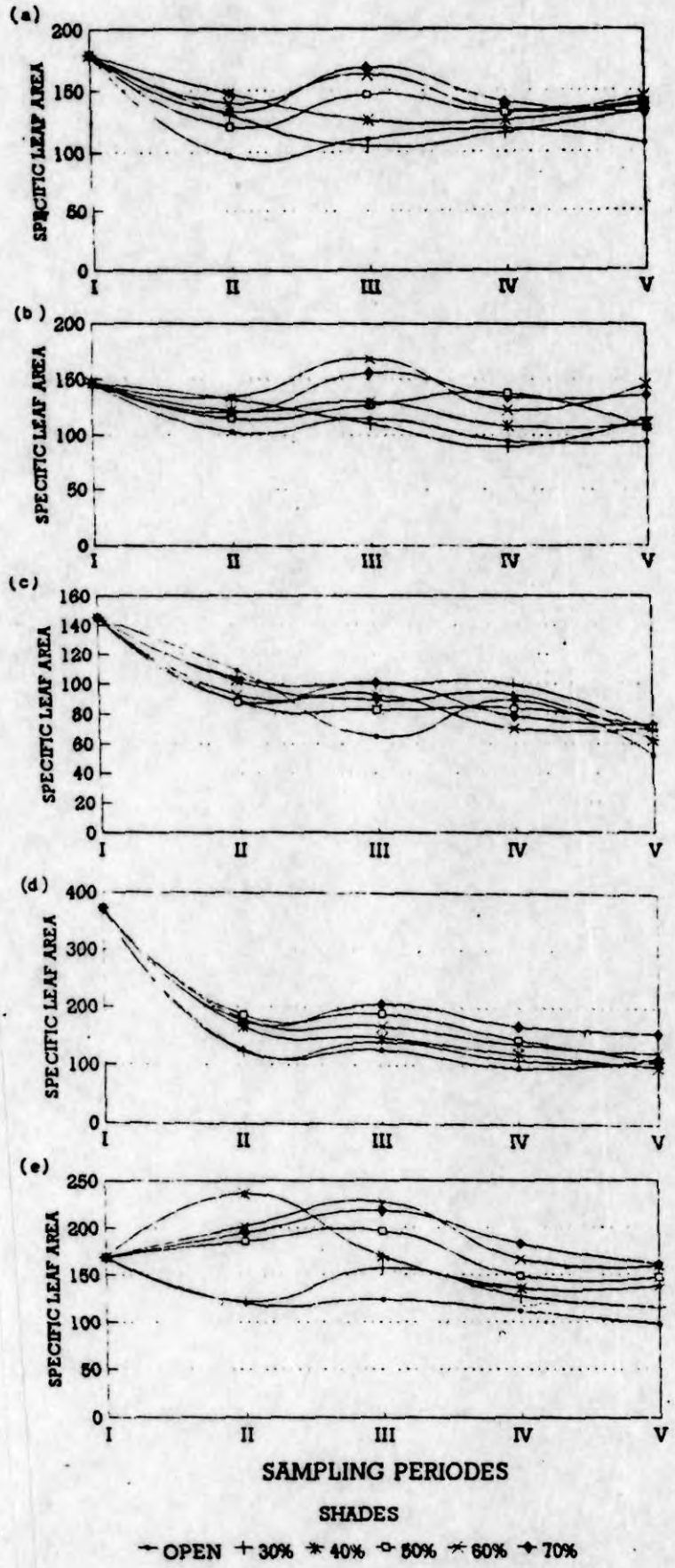


Figure 12. Specific leaf area (cm^2/g) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 15 **Leaf weight ratio in shade treated medicinal plants at different periods of analysis**

	Sampling periods					
	Shade treatments	I	II	III	IV	V
a. *Adhatoda beddomei*	Open	0.4731	0.325	0.192 B	0.087 D	0.119
	30%	0.4731	0.320	0.258 A	0.122 BC	0.119
	40%	0.4731	0.308	0.25 A	0.127 ABC	0.115
	50%	0.4731	0.331	0.23 AB	0.139 AB	0.113
	60%	0.4731	0.320	0.24 A	0.151 A	0.143
	70%	0.4731	0.305	0.189 B	0.113 CD	0.105
	SE±	0.0038	0.024	0.015	0.009	0.011
	CD(P=0.05)	NS	NS	0.045	0.026	NS
b. *Adhatoda vasica*	Open	0.467	0.30 C	0.201 C	0.185 AB	0.139 B
	30%	0.467	0.33 BC	0.293 A	0.159 B	0.147 B
	40%	0.467	0.36 AB	0.270AB	0.150 B	0.141 B
	50%	0.467	0.36 AB	0.297 A	0.159 B	0.208 A
	60%	0.467	0.35 AB	0.243 BC	0.180 AB	0.184 AB
	70%	0.467	0.39 A	0.306 A	0.225 A	0.213 A
	SE±	0.03	0.014	0.015	0.015	0.019
	CD(P=0.05)	NS	0.04	0.045	0.044	0.056
c. *Alpinia galanga*	Open	0.266	0.363 D	0.409	0.198 D	0.219 C
	30%	0.266	0.424 C	0.345	0.231 CD	0.299 B
	40%	0.266	0.401 CD	0.409	0.256 BC	0.306 B
	50%	0.266	0.434 BC	0.418	0.290 B	0.376 A
	60%	0.266	0.483 A	0.395	0.379 A	0.380 A
	70%	0.266	0.473 AB	0.438	0.354 A	0.371 A
	SE±	0.026	0.015	0.019	0.015	0.012
	CD(P=0.05)	NS	0.045	NS	0.044	0.035
d. *Plumbago rosea*	Open	0.27	0.38	0.26	0.16 B	0.09 B
	30%	0.27	0.33	0.27	0.15 B	0.10 AB
	40%	0.27	0.32	0.26	0.16 B	0.08 B
	50%	0.27	0.31	0.26	0.17 B	0.10 AB
	60%	0.27	0.34	0.30	0.24 A	0.13 A
	70%	0.27	0.36	0.28	0.23 A	0.13 A
	SE±	0.05	0.03	0.04	0.02	0.01
	CD(P=0.05)	NS	NS	NS	0.05	0.03
e. *Strobilanthes heyneanus*	Open	0.339	0.299	0.246	0.217	0.174 BC
	30%	0.339	0.279	0.238	0.202	0.157 C
	40%	0.339	0.278	0.239	0.220	0.209 AB
	50%	0.339	0.289	0.251	0.257	0.227 A
	60%	0.339	0.313	0.282	0.229	0.221 A
	70%	0.339	0.293	0.282	0.251	0.215 AB
	SE±	0.022	0.011	0.012	0.014	0.015
	CD(P=0.05)	NS	NS	NS	NS	0.043

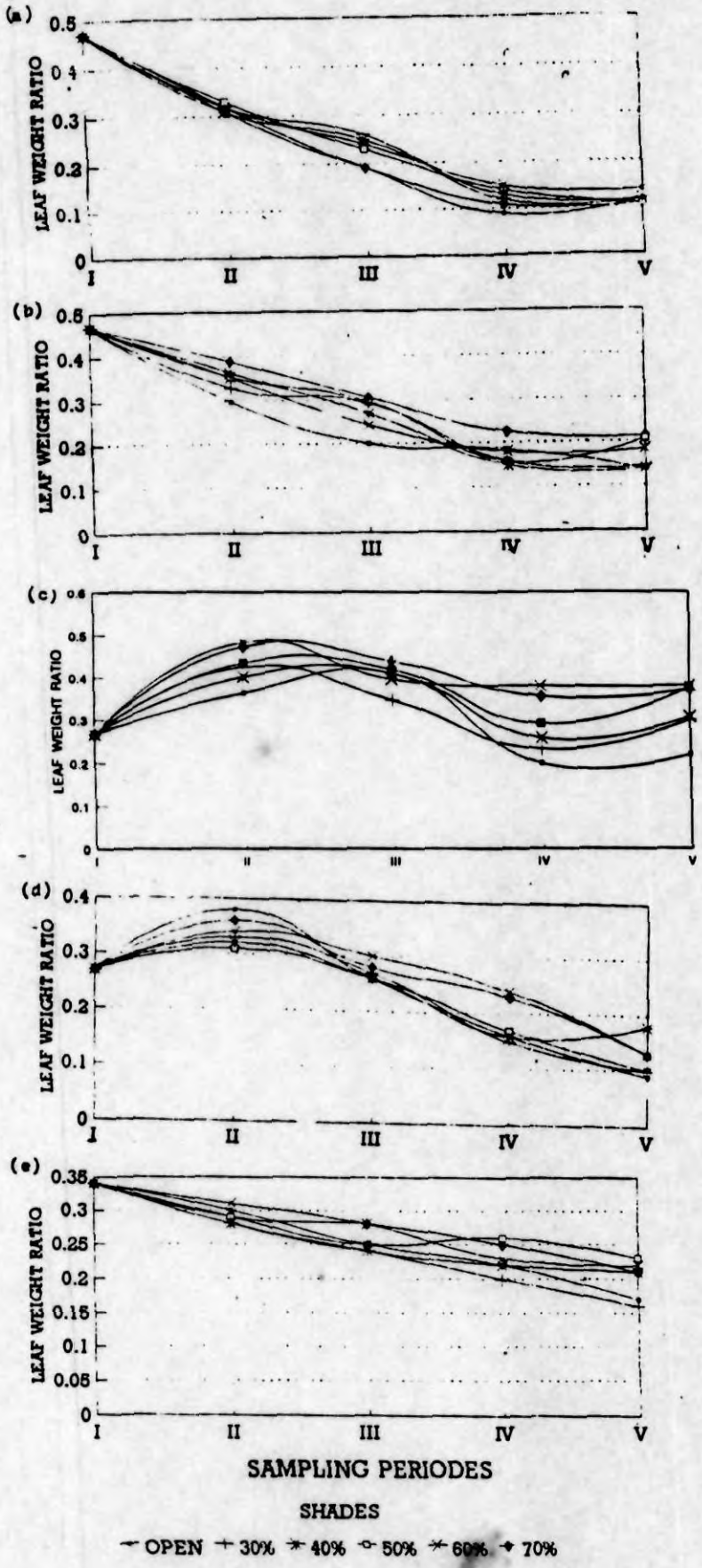


Figure 13. Leaf weight ratio in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 16 **Crop growth rate (g/plant/day) in shade treated medicinal plants at different periods of analysis**

a. *Adhatoda beddomei*

Shade treatments	Sampling periods I	II	III	IV
Open	0.1920 C	0.0107	0.0067	0.0694 A
30%	0.2530 B	0.0129	0.0067	0.0575 A
40%	0.2753 B	0.0098	0.0056	0.0821 A
50%	0.3291 A	0.0147	0.0437	-0.012
60%	0.3415 A	0.0228	0.0425	0.0274 A
70%	0.3451 A	-0.083	0.0948	-0.15 B
SE±	0.018	0.039	0.056	0.031
CD(P=0.05)	0.053	NS	NS	0.092

b. *Adhatoda vasica*

Open	0.1901 C	0.0902	-0.075	0.0266
30%	0.2379 B	0.0415	0.0139	0.0262
40%	0.2426 B	0.0348	0.0429	0.0401
50%	0.2701 AB	0.0790	0.0004	0.0470
60%	0.3157 A	0.0205	0.0115	0.0397
70%	0.3036 A	0.1058	0.1147	0.0008
SE±	0.015	0.042	0.049	0.046
CD(P=0.05)	0.045	NS	NS	NS

c. *Alpinia galanga*

Open	0.152	0.366	0.292 D	0.3897 A
30%	0.183	0.451	0.419 C	0.2048 B
40%	0.198	0.457	0.463 B	-0.068 C
50%	0.237	0.498	0.519 A	-0.068 C
60%	0.209	0.512	0.449BC	-0.063 C
70%	0.196	0.333	0.470 B	-0.074 C
SE±	0.019	0.056	0.043	0.029
CD(P=0.05) NS		NS	0.127	0.087

d. *Plumbago rosea*

Open	0.277 B	0.391	0.069	-0.079
30%	0.419 A	0.351	0.046	0.009
40%	0.473 A	0.283	0.127	-0.066
50%	0.487 A	0.480	0.064	-0.046
60%	0.467 A	0.554	0.179	-0.020
70%	0.485 A	0.587	0.155	-0.028
SE±	0.04	0.09	0.11	0.04
CD(P=0.05)	0.12	NS	NS	NS

e. *Strobilanthes heyneanus*

Open	0.463	0.365 B	0.28 C	0.236 AB
30%	0.519	0.382 B	0.38 C	0.598 A
40%	0.523	0.445 B	0.644 C	-0.13 BC
50%	0.671	1.213 A	1.958 A	-0.37 C
60%	0.539	1.383 A	1.579 B	-0.23 C
70%	0.545	0.928 A	1.335 B	-0.3 C
SE±	0.05	0.15	0.19	0.14
CD(P=0.05)	NS	0.44	0.58	0.42

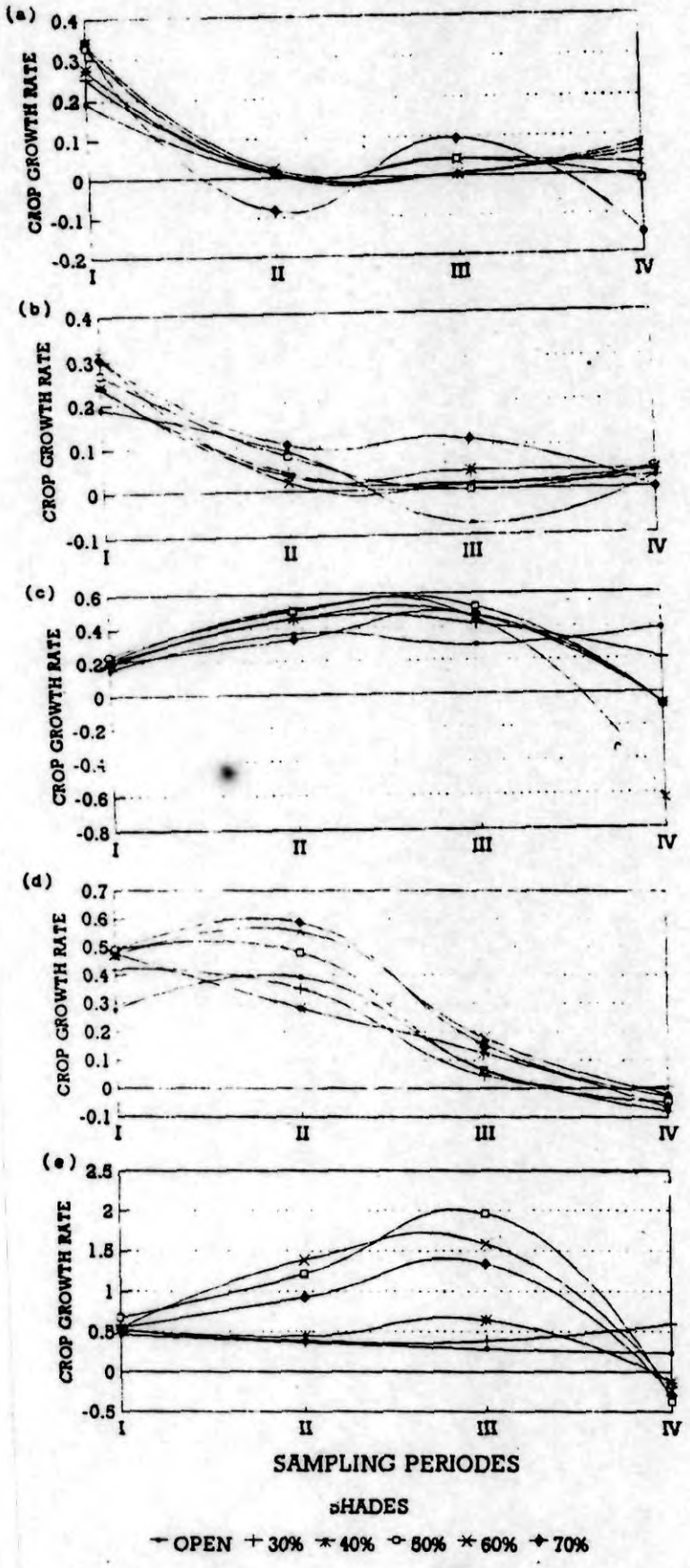


Figure 14.Crop growth rate (g/plant/day) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*

(c) *Alpinia galanga* (d) *Plumbago rosea*

(e) *Strobilanthes heyneanus*

Table 17 **Relative growth rate (g/g/day) in shade treated medicinal plants at different periods of analysis**

a. *Adhatoda beddomei*

Shade treatments	Sampling periods I	II	III	IV
Open	0.0149	0.0004	0.0003	0.00258 A
30%	0.0180	0.0005	0.0002	0.00176 A
40%	0.0188	0.0003	0.0002	0.00232 A
50%	0.0204	0.0003	0.0013	-0.0004 A
60%	0.0208	0.0006	0.0011	0.00062 A
70%	0.0208	-0.0020	0.0028	-0.0044 B
SE±	0.0015	0.0013	0.0012	0.00092
CD(P=0.05)	NS	NS	NS	0.0027

b. *Adhatoda vasica*

Open	0.0200 B	0.0025	-0.002	0.0012
30%	0.0221 AB	0.0017	0.0005	0.0010
40%	0.0222 AB	0.0014	0.0016	0.0012
50%	0.0234 A	0.0026	7E-05	0.0014
60%	0.0249 A	0.0004	0.0004	0.0012
70%	0.0245 A	0.0031	0.0027	1E-05
SE±	0.0009	0.0016	0.221	0.0014
CD(P=0.05)	0.0028	NS	NS	NS

c. *Alpinia galanga*

Open	0.0153	0.0133	0.0062	0.00565 A
30%	0.0168	0.0141	0.0072	0.00258 B
40%	0.0175	0.0137	0.0075	-0.0008 C
50%	0.0191	0.0130	0.0076	-0.007 C
60%	0.0180	0.0143	0.0068	-0.0007 C
70%	0.0175	0.0107	0.0087	-0.0009 C
SE±	0.0013	0.0018	0.0008	0.00061
CD(P=0.05)	NS	NS	NS	0.0018

d. *Plumbago rosea*

Open	0.0379 B	0.0109	0.0016	-0.0017
30%	0.0422 A	0.0075	0.0007	0.00012
40%	0.0436 A	0.0056	0.0020	-0.0009
50%	0.0440 A	0.0082	0.0009	-0.0006
60%	0.0435 A	0.0098	0.0021	-0.0003
70%	0.0438 A	0.0101	0.0019	-0.0003
SE±	0.0013	0.0021	0.0016	0.00066
CD(P=0.05)	0.0038	NS	NS	NS

e. *Strobilanthes heyneanus*

Open	0.0171	0.0057 C	0.0033 C	0.00248 AB
30%	0.0181	0.0056 C	0.0042 BC	0.00458 A
40%	0.0179	0.0065 BC	0.0064 ABC	-0.0009 B
50%	0.0203	0.0119 AB	0.0101 A	-0.0012 B
60%	0.0184	0.0148 A	0.0085 AB	-0.0009 B
70%	0.0185	0.011 ABC	0.0089 AB	-0.0013 B
SE±	0.0011	0.0018	0.0015	0.0012
CD(P=0.05)	NS	0.0054	0.0045	0.0036

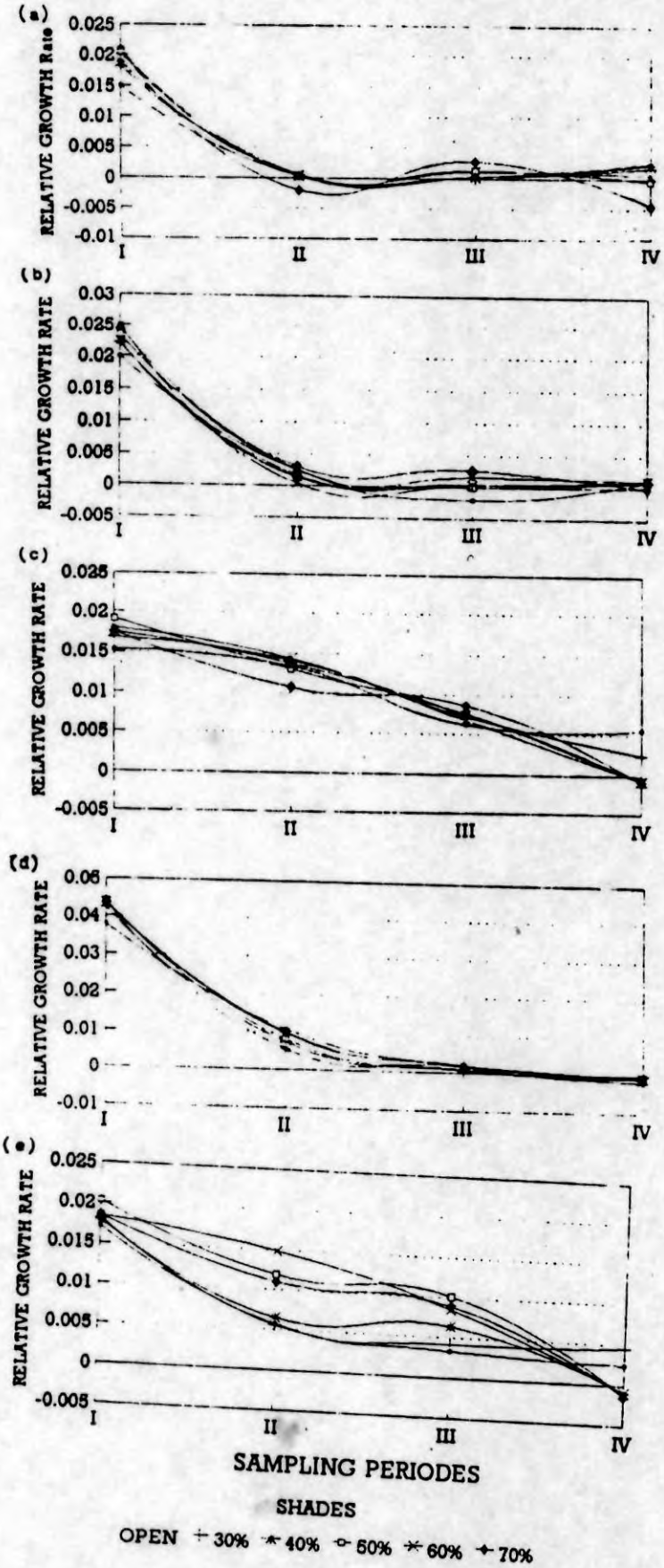


Figure 15. Relative growth rate (g/g/day) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 18 **Net assimilation rate (g cm^{-2} leaf area day^{-1}) in shade treated medicinal plants at different periods of analysis**

a. *Adhatoda beddomei*

Shade treatments	Sampling periods I	II	III	IV
Open	0.0003	3.1 E-06	0.00002	0.00024
30%	0.0003	0.000015	0.000016	0.00012
40%	0.0003	8.3 E-06	0.00001	0.00016
50%	0.0004	0.000012	0.00005	-2E-05
60%	0.0004	0.000012	0.000037	0.00003
70%	0.0004	-6.2 E-05	0.00013	-0.0003
SE±	3E-05	0.000042	0.000062	0.00031
CD(P=0.05)	NS	NS	NS	NS

b. *Adhatoda vasica*

Open	0.0005	0.0002	-0.0002	0.00009
30%	0.0004	4E-05	0.00002	0.00007
40%	0.0004	4E-05	0.00006	0.00007
50%	0.0005	7E-05	5E-06	0.00006
60%	0.0005	1E-05	0.00002	0.00005
70%	0.0005	7E-05	0.00007	-1E-06
SE±	4E-05	4E-05	0.00006	0.00007
CD(P=0.05)	NS	NS	NS	NS

c. *Alpinia galanga*

Open	0.00040	0.00043	0.00029	0.00041 A
30%	0.00042	0.00037	0.00026	0.00012 B
40%	0.00045	0.00036	0.00026	-4E-05 C
50%	0.00051	0.00036	0.00026	-3E-05 C
60%	0.00043	0.00036	0.00022	-3E-05 C
70%	0.00044	0.00025	0.00025	-3E-05 C
SE±	0.00004	5E-06	0.00022	0.00002
CD(P=0.05)	NS	NS	NS	0.00007

d. *Plumbago rosea*

Open	0.0007	0.00028	7E-05	-0.0002
30%	0.0009	0.00019	3E-05	4E-06
40%	0.0008	0.00012	8E-05	-7E-05
50%	0.0007	0.00016	3E-05	-4E-05
60%	0.0007	0.00018	5E-05	-1E-05
70%	0.0006	0.00017	4E-05	-1E-05
SE±	SE-05	0.00005	6E-05	0.00006
CD(P=0.05)	NS	NS	NS	NS

e. *Strobilanthes heyneanus*

Open	0.00040 AB	0.00017	0.00012	0.00016 AB
30%	0.00044 A	0.00016	0.00014	0.00023 A
40%	0.00030 D	0.00012	0.00019	-3E-05 B
50%	0.00037 BC	0.00023	0.00023	-3E-05 B
60%	0.00030 D	0.00023	0.00018	-2E-05 B
70%	0.00032 CD	0.00019	0.00017	-3E-05 B
SE±	0.00002	0.00004	0.00004	0.00007
CD(P=0.05)	0.00006	NS	NS	0.00021

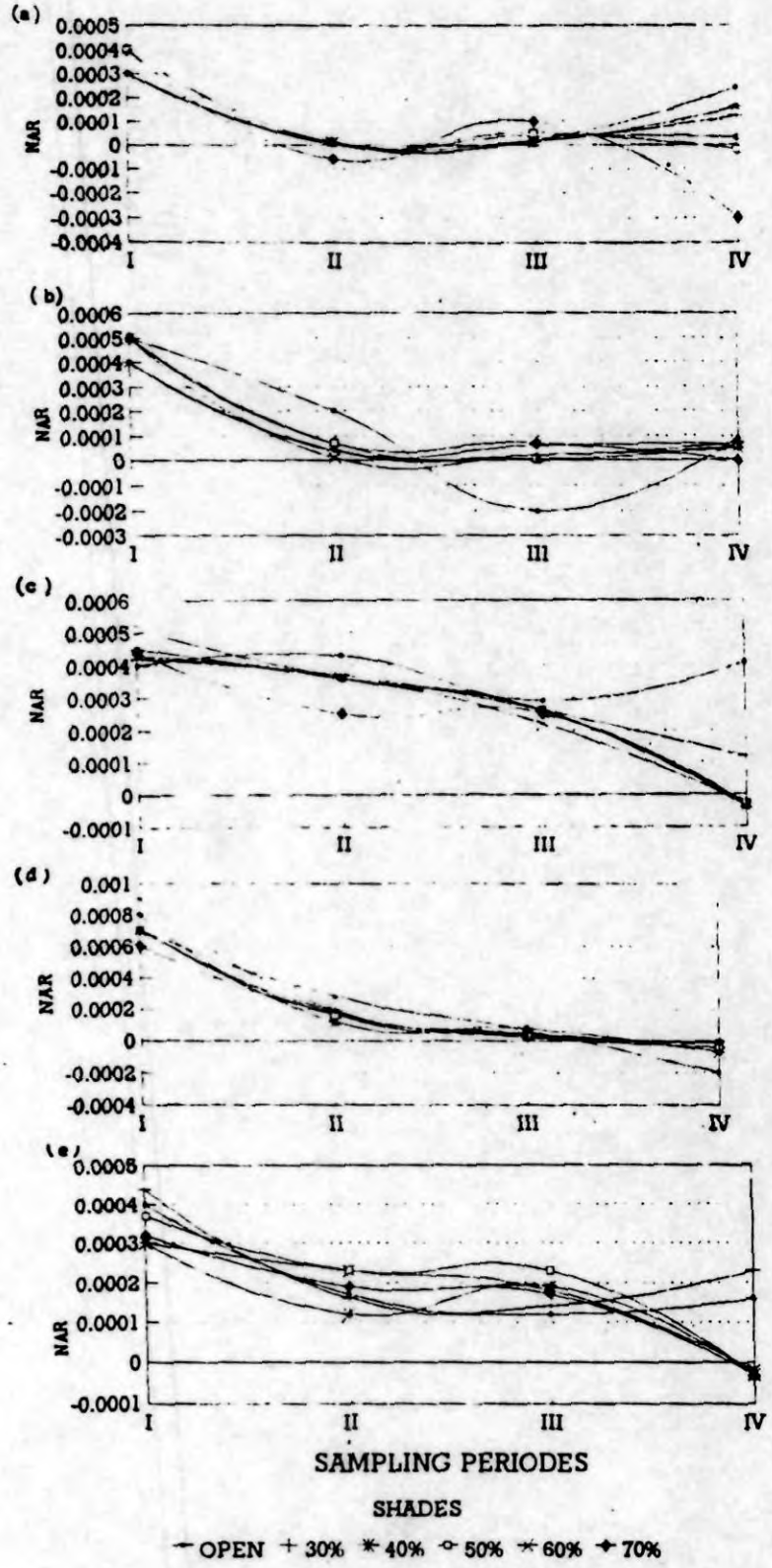


Figure 16. Net assimilation rate (g cm^{-2} leaf area day^{-1}) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 19 **Leaf area ratio in shade treated medicinal plants at different periods of analysis**

	Sampling periods				
	Shade treatments	I	II	III	IV
a. *Adhatoda beddomei*	Open	47.369	25.754 C	15.120	11.376 C
	30%	54.842	33.513 B	19.822	14.877 BC
	40%	57.007	37.531 AB	22.582	15.959 B
	50%	53.106	36.565 AB	24.963	16.961 B
	60%	56.333	41.226 A	28.300	20.409 A
	70%	53.437	36.006 B	22.241	14.536 BC
	SE±	2.14	1.54	3.16	1.15
	CD(P=0.05)	NS	4.58	NS	3.41
b. *Adhatoda vasica*	Open	41.391	24.25 C	18.516 D	15.157 C
	30%	51.250	37.762 B	21.870 D	15.324 C
	40%	51.370	38.617 B	23.988 CD	15.58 C
	50%	49.083	39.18 B	28.414 BC	21.345 B
	60%	54.001	43.179 AB	29.664 B	23.472 B
	70%	53.438	47.279 A	38.111 A	29.667 A
	SE±	3.27	1.96	1.79	1.4
	CD(P=0.05)	NS	5.83	5.33	4.16
c. *Alpinia galanga*	Open	38.7	31.4 C	21.2 D	14.1 C
	30%	41.2	38.2 B	27.5 C	21.5 B
	40%	39.4	38.1 B	29.0 BC	21.2 B
	50%	37.8	35.9 B	28.5 BC	25.4 A
	60%	41.9	39.8 AB	30.8 B	26.6 A
	70%	40.1	42.9 A	34.5 A	27.4 A
	SE±	1.39	1.36	0.93	0.74
	CD(P=0.05)	NS	4.03	2.75	2.19
d. *Plumbago rosea*	Open	56.9	38.8 B	22.2 E	12.3 D
	30%	49.8	39.1 B	26 DE	13.3 CD
	40%	59.6	44.2 B	27.2 D	12.3 D
	50%	64.2	52.9 A	34.8 C	16.3 C
	60%	67.0	55.2 A	40.5 B	22.9 B
	70%	68.4	59.7 A	46.9 A	27.6 A
	SE±	4.41	2.76	1.29	1.06
	CD(P=0.05)	NS	8.2	3.84	3.15
e. *Strobilanthes heyneanus*	Open	42.67 B	32.89 C	27.08 D	20.19 C
	30%	41.41 B	35.69 C	30.82 CD	21.26 C
	40%	61.57 A	50.69 B	34.50 C	29.43 B
	50%	54.51 A	51.34 B	43.01 B	35.56 A
	60%	60.69 A	63.75 A	48.83 AB	36.54 A
	70%	56.89 A	59.29 A	52.43 A	39.59 A
	SE±	2.919	2.549	1.992	1.944
	CD(P=0.05)	8.674	7.573	5.919	5.775

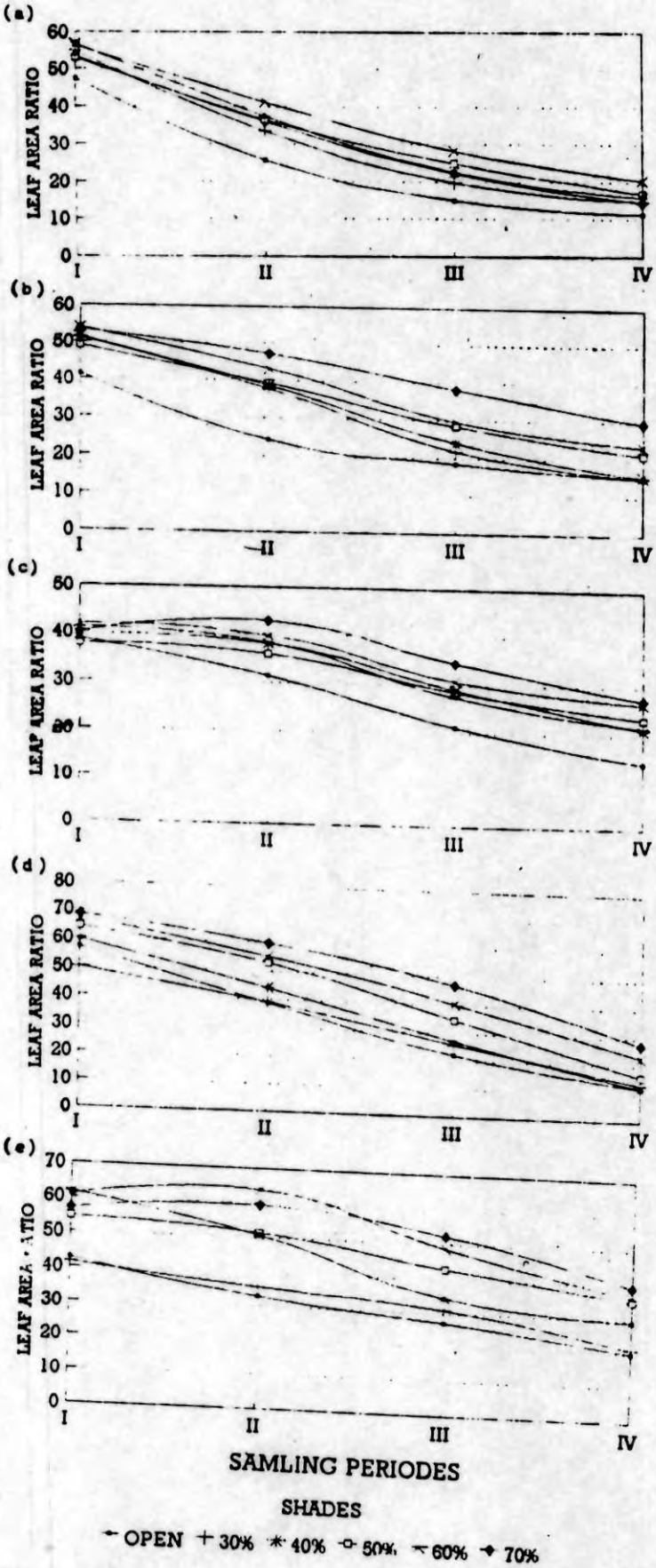


Figure 17. Leaf area ratio in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga* (d) *Plumbago rosea*
(e) *Strobilanthes heyneanus*

Table 20 **Leaf area growth rate (cm^2/day) in shade treated medicinal plants at different periods of analysis**

	Sampling periods			
Shade treatments	I	II	III	
a. *Adhatoda beddomei*				
Open	2.8158 C	-3.941	-4.267	1.6379 A
30%	7.7953 B	-6.942	-5.932	1.6873 A
40%	9.7377 AB	-6.880	-7.635	1.3961 A
50%	10.499 AB	-3.869	-7.936	-1.873 AB
60%	12.522 A	-2.606	-10.31	0.885 A
70%	11.377 AB	-8.779	-6.567	-3.392 B
SE±	1.16	2.65	2	1.24
CD(P=0.05)	3.45	NS	NS	3.69
b. *Adhatoda vasica*				
Open	4.3245 C	-3.201 BC	-1.213 A	-1.166
30%	9.4705 B	-3.797 C	-7.664 B	1.4641
40%	9.5267 B	-2.994 BC	-7.197 B	0.4322
50%	9.9304 B	1.4274 AB	-8.617 B	1.5298
60%	14.137 A	-4.367 C	-8.592 B	2.7417
70%	13.344 A	5.4918 A	-6.61 B	-1.254
SE±	0.95	1.55	1.61	1.32
CD(P=0.05)	2.82	4.6	4.77	NS
c. *Alpinia galanga*				
Open	6.14 B	4.9 B	0.13	-1.2
30%	8.11 AB	12.2 A	0.60	2.2
40%	8.19 AB	14.9 A	1.27	-0.1
50%	8.95 A	15.3 A	4.04	-2.5
60%	9.60 A	15.4 A	3.55	-1.8
70%	8.42 A	15.4 A	2.51	-1.8
SE±	0.68	1.96	1.93	1.34
CD(P=0.05)	2.02	5.83	NS	NS
d. *Plumbago rosea*				
Open	12.9 C	5.31 C	-12	-4.6 C
30%	15.8 C	13.00 BC	-19	-6.6 C
40%	24.0 B	9.17 ABC	-16	1.99 B
50%	27.8 AB	15.80 BC	-26	2.94 AB
60%	27.9 AB	20.80 AB	-16	4.43 AB
70%	30.0 A	28.60 A	-16	5.21 A
SE±	1.59	4.21	5.1	0.93
CD(P=0.05)	4.73	12.5	NS	2.76
e. *Strobilanthes heyneanus*				
Open	13.99 B	6.539 C	-0.5 C	-5.83
30%	15.04 B	17.18 C	-4.39 C	-3.35
40%	34.19 A	-5.80 C	4.728 BC	-3.71
50%	36.19 A	54.60 B	49.45 A	-7.98
60%	34.90 A	89.84 A	1.604 C	-6.2
70%	31.60 A	59.97 AB	35.96 AB	-2.56
SE±	3.89	10.91	10.91	4.89
CD(P=0.05)	11.55	32.41	32.41	NS

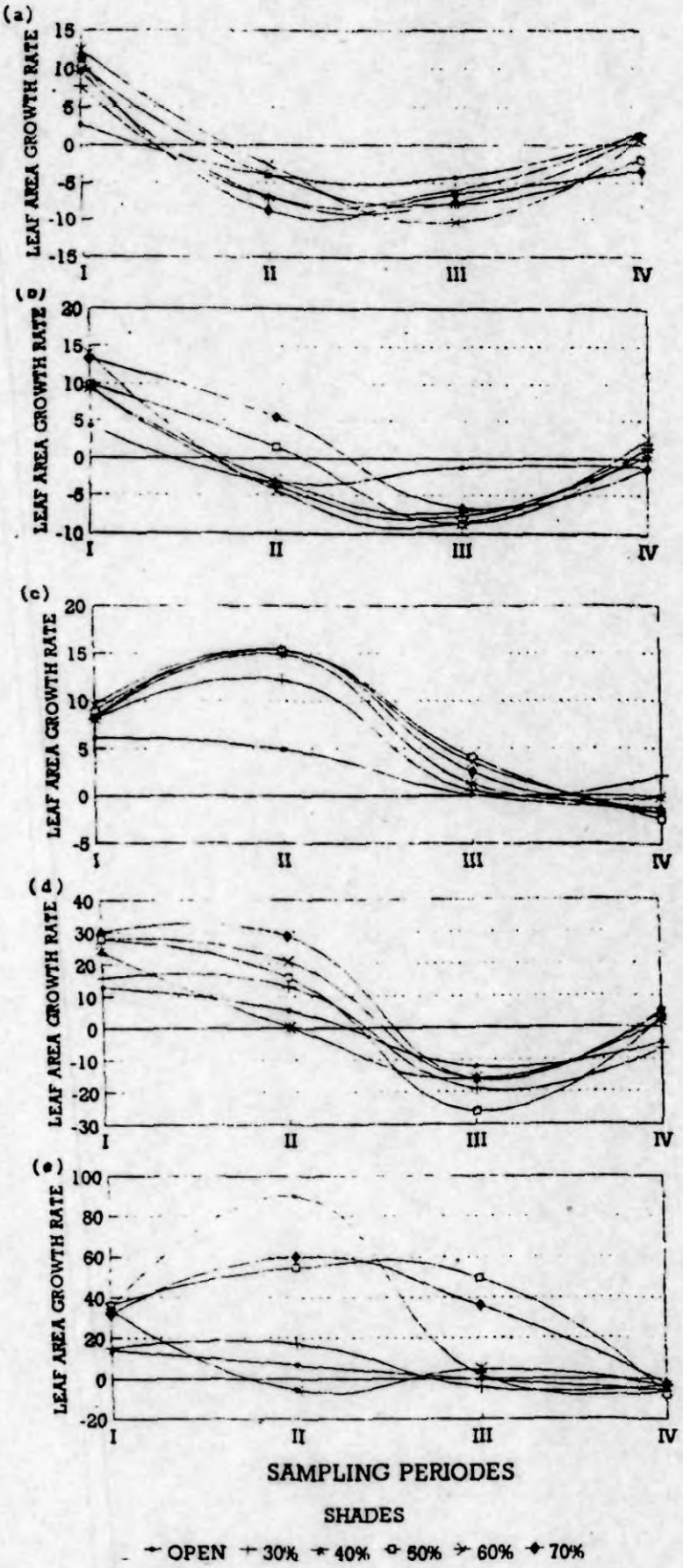


Figure 18. Leaf area growth rate (cm^2/day) in shade treated medicinal plants at different periods of analysis

(a) *Adhatoda beddomei* (b) *Adhatoda vasica*

(c) *Alpinia galanga* (d) *Plumbago rosea*

(e) *Strobilanthes heyneanus*

Table 21 **Leaf area duration in shade treated medicinal plants**

Shade treatments	Species				
	Adhatoda beddomei	*Adhatoda vasica*	*Alpinia galanga*	*Plumbago rosea*	*Strobilanthes heyneanus*
Open	146036 E	116589 E	214607.77 B	250771 A	505100 A
30%	200462 D	184796 D	328342.17 A	333076 A	600413 A
40%	230495 C	193616 D	-319488.83 C	49257.4 B	-662660 B
50%	263932 B	233835 C	-488243.32 E	39485.3 B	-2E+06 C
60%	308074 A	273497 B	-456632.78 E	-131625 C	-2E+06 C
70%	244922 BC	345978 A	-427516.78 D	-208165 C	-2E+06 C
SE±	6799.3	8363.7	3614.69	38621.9	151889
CD(P=0.05)	20203	24851	10740.21	114756	451301

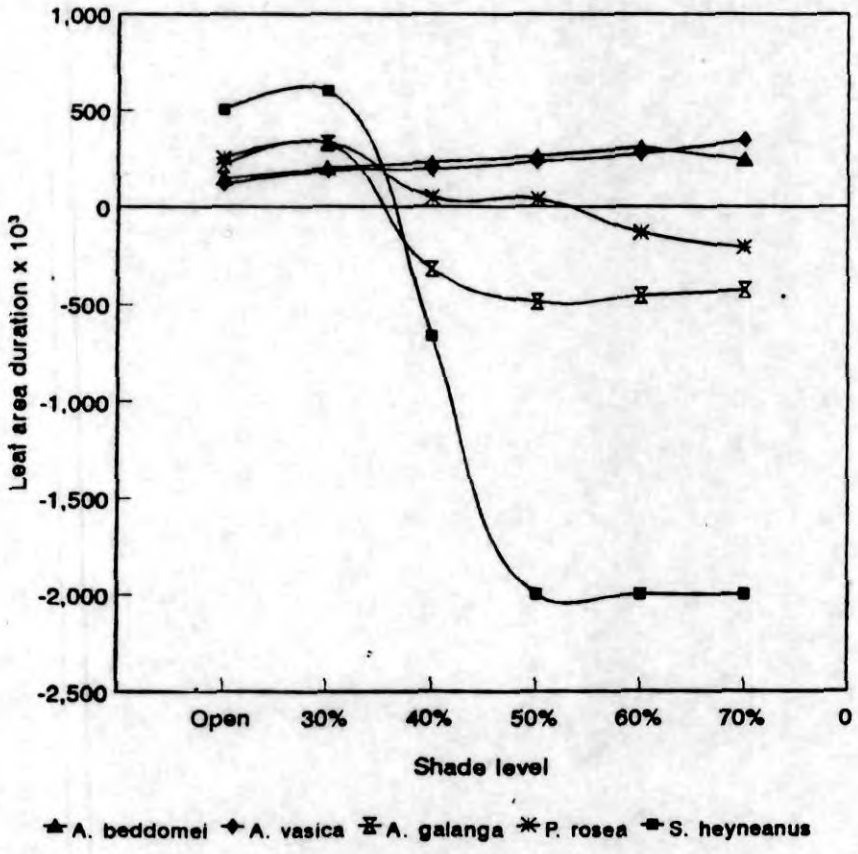


Figure 19. Leaf area duration in shade treated medicinal plants

4.2 Impact of Shade on Foliar Anatomy

Leaves of *Adhatoda beddomei, Adhatoda vasica, Plumbago rosea* and *Strobilanthes heyneanus* were dorsiventral whereas the leaves of *Alpinia galanga* were isobilateral. The internal leaf structure was organised into three different zones, viz. epidermis, mesophyll and vascular tissues. The general leaf anatomy and the effect of shade on the anatomical features in all the species under open sunlight and shade (70%) are described below.

i) *Adhatoda beddomei*

The epidermal cells were found to be polygonal in shape, interrupted by stomata and hairs. Leaves are amphistomatic.

The leaves of plants grown under 70% shade showed a decrease in the frequency of stomata per unit leaf area as compared to the leaves of open grown plants. In transection, leaves grown under direct light had three to four layered compactly arranged palisade (Plate V.1) whereas in shade leaves only 2-3 layers could be observed (Plate V.2). Intercellular spaces of spongy cells were also reduced under shade. However, the proportion of total leaf thickness occupied by the palisade zone alone in both open and shade leaves were found to be the same, i.e., 42%. Similarly the spongy layer occupies 38 and 37% respectively in both the treatments.

ii) *Adhatoda vasica*

The lower epidermis consisted of elongated cells interrupted by stomata, hairs and multicellular glands. The leaves were amphistomatic.

Stomatal intensity per unit leaf area in the shade leaves showed a decrease over that of open leaves. Transection of plants grown in open showed two to three

rows of compactly arranged palisade cells and loosely arranged spongy cells (Plate V.3). Vascular bundles had selerenchymatous bundle sheath extensions. The shade leaves also had a two to three layered palisade (Plate V.4), but the cell size was reduced. The palisade parenchyma occupied 44 and 45% of the total leaf thickness of shade and open leaves respectively. Likewise, the spongy mesophyll cells constituted 33 and 46% respectively of shade and open leaves.

iii) ***Alpinia galanga***

Leaves grown under full sunlight had a single layered epidermis except for certain regions where there was an additional row of cells (Plate V.5). In shade leaves, the epidermis was consistently two layered (Plate V.6). The outermost cells were rectangular, while the inner cells were polygonal or oval in shape. Palisade was one to two layered with abundant chloroplast. The spongy cells were irregular in shape with intercellular spaces. Vascular bundles have a bundle sheath with sclerenchymatous extensions reaching upto the lower and upper epidermis. Bundle sheath extension was more developed in open leaves. The large sized epidermal cells contributed to the major portion of the total leaf thickness occupying 41 and 47% respectively whereas the palisade zone occupied 28 and 17% respectively for the open and shade leaves.

iv) ***Plumbago rosea***

The epidermal cells were oval in shade and were compactly arranged. Leaves were amphistomatic and the stomatal density per unit leaf area in the shade leaves showed a decrease over that of the open leaves.

Transection showed two rows of compactly arranged elongated palisade cells, of which the upper layer was more or less uniform and regular (Plate V.7).

Plate V. Transection of open and shade leaves x 125

(1) & (2) *Adhatoda beddomei* - Open and 70%

(3) & (4) *Adhatoda vasica* - Open and 70%

(5) & (6) *Alpinia galanga* - Open and 70%

(7) & (8) *Plumbago rosea* - Open and 70%

(9) & (10) *Strobilanthes heyneanus* - Open and 70%

Spongy zone was four to seven layered with intercellular spaces. Both palisade and spongy cells possessed chlorophyll but its colouration was more deep in the upper zone. Many of the ground tissue possessed tannin (Plate V.7). Vascular bundles were conjoint, collateral and ensheathed by a parenchymatous sheath. In shade leaves the palisade zone consisted of a single layer of cells, but in certain regions, an additional layer of small cells was present (Plate V.8). Similarly, in spongy layer also the number of cell layers was reduced with less intercellular spaces. In open leaves, out of the total leaf thickness, 35.6% was occupied by palisade cells, while in shade leaves it was 30.8%. Similarly the spongy layer in open and shade leaves was 52.5% and 43.3% respectively

v) ***Strobilanthes heyneanus***

A distinguishing feature of the shade plants of this species was the appearance of wavy cell margins in the epidermis, whereas in the open grown plants the cells were polygonal. In T. S two rows of long, uniform and regular palisade cells were present in open condition. Spongy mesophyll cells were irregular in shape (Plate V.9). However, in shade leaves usually a single layered palisade was present except for certain regions where an additional layer of small cells were found (Plate V.10). The spongy mesophyll layer of shade leaves showed fewer cells than leaves under the open condition. The palisade parenchyma alone contributed to 47 and 40% in open as well as shade plants respectively whereas in the case of spongy mesophyll, the respective figures were 29 and 34%.

The actual measurements of thickness of various compartments obtained for the different species under study are summarised in Table 22.

Table 22 **Foliar anatomy of open and shade (70%) plants**

Species	Treatment	Thickness in μm			
		Epidermis	Palisade parenchyma	Spongy mesophyll	Total
Adhatoda beddomei	Open	50	105*	95*	250*
	70% shade	45	90	80	215
Adhatoda vasica	Open	25*	100	105*	230*
	70% shade	45	95	70	210
Alpinia galanga	Open	95	65*	70*	230
	70% shade	110	40	85	235
Plumbago rosea	Open	35*	105*	155*	295*
	70% shade	55	60	85	200
Strobilanthes heyneanus	Open	55	105*	65	225*
	70% shade	45	70	60	175

* Significantly superior as revealed by t-test

It was observed that the thickness of palisade as well as spongy mesophyll cells showed a decline in the plants which were grown under 70% shade as compared to the open plants for all the species. Correspondingly, the total leaf thickness of the different species also decreased in the shade plants, except in the case of *Alpinia galanga*. In general, the expression of shade adaptation with respect to cellular dimensions varied considerably within the different species studied. For instance, in the case of *Alpinia galanga*, the epidermis in the shade plants was consistently two layered whereas in *Adhatoda beddomei* the shade plants were characterised by a reducation in the number of palisade layers, indicating also a reduction in their cell number. Similar reduction in palisade and spongy cells in shade plants was also exhibited by *Plumbago rosea* and *Strobilanthes heyneanus*

4.3 Impact of Shade on Photosynthesis and Other Related Parameters

4.3.1 Photosynthesis

4.3.1.1 Diurnal changes in photosynthetic characteristics

Diurnal course of photosynthetic rate and other related characteristics was recorded in all the five species *Adhatoda beddomei, Adhatoda vasica, Alpinia galanga, Plumbago rosea* and *Strobilanthes heyneanus* grown under open sunlight and 70% shade. The results are described below.

The diurnal variation in meteorological variables in the open and under shaded conditions is presented in Figure 20. It is observed that solar radiation, leaf temperature and vapour pressure deficit (VPD) increases upto mid-day and declined thereafter but the relative humidity (RH) followed the reverse trend. The environmental conditions under shade showed similar trend as under open sunlight but the values were lower except for RH.

The diurnal changes of Pn and other characteristics as recorded in the species studied under the open condition and under shade (Figure 21, 22 and 23) are as follows.

Adhatoda beddomei

Under normal sunlight peak photosynthetic rate (Pn) observed was 17.9μ mol CO_2 $m^{-2}s^{-1}$ at 10.0 h. whereas it was 7.9μ mol $m^{-2}s^{-1}$ at 11.0 h under shade condition. Similarly maximum conductance (Cs) under open condition was 0.64 mol m^{-2} s^{-1} recorded at 11.0 h and in the plants subjected to shade it was 0.61 mol $m^{-2}s^{-1}$. Maximum transpiration (E) was 26.5 and 20.6μ mol m^{-2} s^{-1} respectively.

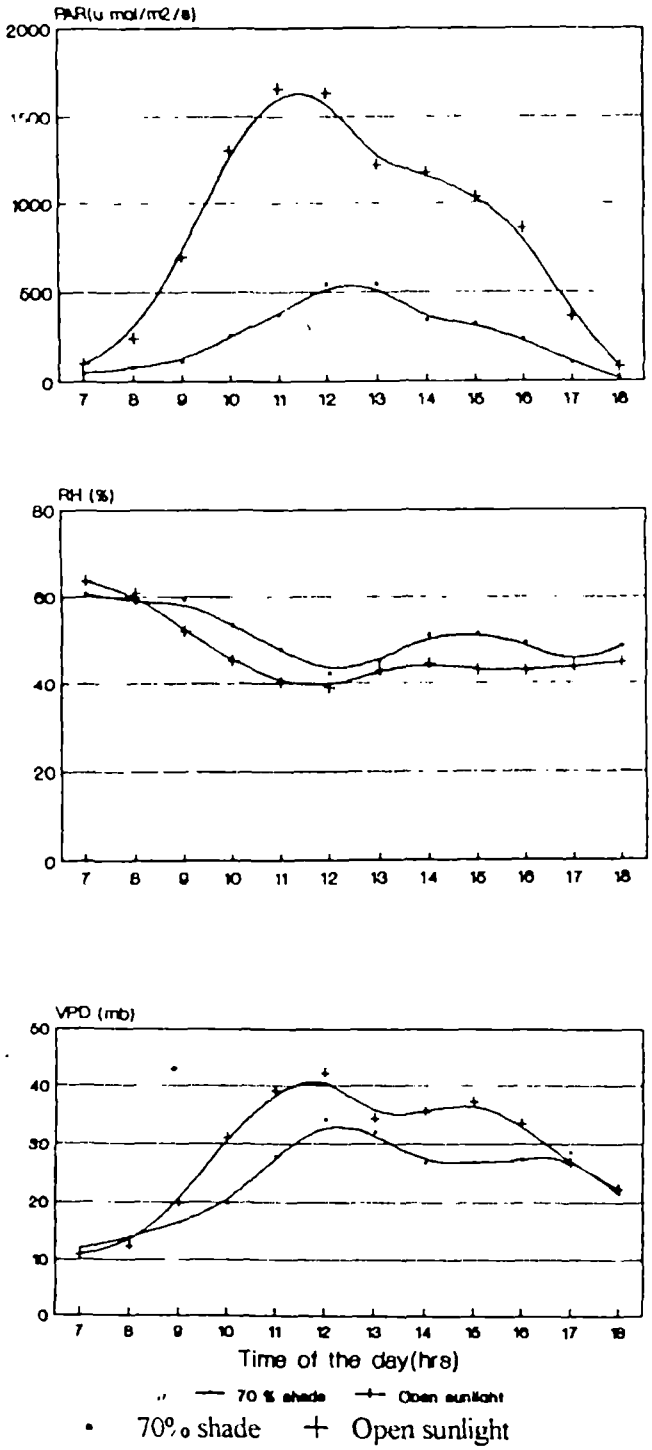


Figure 20. Diurnal variation in meteorological variables in medicinal plants grown under open sunlight and 70% shade

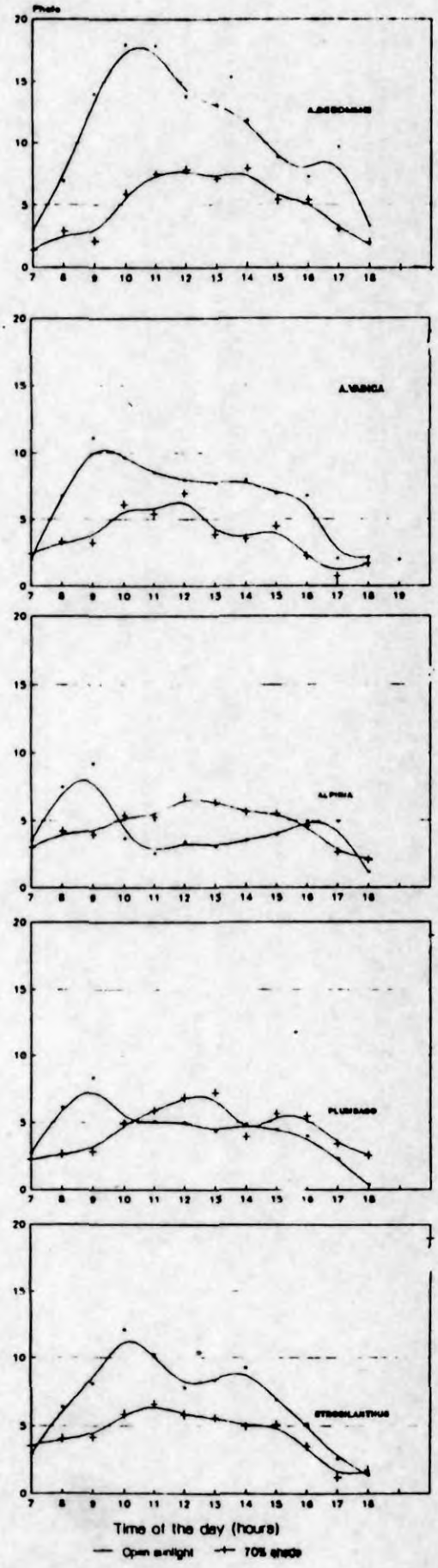


Figure 21. Diurnal variation in photosynthetic rate (μmol/m^2/s) under open sunlight and 70% shade in five species of medicinal plants

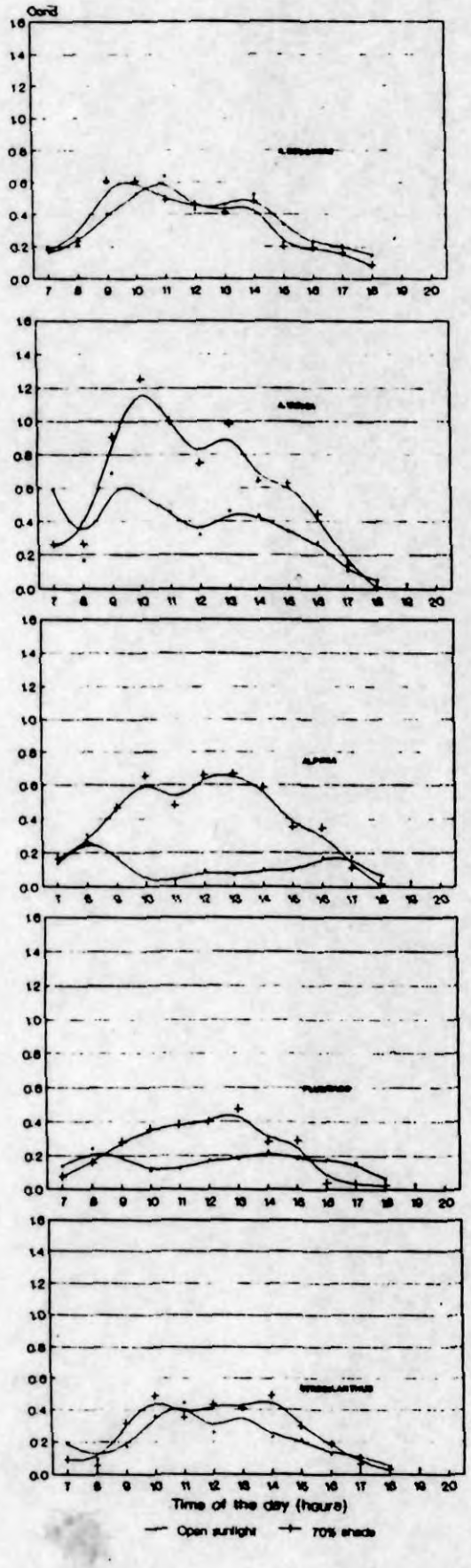


Figure 22. Diurnal variation in conductance (mol/m^2/s) under open sunlight and 70% shade in five species of medicinal plants

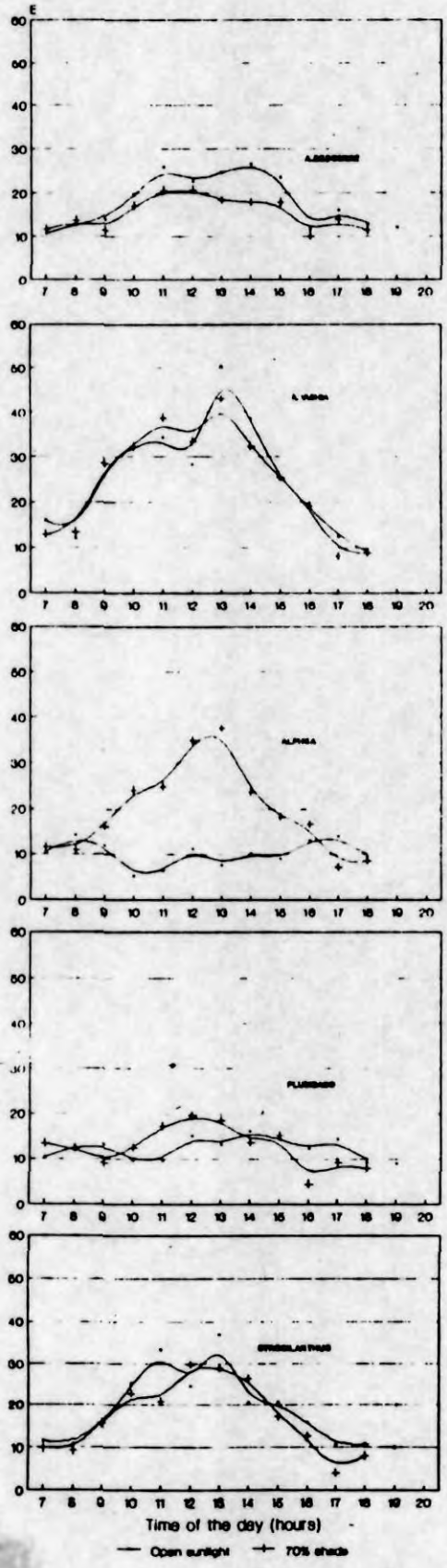


Figure 23. Diurnal variation in transpiration (μmol/m^2/s) under open sunlight and 70% shade in five species of medicinal plants

Adhatoda vasica

Peak photosynthesis was recorded at 9 h and 12 h, for the open and shade grown plants. Pn was 11.14μ mol $m^{-2}s^{-1}$ in the former and 6.96μ mol m^{-2} s^{-1} in the latter. As regards stomatal conductance the measurements were 0.691 and 0.998 respectively and maximum conductance observed under shade was at 11.0 h. Under open sunlight maximum transpiration rate was 50.37 whereas it was 42.96 for the shade plants, both observed at 13 h.

Alpinia galanga

The maximum photosynthetic rate recorded under shade was 6.8μ mol CO_2m^{-2} s^{-1} at 12 h. In open condition, this was 9.2μ mol m^{-2} s^{-1} at 9 h. Stomatal conductance was maximum at 13 h in shade plants and recorded 0.67 as against 0.31 in open conditions. Transpiration rate for both the treatments was 37.64 and 14.18 respectively, thus showing maximum E under shade.

Plumbago rosea

The peak photosynthetic rate for *Plumbago rosea* was found to be 8.37μ mol $m^{-2}s^{-1}$ and was observed at 9 h under open. The maximum Pn under shade condition was however 7.25. Maximum stomatal conductance was recorded under shade (0.47) than under light (0.24). So also, transpiration showed a high of 19.43 in the shaded plants.

Strobilanthes heyneanus

Strobilanthes heyneanus showed a peak Pn (12.07μ mol $m^{-2}s^{-1}$) at 10 h under open conditions and it was 6.61 under shade. Here also, the maximum

conductance (0.44) observed in the control plants was at 11 h whereas it showed a peak of 0.49 in the shade plants at 10 h. Transpiration rate was maximum (36.91) in the former, in comparison to 29.73 in latter.

Under normal sunlight, the peak Pn was observed at 09.00 h for *Adhatoda vasica*, *Alpinia galanga* and *Plumbago rosea* while for *Adhatoda beddomei* and *Strobilanthes heyneanus* it was at 10.0 h. Under shade conditions peak Pn was observed for all the species at 10.00 or 1.00 h and continued for 3 to 4 hours. Lowest Pn was recorded for all the species either in the morning (07.00 h) or in the afternoon (18.00 h).

Maximum Pn under shade was lower than in open sunlight irrespective of species. Between species, the highest rate (7.8μ mol CO_2 $m^{-2}s^{-1}$) was recorded for *Adhatoda beddomei* and the lowest rate (6.6μ mol CO_2 $m^{-2}s^{-1}$) for *Strobilanthes heyneanus* under shade. Maximum Cs value was recorded under shade than under light in all species except *Adhatoda beddomei*. Among the species, *Adhatoda vasica* showed the highest value both under light (0.69) and shade (1.25). Transpiration rate (E) showed a similar trend like Pn and Cs in all the species (Figure 4). Among the species, *Adhatoda vasica* showed the highest E both under light (50.3 m mole $m^{-2}s^{-1}$) and shade (42.9).

4.3.1.2 Maximum photosynthetic rate

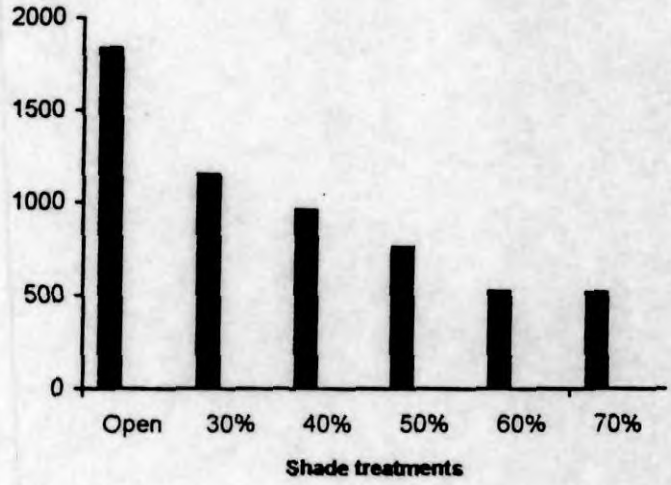
Maximum photosynthetic rate (μmol $m^{-2}s^{-1}$) of the five shade adapted medicinal plants *Adhatoda beddomei*, *Adhatoda vasica*, *Alpinia galanga*, *Plumbago rosea* and *Strobilanthes heyneanus* at different light intensities (open, 30%, 40%, 50%, 60% and 70% shade) in the month of February under clear sky

condition is given in the Table 24 (Figure 24) and the PAR received in different treatments, at the time of photosynthesis measurements is given in Table 23.

Table 23 **Photosynthetically active radiation (PAR) recorded in different treatments in the month of February under clear sky condition**

	Shade treatments					
	Open	30%	40%	50%	60%	70%
PAR	1836*	1152*	959*	764*	525	516

SE± 22
CD 6945
(P=0.05)



From diurnal variation, it is observed that maximum photosynthetic rate is at different time in different treatments. Hence the P_{max} is recorded at different time in different treatments.

Adhatoda beddomei

Maximum photosynthetic rate of 17.91 µmol $m^{-2}s^{-1}$ was recorded under the open condition. All levels of shade inhibited the maximum rate of photosynthesis. Among the shade treatments, the maximum photosynthetic rate observed under 30% shade was significantly superior to that of all other shade levels. The maximum photosynthetic rate under 40% is significantly superior to those under 70% shade. There was no significant difference between the maximum photosynthetic rate under 50, 60 and 70% shade levels.

Table 24 **Maximum photosynthetic rate (µmol/m²/s) in different treatments in the month of February under clear sky condition**

Shade treatment	Species				
	A. beddomei	*A. vasica*	*A. galanga*	*P. rosea*	*S. heyneanus*
Open	17.91*	11.14*	9.23	8.37	12.07*
30%	10.94*	9.71*	10.61*	9.52*	11.14*
40%	9.37*	7.68	9.98*	8.36	10.90*
50%	8.84	7.57	9.58*	7.43	7.32
60%	8.38	7.05	7.70	7.35	7.03
70%	7.81	6.96	6.80	7.25	6.61
SE±	0.41	0.38	0.42	0.49	0.46
CD (P=0.05)	1.28	1.18	1.28	1.51	1.43

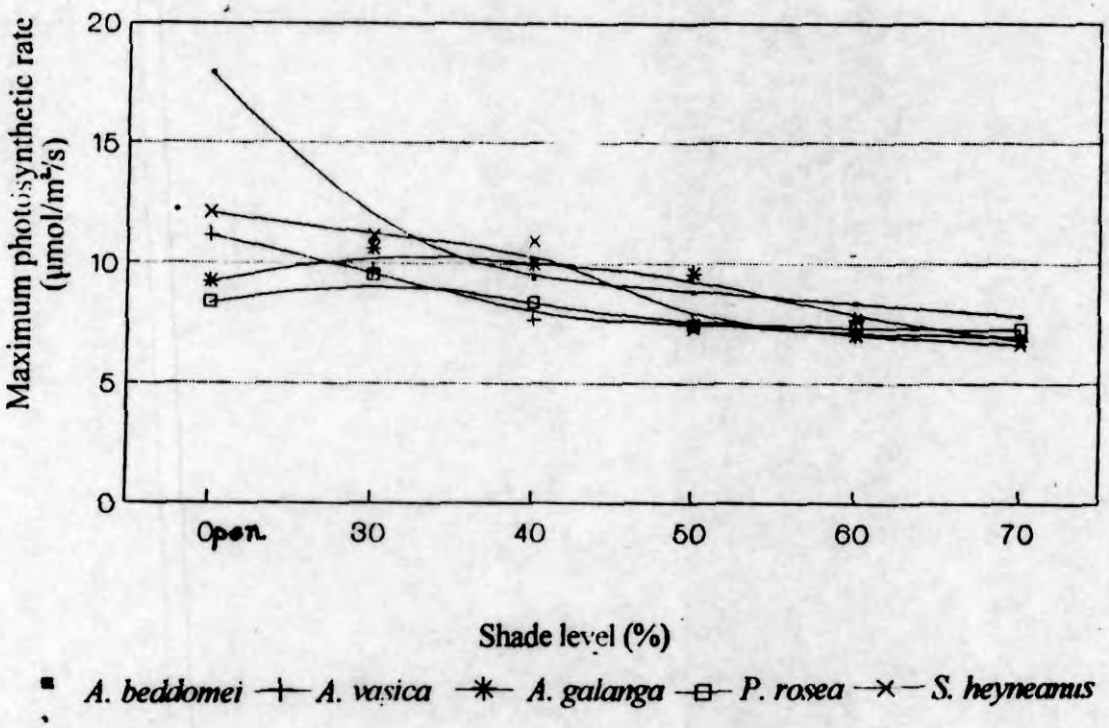


Figure 24. Maximum photosynthetic rate (µmol/m²/s) in different treatments in the month of February under clear sky conditions

Adhatoda vasica

The maximum photosynthetic rate did not vary significantly among treatments of 40, 50, 60 and 70% shade. The rate was significantly higher under 3% shade compared to other shade treatments. The maximum photosynthetic rate under open sunlight was higher than that of all shade treatments.

Alpinia galanga

The maximum photosynthetic rate of 10.61μ mol $m^{-2}s^{-1}$ was observed under 30% shade level and this treatment was significantly superior to that of the open sunlight. A decrease in maximum photosynthetic rate was observed with progressive increase in shade. Shade levels upto 50% was significantly superior to 60 and 70%.

Plumbago rosea

As in the previous case, the optimum shade treatment was found to be 30% which also exhibited the highest maximum photosynthetic rate. Open sunlight is slightly injurious and so also shade above 40% was found to be inhibitory.

Strobilanthes heyneanus

A tolerance of upto 40% shade was observed for this species. There was no significant difference in maximum photosynthetic rate between open, 30 and 40% shade. The maximum photosynthetic rates at higher shade levels are also in par among themselves.

On the whole, 30% shade treatment was found to be optimum in the case of *Alpinia galanga* and *Plumbago rosea* while open sunlight was optimum in the case

of *Adhatoda beddomei* and *Adhatoda vasica*. *Strobilanthes heyneanus* tolerates upto 40% shade. Open condition was slightly injurious in the case of *Plumbago rosea*. The higher levels of 50 to 70% shade was inhibitory for all the species.

4.3.2 Photosynthetic pigments

4.3.2.1 Chlorophyll contents

The effect of shade on chlorophyll contents, in all the five species of medicinal plants; *Adhatoda beddomei*, *Adhatoda vasica*, *Alpinia galanga*, *Plumbago rosea* and *Strobilanthes heyneanus* at different light intensities (open, 30%, 40%, 50%, 60% and 70% shade) was studied by measuring the following parameters: total chlorophyll, chlorophyll *a*, chlorophyll *b* and chlorophyll *a b* ratio.

Adhatoda beddomei

The chlorophyll content was significantly high in plants grown under 50%, 60% and 70% shade levels as compared to those under open condition in all phases of growth except the third sampling, corresponding to the 301st day of growth. Chlorophyll *a* is significantly high in plants grown under 40%, 50%, 60% and 70% shade compared to the plants under open sunlight in all sampling periods except during the third sampling period. Chlorophyll *b* is significantly higher under 60% and 70% shade compared to the chlorophyll *b* content under full sunlight in all sampling periods except during the third sampling period. Chlorophyll *a b* ratio is significantly low in 60% and 70% shade levels compared to the *a/b* ratio under open condition in the final phase of growth (Table 25, Figure 25).

Table 25 **Chlorophyll contents (mg/g dry weight) in shade treated *Adhatoda beddomei* at different periods of analysis**

Total chlorophyll

	Sampling period			
	I	II	III	IV
Open	1.13	1.50	2.67	2.45
30%	2.26	1.97	3.02	3.25
40%	2.71	2.66	3.04	3.89
50%	2.84	2.51	3.66	4.10
60%	2.77	4.04	3.64	4.44
70%	4.04	4.64	4.98	6.37
SE ±	0.33	0.29	0.46	0.56
CD(P=0.05)	0.97	0.86	1.38	1.65

Chlorophyll a

	Sampling period			
	I	II	III	IV
Open	0.70	1.02	1.96	1.82
30%	1.32	1.33	2.24	2.40
40%	1.80	1.87	2.32	2.82
50%	1.73	1.94	2.78	2.52
60%	1.79	2.86	2.82	3.11
70%	2.70	3.22	3.70	4.51
SE ±	0.23	0.20	0.35	0.33
CD(P=0.05)	0.67	0.60	1.05	0.98

Clorophyll b

	Sampling period			
	I	II	III	IV
Open	0.43	1.02	0.71	0.64
30%	0.94	1.33	0.78	0.85
40%	0.90	1.87	0.73	1.01
50%	1.12	1.94	0.88	1.08
60%	0.98	2.86	0.82	1.33
70%	1.34	3.22	1.28	1.87
SE ±	0.13	0.20	0.11	0.16
CD(P=0.05)	0.39	0.60	0.33	0.46

Chlorophyll a/b

	Sampling period			
	I	II	III	IV
Open	1.61	2.13	2.75	2.84
30%	1.54	2.18	2.81	2.84
40%	2.01	2.35	3.20	2.65
50%	1.55	2.35	3.22	2.80
60%	1.86	2.42	3.39	2.36
70%	2.01	2.26	2.89	2.42
SE ±	0.16	0.10	0.09	0.07
CD(P=0.05)	0.46	0.29	0.28	0.22

Adhatoda vasica

Total chlorophyll content, chlorophyll *a* and chlorophyll *b* in 70% shade are significantly high as compared to those of plants grown under open conditions on all the sampling periods. On the fourth sampling, corresponding to 364th day of growth, total chlorophyll content and chlorophyll *a* are significantly higher under 50%, 60% and 70% shade compared to that under full sunlight. Chlorophyll *a/b* is significantly higher under 70% shade compared to the plants grown under open condition in all growth phases (Table 26, Figure 26).

Table 26 **Chlorophyll contents (mg/g dry weight) in shade treated *Adhatoda vasica* at different periods of analysis**

Total chlorophyll

	Sampling period			
	I	II	III	IV
Open	1.57	1.88	2.70	1.57
30%	1.61	1.78	2.99	2.86
40%	1.89	2.14	3.20	2.88
50%	2.40	2.22	3.17	4.18
60%	2.87	3.05	3.08	5.82
70%	3.93	3.88	5.07	6.19
SE ±	0.40	0.34	0.24	0.45
CD(P=0.05)	1.20	1.00	0.71	1.34

Chlorophyll a

	Sampling period			
	I	II	III	IV
Open	1.02	1.25	2.23	1.16
30%	1.10	1.42	2.29	2.12
40%	1.26	1.37	2.39	2.14
50%	1.63	1.50	2.40	3.06
60%	2.00	1.96	2.34	4.23
70%	2.70	2.57	3.71	4.30
SE ±	0.27	0.24	0.23	0.33
CD(P=0.05)	0.81	0.72	0.68	0.98

Clorophyll b

	Sampling period			
	I	II	III	IV
Open	0.55	0.63	0.73	0.41
30%	0.51	0.61	0.71	0.75
40%	0.63	0.74	0.81	0.72
50%	0.77	0.72	0.77	1.12
60%	0.88	1.09	0.74	1.69
70%	1.23	1.32	1.37	1.89
SE	0.13	0.11	0.06	0.13
CD(P=0.05)	0.40	0.34	0.18	0.38

Chlorophyll a/b

	Sampling period			
	I	II	III	IV
Open	1.77	2.03	2.70	2.79
30%	2.13	1.94	3 25	2.86
40%	2.03	1.82	2.95	2.92
50%	2.13	2.18	3.15	2.74
60%	2.29	1.79	3.18	2.66
70%	2.25	1.93	2.71	2.27
SE±	0.15	0.09	0.11	0.06
CD(P=0.05)	0.44	0.28	0.32	0.17

Alpinia galanga

Total chlorophyll content and chlorophyll *a* were significantly high in 50%, 60% and 70% shade grown plants compared to open grown plants in all sampling periods except the first sampling period corresponding to the 182nd day of growth. Chlorophyll *b* is significantly higher under 60% and 70% shade compared to that under full sunlight in all sampling periods. Chlorophyll *a*/*b* ratio at various shade levels is on par with that of open grown plants (Table 27, Figure 27).

Table 27 **Chlorophyll contents (mg/g dry weight) in shade treated *Alpinia galanga* at different periods of analysis**

Total chlorophyll

	Sampling period			
	I	II	III	IV
Open	1.94	2.28	2.48	2.56
30%	2.10	2.64	2.79	2.59
40%	2.79	3.12	3.75	3.80
50%	2.91	5.07	4.77	4.80
60%	3.06	5.72	6.96	8.36
70%	3.43	5.87	7.92	8.33
SE ±	0.44	0.67	0.75	0.50
CD(P=0.05)	1.29	2.00	2.24	1.48

Chlorophyll a

	Sampling period			
	I	II	III	IV
Open	1.41	1.48	1.77	1.82
30%	1.52	1.78	1.97	1.82
40%	1.86	2.10	2.68	2.73
50%	2.18	3.28	3.48	3.40
60%	2.21	3.73	4.84	5.93
70%	2.35	3.67	5.48	5.96
SE ±	0.34	0.45	0.53	0.34
CD(P=0.05)	1.02	1.33	1.59	1.02

Clorophyll b

	Sampling period			
	I	II	III	IV
Open	0.54	0.80	0.71	0.74
30%	0.58	0.86	0.82	0.77
40%	0.93	1.03	1.07	1.07
50%	0.73	1.79	1.29	1.40
60%	0.85	1.99	2.12	2.45
70%	1.09	2.20	2.44	2.36
SE ±	0.11	0.24	0.22	0.16
CD(P=0.05)	0.31	0.70	0.66	0.48

Chlorophyll a/b

	Sampling period			
	I	II	III	IV
Open	2.60	1.80	2.47	2.46
30%	2.60	2.06	2.40	2.33
40%	2.00	1.87	2.50	2.57
50%	2.84	1.82	3.04	2.43
60%	2.86	1.91	2.26	2.47
70%	2.08	1.70	2.24	2.52
SE ±	0.27	0.13	0.18	0.09
CD(P=0.05)	0.81	0.38	0.55	0.27

Plumbago rosea

Total chlorophyll and chlorophyll *a* were significantly high under 60% and 70% shade as compared to those under full sunlight at different phases of growth whereas, chlorophyll *b* was significantly high under 60% and 70% shades as compared to that of open condition in all sampling periods except the first sampling period corresponding to the 182nd day of growth. Chlorophyll *a/b* ratio was significantly low in 30%, 40%, 60% and 70% shade as compared to this ratio under open condition in the 301st day of growth (Table 28, Figure 28).

Table 28 **Chlorophyll contents (mg/g dry weight) in shade treated *Plumbago rosea* at different periods of analysis**

Total chlorophyll

	Sampling period			
	I	II	III	IV
Open	1.35	1.39	2.06	1.95
30%	1.87	1.74	2.31	2.05
40%	2.02	2.29	2.36	3.26
50%	2.33	2.97	2.39	5.43
60%	2.91	3.25	4 81	6.23
70%	3.53	4.14	4.83	7.08
SE ±	0.42	0.35	0.49	0.90
CD(P=0.05)	1.24	1.03	1.46	2.67

Chlorophyll a

	Sampling period			
	I	II	III	IV
Open	0.87	0.82	1.50	1.34
30%	1.31	1.09	1.63	1.45
40%	1.39	1.51	1.66	2.27
50%	1.58	1.97	1.75	3.97
60%	2.19	2.14	3.28	4.45
70%	2.47	2.68	3.30	4.98
SE ±	0.31	0.25	0.36	0.64
CD(P=0.05)	0.93	0.73	1.06	1.91

Clorophyll b

	Sampling period			
	I	II	III	IV
Open	0.48	0.57	0.55	0.61
30%	0.57	0.64	0 68	0.60
40%	0.63	0.79	0.70	0.99
50%	0.75	1.00	0.64	1.47
60%	0.72	1.11	1.53	1.78
70%	1.06	1.45	1.53	2.11
SE ±	0.11	0.11	0.14	0.26
CD(P=0.05)	0.32	0.33	0.40	0.76

Chlorophyll a/b

	Sampling period			
	I	II	III	IV
Open	1.76	1.38	2.80	2.08
30%	2.32	1.67	2.41	2.43
40%	2.23	1.88	1.95	2.24
50%	2.15	1.97	2.74	2.84
60%	3.04	1.93	2.15	2.48
70%	2.27	1.85	2.16	2.36
SE ±	0.12	0.14	0.12	0.14
CD(P=0.05)	0.36	0.43	0.35	0.40

Strobilanthes heyneanus

The total chlorophyll content and chlorophyll *a* contents in 50%, 60% and 70% shade were significantly high as compared to those of the plants grown under open condition on all sampling periods except the second sampling (238th day) whereas, chlorophyll *b* in 50%, 60% and 70% shade levels were significantly high compared to that of open condition on all sampling periods except the second and third sampling periods corresponding to 238th and 301st days of growth.

Table 29 **Chlorophyll contents (mg/g dry weight) in shade treated *Strobilanthes heyneanus* at different periods of analysis**

Total chlorophyll

	Sampling period			
	I	II	III	IV
Open	2.00	2.69	3.12	4.03
30%	2.19	3.16	3.96	5.10
40%	2.82	3.92	4 67	5.44
50%	4.29	4.01	6.30	9.17
60%	5.59	7.69	9.99	11.29
70%	5.66	8.55	10.47	12.20
SE ±	0.73	0.87	0.79	1.04
CD(P=0.05)	2.15	2.57	2.36	3.10

Chlorophyll a

	Sampling period			
	I	II	III	IV
Open	1.45	1.71	2.11	2.92
30%	1.57	2.02	3.03	3.70
40%	1.81	2.51	3.47	4.06
50%	3.71	2.57	4.64	6.60
60%	4.00	4.17	7.16	7.99
70%	3.75	4.88	7.40	8.62
SE ±	0.53	0.50	0.58	0.72
CD(P=0.05)	1.56	1.47	1.73	2.14

Clorophyll b

	Sampling period			
	I	II	III	IV
Open	0.55	0.98	1.01	1.11
30%	0.62	1.14	0.93	1.42
40%	1.01	1.41	1.20	1.38
50%	1.09	1.44	1.66	2.57
60%	1.59	3.53	2.83	3.30
70%	1.92	3.68	3.07	3.58
SE ±	0.16	0.41	0.22	0.33
CD(P=0.05)	0.48	1.23	0.66	0.98

Chlorophyll a/b

	Sampling period			
	I	II	III	IV
Open	2.66	1.72	2.11	2.62
30%	2.66	1.77	3.27	2.56
40%	1.79	1.76	2.89	2.97
50%	3.32	1.78	2.79	2.61
60%	2.49	1.30	2.54	2.43
70%	1.92	1.34	2.40	2.40
SE ±	0.20	0.14	0.15	0.10
CD(P=0.05)	0.58	0.41	0.46	0.31

Chlorophyll *a/b* ratio is significantly low in 70% and 40% shade as compared to the *a/b* ratio under full sunlight in the first sampling. In the second sampling, the *a/b* ratio was significantly low in 60% shade level as compared to those under open condition (Table 29, Figure 29).

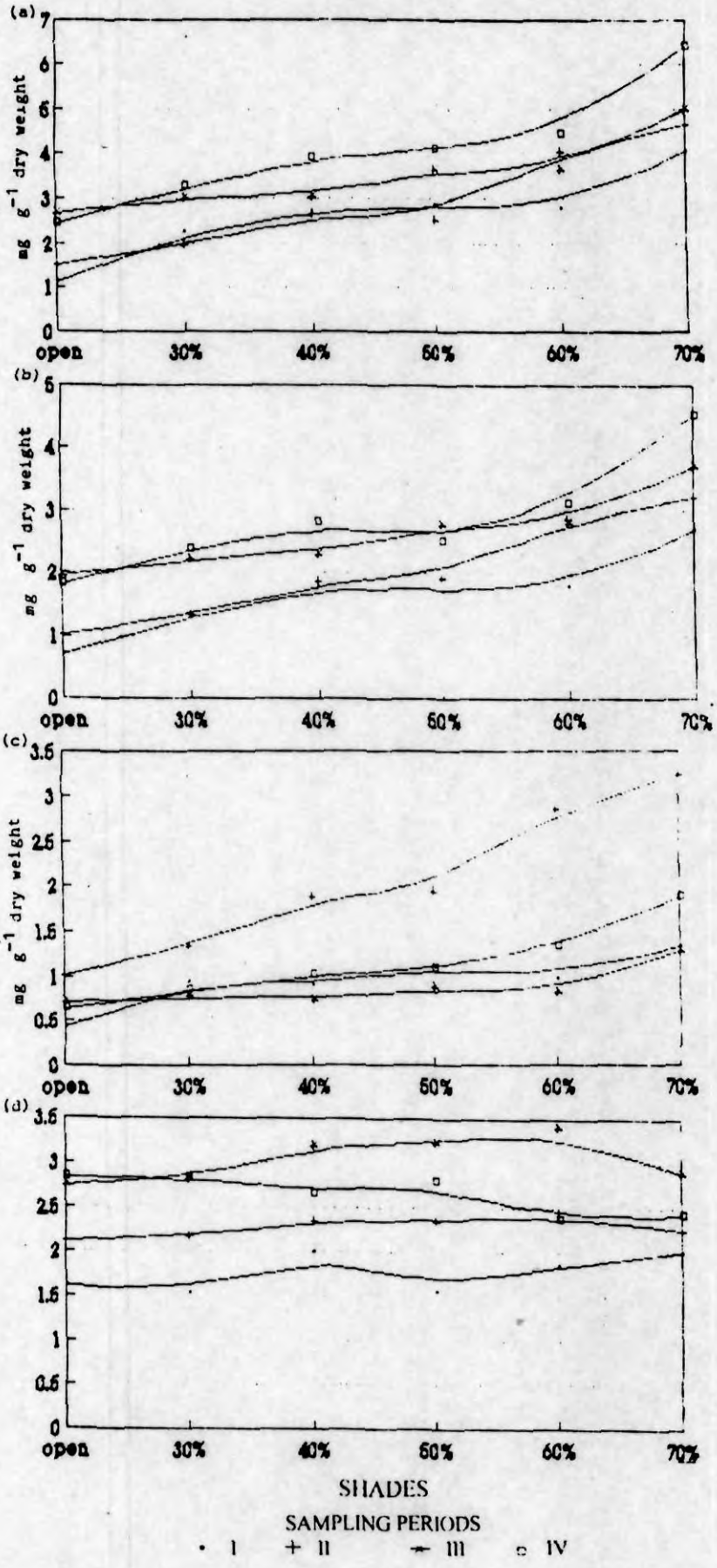


Figure 25. Chlorophyll contents (mg/g dry weight) in shade treated *Adhatoda beddomei* at different periods of analysis
(a) Total chlorophyll (b) Chlorophyll a
(c) Chlorophyll b (d) Chlorophyll a/b ratio

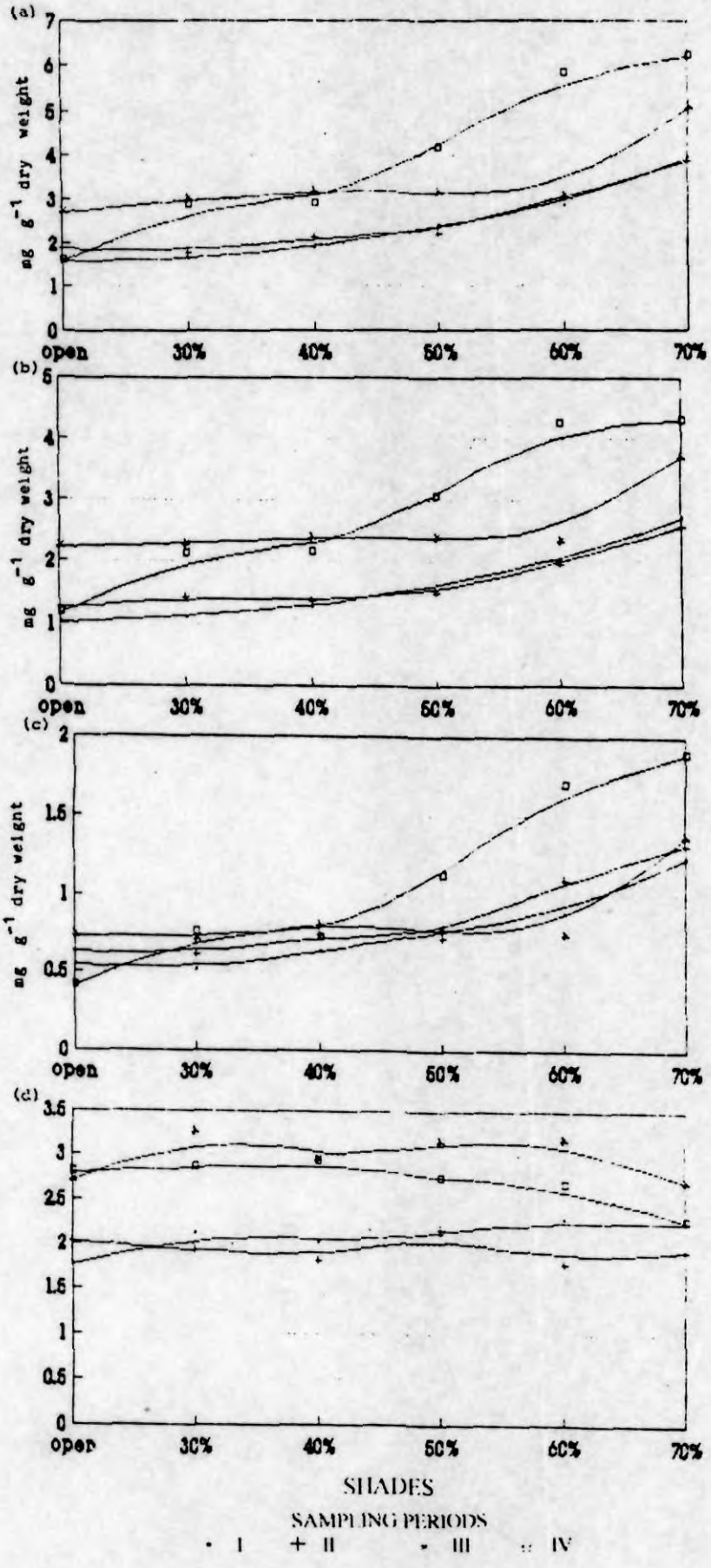


Figure 26 Chlorophyll contents (mg/g dry weight) in shade treated *Adhatoda vasica* at different periods of analysis
(a) Total chlorophyll (b) Chlorophyll a
(c) Chlorophyll b (d) Chlorophyll a:b ratio

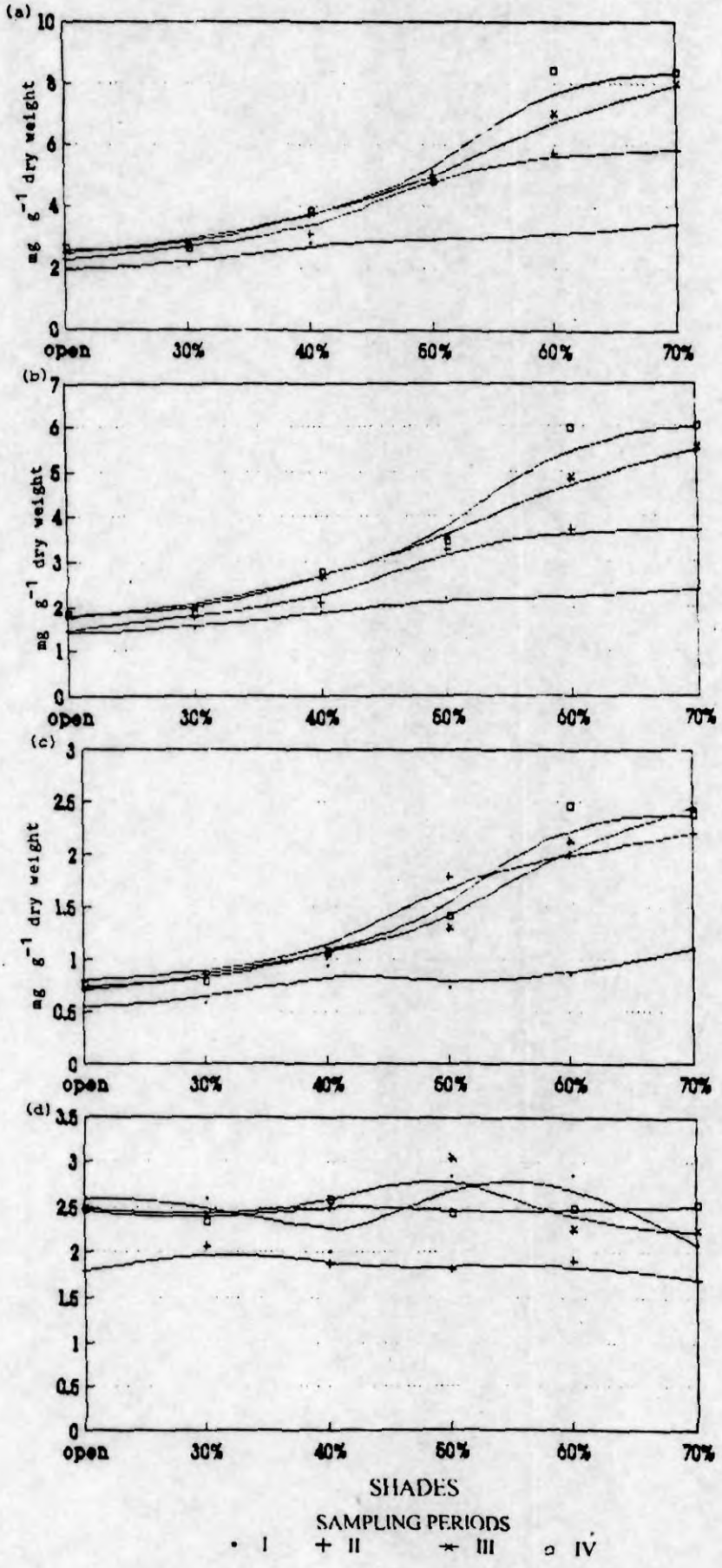


Figure 27. Chlorophyll contents (mg/g dry weight) in shade treated *Alpinia galanga* at different periods of analysis
(a) Total chlorophyll (b) Chlorophyll a
(c) Chlorophyll b (d) Chlorophyll a/b ratio

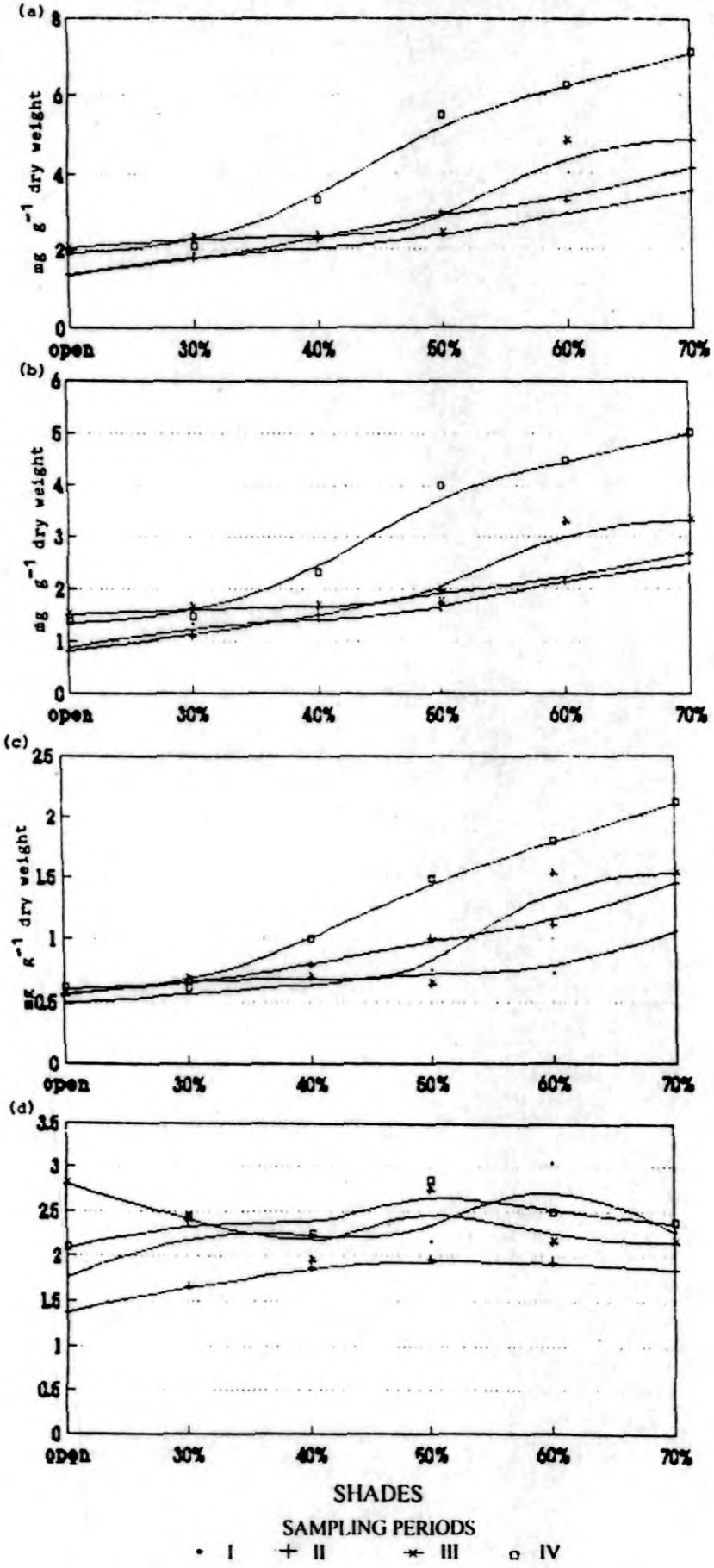


Figure 28 Chlorophyll contents (mg/g dry weight) in shade treated *Plumbago rosea* at different periods of analysis

(a) Total chlorophyll (b) Chlorophyll a

(c) Chlorophyll b (d) Chlorophyll a/b ratio

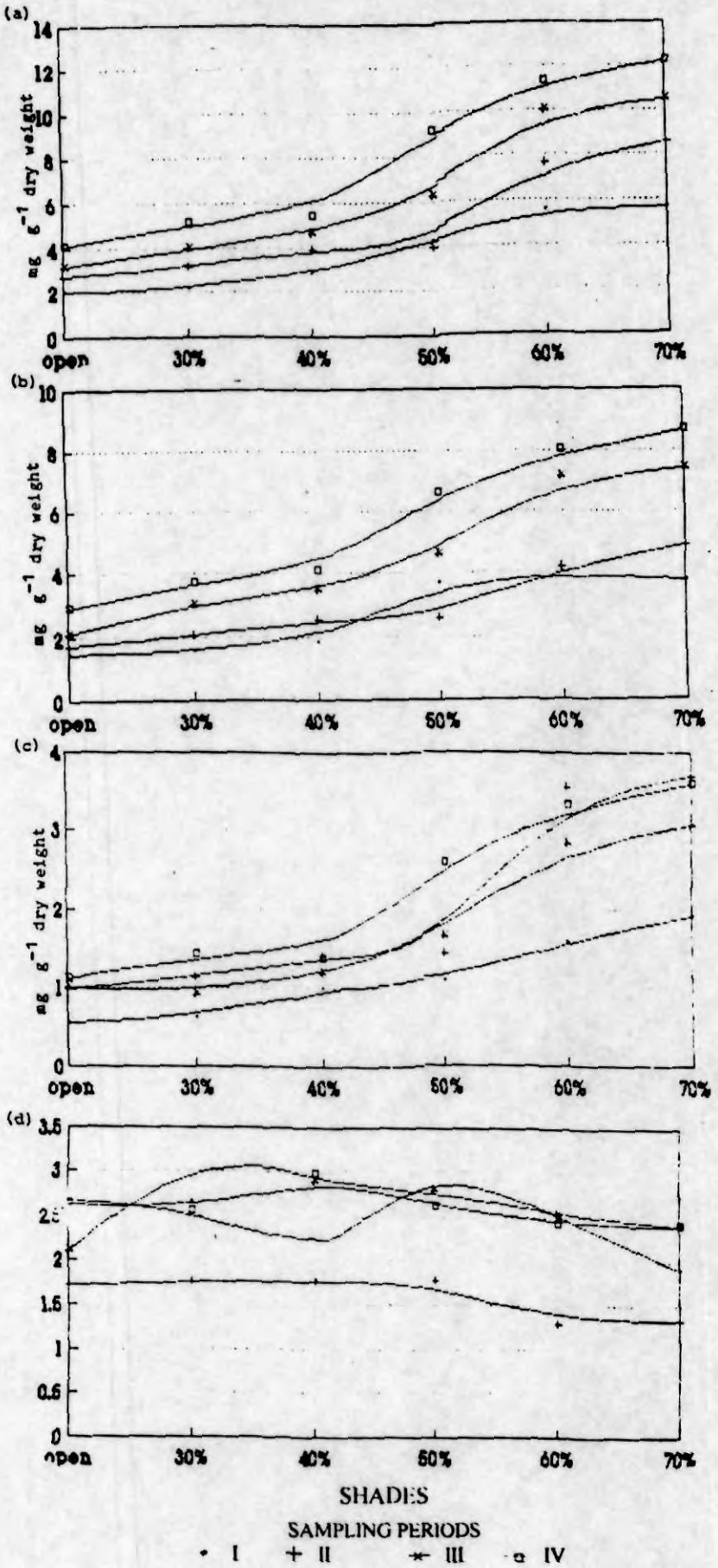


Figure 29. Chlorophyll contents (mg/g dry weight) in shade treated *Strobilanthes heyneanus* at different periods of analysis
(a) Total chlorophyll (b) Chlorophyll a
(c) Chlorophyll b (d) Chlorophyll a/b ratio

4.3.2.2 Carotenoid contents

The effect of shade on carotenoid contents in all the five species of medicinal plants: *Adhatoda beddomei*, *Adhatoda vasica*, *Alpinia galanga*, *Plumbago rosea* and *Strobilanthes heyneanus* at different light intensities (open, 30%, 40%, 50% and 70% shade) are given below (Table 30, Figure 30 and 31).

Adhatoda beddomei

Carotenoid content is significantly high in 70% shade compared to that under full sunlight in all sampling periods except the first sampling period corresponding to 182nd day of growth.

Adhatoda vasica

Carotenoid content was significantly high in 60% and 70% shade levels as compared to that under open condition in all phases of growth except the third sampling period. In the final phase of growth the carotenoid amount is significantly high in plants grown under 40%, 50%, 60% and 70% shade levels as compared to the amounts in plants grown under open condition.

Alpinia galanga

Carotenoid content in 50%, 60% and 70% shade are significantly high as compared to that under full sunlight in all phases of growth.

Plumbago rosea

Carotenoid content was significantly high in 60% and 70% shade levels in all sampling periods compared to that of open condition.

Strobilanthes heyneanus

Carotenoid content in plants grown under 60% and 70% shade levels were significantly high as compared to plants grown under open condition in all phases of growth.

Table 30 **Catotenoid contents (mg/g dry weight) in shade treated medicinal plants at different periods of analysis**

Adhatoda beddomei

	I	II	III	IV
Open	0.04	0.05	0.09	0.09
30%	0.05	0.07	0.10	0.11
40%	0.07	0.07	0.09	0.12
50%	0.07	0.08	0.10	0.11
60%	0.08	0.10	0.09	0.12
70%	0.13	0.11	0.14	0.15
SE ±	0.01	0.01	0.01	0.01
CD(P=0.05)	0.03	0.02	0.03	0.04

Adhatoda vasica

	I	II	III	IV
Open	0.06	0.05	0.09	0.05
30%	0.06	0.05	0.08	0.11
40%	0.06	0.06	0.10	0.09
50%	0.08	0.06	0.08	0.11
60%	0.09	0.08	0.08	0.14
70%	0.10	0.11	0.13	0.16
SE ±	0.01	0.01	0.01	0.01
CD(P=0.05)	0.03	0.03	0.01	0.04

Alpinia galanga

	I	II	III	IV
Open	0.09	0.13	0.10	0.13
30%	0.11	0.13	0.14	0.15
40%	0.12	0.15	0.15	0.16
50%	0.14	0.20	0.19	0.20
60%	0.14	0.22	0.25	0.30
70%	0.15	0.22	0.26	0.28
SE ±	0.01	0.02	0.02	0.02
CD(P=0.05)	0.04	0.07	0.06	0.05

Plumbago rosea

	I	II	III	IV
Open	0.06	0.07	0.10	0.09
30%	0.08	0.08	0.10	0.11
40%	0.09	0.10	0.10	0.13
50%	0.10	0.11	0.12	0.20
60%	0.10	0.12	0.14	0.22
70%	0.15	0.15	0.15	0.22
SE ±	0.01	0.01	0.01	0.03
CD(P=0.05)	0.04	0.04	0.04	0.08

Strobilanthes heyneanus

	I	II	III	IV
Open	0.07	0.13	0.15	0.17
30%	0.08	0.15	0.14	0.15
40%	0.09	0.15	0.16	0.21
50%	0.16	0.16	0.19	0.25
60%	0.17	0.23	0.28	0.34
70%	0.18	0.26	0.30	0.35
SE ±	0.02	0.02	0.02	0.03
CD(P=0.05)	0.06	0.05	0.05	0.09

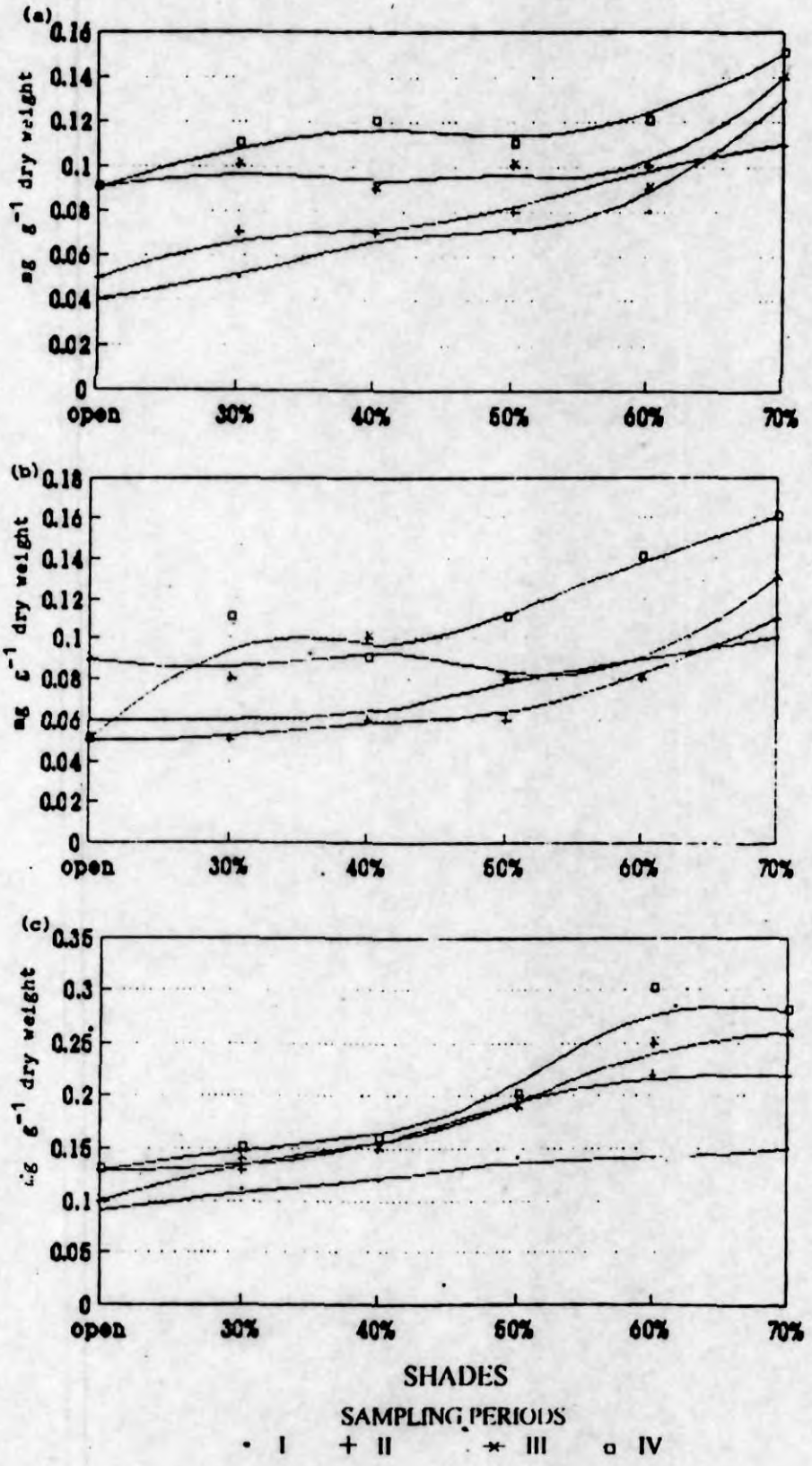


Figure 30. Carotenoid contents (mg/g dry weight) in shade treated medicinal plants at different periods of analysis
(a) *Adhatoda beddomei* (b) *Adhatoda vasica*
(c) *Alpinia galanga*

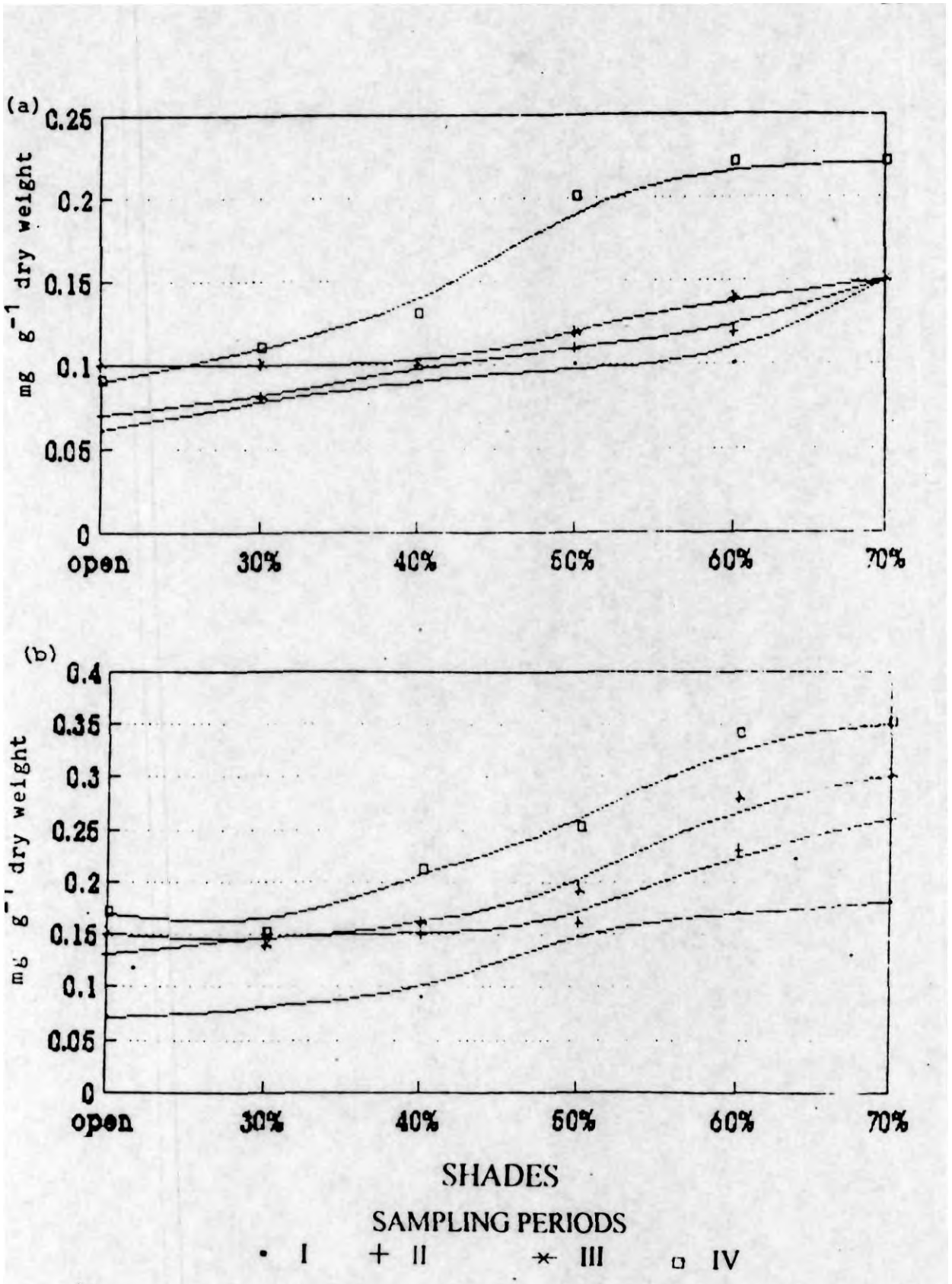


Figure 31. Carotenoid contents (mg/g dry weight) in shade treated medicinal plants at different periods of analysis
(a) *Plumbago rosea* (b) *Strobilanthes heyneanus*

Chapter 5

DISCUSSION

5.1 Impact of Shade on Growth

The results from the present studies reveal the mechanisms of shade adaptation at morphological, anatomical and physiological level.

5.1.1 Morphology

An increase in plant height and internode length was observed under shade in all the species. The tendency for increasing height by shade adapted species for exploitation of better lit conditions under higher levels of canopy have been reported (Aminuddin, 1986; Begonia *et al.*, 1988; Kohyama and Hotta, 1990; Lakshmamma and Rao, 1996 and Venkataramanan and Govindappa, 1988). The observed increase in plant height thus appears to be a possible adaptation for maximisation of light interception by individual leaves. Sturdy (1935) and de Castro *et al.* (1962) reported an increase in the length as well as diameter of internodes in coffee.

High light inhibited branch production in *Adhatoda vasica* and *Plumbago rosea* and the light threshold for branching was 70 per cent and 50 per cent shade respectively. *Adhatoda vasica* appears to have lower thresholds than all the other medicinal plants under study. In *Strobilanthes heyneanus*, total number of branches decreased under shade indicating the highest light threshold for branching for this species.

This differential response exhibited by different species under shade might be due to differences in threshold values of light absorption (Regnier and Stoller, 1989) as well as species variation for branching (Ducrey, 1992).

5.1.2 Classical growth parameters

Among the five species of medicinal plants studied, the optimum shade requirement was different for different species. Among the shade treatments, 70 per cent shade was most favourable for growth of *Adhatoda vasica* and *Plumbago rosea* whereas 60 per cent shade was most suitable for *Adhatoda beddomei* and 50 per cent shade for *Alpinia galanga* and *Strobilanthes heyneanus*. The aforesaid treatment produced plants with increased stem and leaf weight and therefore highest TDM. Shade requirement variation in different species of coffee have been reported earlier (de Castro *et al.*, 1962; Huxley, 1967; Maestri and Gomez, 1961; Venketaramanan and Govindappa, 1987).

In *Alpinia galanga*, *Plumbago rosea* and *Strobilanthes heyneanus*, intermediate shade treatments produced plants with heaviest roots. Inhibition of root growth by exposure to full light and 70 per cent shade is in conformity with earlier reports (de Castro *et al.*, 1962 and Machado, 1946).

An increase in shoot:root ratio with shade, as observed in this investigation, is supported by the findings of Aminuddin (1986) and Marler *et al.* (1994). Popma and Bongers (1988) and Osunkoya *et al.* (1994) also reported a decrease in root:shoot ratio under shade. This indicates that they have proportionally less root tissue to maintain in the shade (Stoller and Myers, 1989). It might also be possible that less root is associated with low water uptake under shade.

Reduced irradiance during growth caused an increase in photosynthetic tissue: support tissue ratio in all the species. To utilise available photosynthetic

photon flux density (PPFD) efficiently, shade adaptable plants maximise the photosynthetically active tissues of the total plant biomass by redistributing dry matter. This in turn, maximises efficiency of light interception by increase in the proportion of dry matter in leaf tissue (Regnier *et al.*, 1988). This increase reflect greater partitioning of plant biomass into leaf tissues that harvest the available PPFD, with less biomass diverted to tissues that deplete photosynthate. The values of the leaf:support tissue ratio indicate that under shades these medicinal plants utilised a noticeable amount of biomass in harvesting the available light, an essential function for shade plants that survive extended periods under the canopy where light levels are commonly very low (Stoller and Myers, 1989).

An increase in cumulative leaf area with increasing intensity and duration of shade, as observed here, is in agreement with earlier reports (Alvim, 1960; Castillo, 1961; Hampson *et al.*, 1996; Huang and Kuo, 1996; Huxley, 1967; Maestri and Gomes, 1961; Marler *et al.*, 1994; Messier *et al.*, 1989; Sturdy, 1935; Venketaraman and Govindappa, 1987). In all species studied, the least leaf area was under full day light. Values for leaf area among the shade treatments followed the same trend as in the case of TDM in all species. For the effect of shade on leaf expansion the inherent anatomical structure of leaf is clearly important because this determines the extent to which it can be modified. Relatively thick leaves are less capable of increasing the leaf area than those with thin leaves (Huxley, 1962 and 1967).

Increased total leaf area in response to shade reported here is associated with both increase in leaf number and size. However, Sturdy (1935) found that coffee under shade had fewer leaves but more total leaf area than in full sun.

Decrease in SLW was noticed under shade in all species studied except *Alpinia galanga*. Leaves in shady environment typically have lower SLW than

leaves grown in sunny conditions. Low SLW represents a complement of leaf characteristics including decreased leaf thickness, decreased palisade cell development, lower photosynthesising cells per unit leaf area, decreased assimilatory apparatus per unit area, lower light saturation point and/or decreased respiration rate. (Boardman, 1977; Chabot and Chabot 1977). Even though maximum photosynthetic rate per unit leaf area is low under shade, total photosynthetic rate per plant is higher due to increased total leaf area per plant under shade. This in turn may cause increased TDM under low irradiance levels, in shade adapted plants. So SLW is a good indicator of photosynthetic capacity, growth of plant and of relative ability to adapt to shade. Comparison of SLW among species must distinguish genetic and environmental effects on SLW. There is undoubtedly a genetic influence on SLW, as shown by comparisons among and within species grown under the same conditions (Jurik, 1986), although the magnitude of genetic differences in SLW are generally much less than differences due to environmental effects.

The thin shade grown leaves with low SLW also maximise the exposure of the radiation harvesting apparatus to the limited number of usable photons (Bjorkman *et al.*, 1972a, b; Blackman, 1960; Goodchild *et al.*, 1972; Mahmoud and Grime, 1974; Myerscough and Whitehead, 1966; Patterson, 1979). The decrease in SLW under shade as observed in the present investigation is in conformity with the earlier reports (Beurlein and Pendleton, 1971; Bjorkman *et al.*, 1972a, b; Blackman, 1960; Bongers *et al.*, 1988; Bowes *et al.*, 1972; Evans and Hughes, 1961; Hampson *et al.*, 1996; Jurik, 1986; Mahmoud and Grime, 1974; Messier *et al.*, 1989; Osunkoya *et al.*, 1994; Popma and Bongers, 1988; Regnier *et al.*, 1988 and Utsunomiya and Higuchi, 1996).

In the present study shading during growth caused increased SLA. This is due to increased distribution of leaf biomass contributed by significantly increased leaf area due to shading as reported by Begonia *et al.* (1988). Differences in SLA reflect changes in structure and thickness of leaves. The thinner leaves characteristically produced under shade have greater SLA than leaves produced under high PAR (Huxley, 1967; Boardman, 1977 and Patterson, 1980b). Increased LAR in shaded plants was due primarily to increases in SLA rather than LWR (Regnier *et al.*, 1988). Rate of increase of SLA is greater than LWR in plants grown at reduced irradiance. The greater sensitivity of SLA than LWR to irradiance level has been reported for other species (Evans and Hughes, 1961; Cooper, 1967). Thus this species compensates for low irradiance by increasing the amount of photosynthetically active area in proportion to above ground plant mass, primarily by decreasing the leaf thickness, as indicated by increased SLA. This response has been associated more frequently with shade than sun adapted species (Regnier *et al.*, 1988). The increase in SLA under shade as observed in the present investigation is in conformity with the earlier report of Ducrey (1992, 1994), Groninger *et al.* (1996), Huang and Kuo (1996), Klinka *et al* (1992), McKendrick (1996) and Regnier and Harison (1993).

An increase in LWR with shade as observed in this work is supported by earlier reports (Huxley, 1967; Begonia et al., 1988 and Regnier et al., 1988). This means that in response to decreased PAR the plant invested more of its biomass into the development of the leaf components. The change in leaf weight ratio with increase in shading is small over the whole range of treatments, as is generally the case of dicotyledonous plants with dorsiventral leaves.

An increase in LAR with increasing intensity of shade is observed in this investigation. Several shade adapted species exhibit an increase in leaf area ratio

when grown at low irradiance (Alvin, 1960; Begonia *et al.*, 1988; Blackman and Wilson, 1951a, b; Castillo, 1961; Cooper, 1967; Huerta, 1954; Huxley, 1967; Maestri and Gomez, 1961; Osunkoya *et al.*, 1994; Patterson, 1985, Pompa and Bongers, 1988; Regnier *et al.*, 1988; Stoller and Myers, 1989; Utsunomiya and Higuchi, 1996; Venkataramanan and Govindappa, 1987 and Whitehead, 1973), a response found less frequently among sun adapted species (Blackman and Wilson, 1951a, b; Cooper, 1967 and Patterson *et al.*, 1978). This response compensates for reduced irradiance by increasing light interception in proportion to total plant tissue. The increase in LAR with shading represents an adaptation to low PAR because a greater LAR results from a greater allocation of plant materials into photosynthetic light harvesting structures, thus corroborating previous observations (Patterson, 1979, 1980a). Photosynthate distribution efficiency has also been expressed by LAR (Patterson, 1985). By having the highest proportion of its biomass in efficient light harvesting tissues, all species studied seem to be best equipped, morphologically, to utilise the available irradiance at low light intensities (Stoller and Myers, 1989). The decrease of LAR with the increase in age of the plants, noted in the present investigation, has also been observed in coffee (Venkataramanan and Govindappa, 1987) and in sweet pepper (Nilwik, 1981).

Decrease in NAR under shade was observed in *Alpinia galanga* and *Strobilanthes heyneanus* whereas the effects were non-significant in all other species studied. The unshaded plants exhibited maximum NAR in *Alpinia galanga* whereas the least shade i.e. 30 per cent showed more NAR than in the unshaded plants in *Strobilanthes heyneanus*. But in general, NAR decreases under heavy shades. Maximum NAR in unshaded plants of coffee has been reported earlier (Huerta, 1954; Castillo, 1961; Orlando, 1963). Similar reports are available with

other species also (Blackman and Wilson, 1951a, b; Mc Laren and Smith, 1978; Patterson, 1979; Regnier *et al.*, 1988; Rincon and Huante, 1993).

In *Helianthus annuus* (Blackman and Black, 1959; Huxley, 1963a) NAR increases with increasing radiation income up to the maximum values provided by the environment. But this was not observed for seedlings of citrus in Israel (Monselise, 1951) and Cacao in Ghana (Goodall, 1955) but it cannot be assumed that water was not limiting, particularly in the latter case. The reduced NAR under heavy shades was a reflection of a decrease in radiant energy available for photosynthesis under shade (Begonia et al., 1988). NAR is one of the important components which determine RGR. In the present investigation, generally lower NAR was associated with low RGR.

NAR follows the pattern observed in maximum photosynthetic rate (leaf area basis) and in leaf thickness. The instantaneous photosynthetic rate of a single leaf in these species, therefore gives an approximate measure of the NAR, which reflects the whole plant's effectiveness in incorporating dry matter over time based on its total leaf area.

In the present investigation, the effect of shade on RGR was found to increase with intensity only during the initial sampling. RGR either remained constant or showed a decline in comparison to the open plant during the final sampling. In the initial samplings, increased LAR fully compensated for decreased NAR which resulted in an increased RGR over shade levels. But in the final samplings, the increase in LAR did not fully compensate for reduced NAR. So there was a reduction in RGR of plants at the final sampling. Foggio and Warrington (1989) and Venkataramanan and Govindappa (1987) found that plants grown at reduced irradiance exhibited an increase in RGR. But reduction in RGR

of plants grown at low irradiance was reported by Osunkoya *et al.* (1994), Regnier *et al.* (1988) and Rincon and Huante (1993).

5.2 Impact of shade on foliar anatomy

Plants grown under open and shade condition show morphological and anatomical variations (Kramer and Kozlowski, 1979). Generally leaves of shade plants are thin and this is evident from the data of a single species grown under different light intensities (Abrams, 1987; Abrams and Kubiske, 1990; Adams et al., 1987; Boardman, 1977; Fahl et al., 1994; Marler et al., 1994; Messier et al., 1989; Regnier et al., 1988; Shiraishi *et al.*, 1996 and Utsunomiya and Higuchi, 1996). In the present study, it was observed that the leaf thickness in all the species grown in shade was reduced as compared with the open grown plants. This was either due to the reduction in the number or size of the internal laminar tissues.

Transection of leaf blades of the open grown plants and shade plants revealed a strong influence of shade on cell size and number of different anatomical variables. Apart from quantitative differences in various tissues, qualitative variation with regard to mesophyll cell size, number of contacts between the cells, extent of air cavities etc. were also observed.

In the present study, it was observed that shade reduced the number of palisade layers in comparsison with the leaves in the open. A reduction in the cell number was also indicated under shade. Photosynthetic tissue per unit leaf area thus decreased. Thicker leaves in plants grown at high irradiance have been attributed primarily to increase in the thickness of the palisade mesophyll layer as reported by Chabot *et al.* (1979), Fails *et al.* (1982), Huang and Kuo (1996), Nobel (1976) and Patterson *et al.* (1977). Reduction in spongy cell number, in shade plants, was also noted. Thicker leaves in unshaded plants than in shaded ones,

because of the increased size of the palisade and spongy parenchyma tissues has been reported by Fahl *et al.* (1994) and Huang and Kuo (1996).

Several workers have discussed in detail the relationship of internal leaf structure and photosynthetic rate (Mansfield and Jones, 1976; Boardman, 1977; Bothar-nordenkampf, 1982). The palisade cells account for major part of the photosynthetic machinery. They contain at least twice or even three to five times as much chlorophyll corpuscles, than the spongy cells in which CO_2 exchange is only a subsidiary function (Haberlandt, 1914). Moreover the elongated palisade cells exposes 1.6 to 3.5 times free surface area than the spongy parenchyma (Turrel, 1936) indicating a higher ratio of internal to external surface area thereby facilitating efficient gas exchange. Thus in the present study the individual palisade layer thickness combined with the total tissue thickness was indicative of the internal exposed surface area and thereby to photosynthetic rate. In alfalfa leaves, Delaney and Dobrenz (1974a, b) obtained significant positive correlation between apparent photosynthesis and thickness of palisade tissue.

Great depth of absorbing tissue is required for high photosynthetic capacity. Plants grown in shade have lesser development of the palisade and spongy mesophyll region than the plants grown in direct sunlight (Boardman, 1977). But though the photosynthetic rate per unit area is low in shade plants, the total output will be high, due to large laminar area. Wilson and Cooper (1969a, b) concluded that photosynthetic rate per unit leaf area is the result of an interaction between the number of mesophyll cells per unit area and leaf thickness whereas on a per leaf basis, the increased palisade cell size coupled with greater leaf surface area collectively contributed to the improved photosynthetic rate under the shade.

Patterson *et al.* (1978) suggested that the greater mesophyll thickness in high irradiance grown plants may lead to chloroplast shading one another within

the leaf, causing photosynthesis to become saturated at higher light intensities than in plants grown at low irradiance. From the present study, it is evident that plants grown in 70% shade showed maximum anatomical adaptation to shade condition.

5.3 Impact of shade on photosynthesis and other related parameters

5.3.1 Photosynthesis

5.3.1.1 Diurnal changes in photosynthetic characteristics

Highest peak Pn at around 09.00 or 10.00 h in the species studied under open sunlight may be due to favourable environmental conditions such as PAR, relative humidity and vapour pressure deficit and plant moisture status. The decline in Pn after 09.00 or 10.00 h can be traced to the closure of stomata in all species. Mid-day depression due to other factors as well has been reported earlier by several authors (Singh *et al.*, 1988 and Xu *et al.*, 1984). A second peak was observed in *Alpinia galanga* and *Adhatoda beddomei* at 16.00 and 17.00 h respectively. Schulze and Hall (1981) ascribed the two-peaked diurnal course of CO_2 uptake mainly to the change in the environmental conditions. The first peak occurs in the early morning, but by noon stomata close to such a degree that CO_2 uptake decreases. The stomata then open again in late afternoon, resulting in the second peak of CO_2 uptake. Only a minor difference was observed in maximum Pn between open and shade grown plants of *Alpinia galanga* and *Plumbago rosea*. However, in the case of plants grown in the open condition a sharp decline in Pn was noticed after the 09.00 h peak. It is widely recognised that shade plants may suffer damage if grown under high irradiance. Also these plants possess only limited capacity for photosynthetic assimilation under high quantum flux densities (Bjorkman, 1981). Under shade, all the species in this study maintained maximum Pn for a longer period. It is a known fact that the leaves must be able to trap the

available light under shade and to convert with the highest possible efficiency. The interesting point to note is that the average daily Pn of leaves of *Alpinia galanga* and *Plumbago rosea* under shade appeared to have a similar rate when compared to those plants grown in open sunlight. A close examination of the diurnal course revealed that at low irradiance the shade grown plants, of the same sp. showed higher Pn than open. For example, the light intensity at 07.00 h in the open light is same as that under shade at 09.00 h, but when we compare the Pn at 07.00 h in the open condition with that at 09.00 h in the shade, of the same species, the latter showed higher values than the former. The daily average Pn of *Strobilanthes heyneanus* grown in open sunlight was moderately higher than the shade grown, whereas the open grown *Adhatoda beddomei* and *Adhatoda vasica* plants showed nearly two times higher values than the shade plants. The oscillation type of diurnal Pn occuring under shade of *Adhatoda beddomei*, *Adhatoda vasica* and *Alpinia galanga* may be related to stomatal behaviour with attempts to maintain leaf turgor as reported by Shirazi *et al.* (1976). Stomata effectively control the diffusion of water vapour from intercellular space in the leaf to ambient atmosphere and also control the diffusion of CO_2 in the opposite direction. Consequently, potential increase in Pn resulting from greater stomatal conductance must be weighted against the costs associated with increase in transpiration.

There was no difference in daily average Cs of *Adhatoda beddomei* and *Strobilanthes heyneanus* plants grown under open and shade conditions, whereas *Adhatoda vasica* and *Alpinia galanga* showed nearly two times and *Plumbago rosea* 50 per cent higher Cs under shade than in the light. Cowan (1986) analysed how stomatal conductance should vary diurnally in response to changing environmental conditions based on maximising total daily photosynthesis for a given daily total amount of transpiration.

Measurements of transpiration per unit leaf area showed that there was not much difference for *Adhatoda beddomei*, *Adhatoda vasica*, *Plumbago rosea* and *Strobilanthes heyneanus* under open and shade conditions whereas *Alpinia galanga* showed nearly two times higher transpiration under shade than open conditions. The E peaked at mid-day or afternoon in all the species and declined thereafter. High VPD at mid-day may be a factor which reduces the Pn and increases the transpiration (Turner *et al.*, 1985). The ratio of average daily transpiration to Pn was the same for open and shade plants of *Plumbago rosea*. Several studies have shown that within a given species, E/Pn remains roughly constant as stomatal conductance varies in response to shift in irradiance and RH (Ball and Farqhar, 1984a, b and Wong *et al.*, 1979).

It is difficult to elucidate the actual mechanism responsible for diurnal course because several environmental factors change under open and shade conditions. The adaptability of species is also a factor. It may be concluded that *Alpinia galanga*, *Plumbago rosea*, *Strobilanthes heyneanus*, *Adhatoda beddomei* and *Adhatoda vasica* may change their mechanism to acclimatise to the light environment where they are grown. Bowas *et al.* (1972) found that Soybean may acclimatise to whichever light intensity it is grown in. Hence further studies are required on environmental interaction with whole plant growth and productivity of these species under different light intensities, before final conclusions on the related physiological mechanisms can be drawn.

5.3.1.2 Maximum photosynthetic rate

The response of these species in photosynthetic activity was analysed as a function of shade adaptation and found a decrease in maximum photosynthetic rate under different shade treatments when it was expressed on a unit leaf area bases.

Greater reduction was associated with the greater percentage shade applied in the experiment.

Many reports are available on the effect of shade on photosynthetic properties (Agata *et al*, 1985; Carter and Teramura, 1988; Ducrey, 1994; Kitajima, 1994; Madsen *et al.*, 1991; Marler *et al.*, 1994; Masarovicova and Elias, 1985; Mckiernan and Baker, 1991; Mori *et al.*, 1990; Mulkey *et al.*, 1991 and Sondergaard and Bonde, 1988). Agata *et al.* (1985), Ducry (1994), Fukuoka *et al.* (1996), Madsen *et al.* (1991) and Mori *et al.* (1990) reported a decrease in photosynthetic rate on a leaf area basis, under shade. Numerous shade and sun adapted plants are known to exhibit thin leaves when grown at low irradiance (Abrams, 1987; Abrams and Kubiske, 1990; Adams *et al.*, 1987; Chabot and Chabot, 1977; Marler *et al.*, 1994; Messier *et al.*, 1989 and Regnier *et al.*, 1988). Considering the difference in the leaf thickness in plants grown under open and shaded conditions, Regnier *et al.* (1988) observed an increase in maximum photosynthetic rate when expressed on a unit leaf volume basis. Traditionally photosynthetic rate is expressed on a leaf area basis, due to the ease of measurement.

Reduced irradiance during growth also causes a decrease in leaf thickness in all species (I'ma *et al.*, 1993). Thinner leaves in plants grown at low irradiance have been attributed primarily to decreases in the thickness of the palisade mesophyll layer (Chabot *et al.*, 1979 and Fails *et al.*, 1982; Nobel, 1976; Patterson *et al.*, 1977 and Paulson and Delucia, 1993). Photosynthetic tissue per unit leaf area is therefore decreased, finally resulting in low photosynthetic rate at low light intensities. Maximum photosynthetic rate was correlated with leaf thickness for all species.

The maintenance of a high leaf surface area in comparison to support tissue may be as important as photosynthesis per unit leaf area to survive under shade. However, accordi.., to Boardman (1977), the capacity of photosynthesis is expected to be independent of the efficiency of light absorption and primary photochemical reaction. It will be influenced by some steps of dark reaction: stomatal resistance for CO_2, activity of RuDP carboxylase and the rate of photosynthetic electron transport. He also reported that high stomatal resistance and mesophyll resistance, whereas low stomatal conductance, and low RuDP carboxylase activity and low rate of photosynthetic electron transport are found in plants when grown under low irradiance. These are probably some of the intrinsic factors that give low maximum photosynthetic rate in shade plants.

5.3.2 Photosynthetic pigments

5.3.2.1 Chlorophyll contents

One of the major effects of shade adaptation in plants is the increase in concentration of chlorophyll pigments in leaves. In the present investigation there was an increase in total chlorophyll and component pigments which was directly proportional to the degree and duration of shades. The leaves of shaded plants were rich in chlorophyll than the leaves of unshaded or open plants. The total chlorophyll contents in 50%, 60% and 70% shade were much higher than that of open condition on all sampling periods, the highest increase being observed in 70% shade. Shade, besides increasing the Chlorophyll a and b, produced a differential increase. Under shade chlorophyll b synthesis increases relative to chlorophyll a synthesis leading to a lower chlorophyll a/b ratio.

An increase in chlorophyll content expressed on a weight basis with increasing intensity of shade as observed in this investigation is supported by the

findings of Adams *et al.* (1987), Adams *et al.* (1988), Andrew *et al.* (1984), Bjorkman (1981), Bjorkman (1968), Bjorkman and Holmgren (1963), Goodchild *et al.* (1972), Hampson *et al.* (1996), Lakshmamma and Rao (1996), Lichtenthaler *et al.* (1981), Rabinowitch (1945), Sandergaard and Bonde (1988) and Shiraishi *et al.* (1996).

Regnier *et al.* (1988) found that chlorophyll contents per unit leaf volumes also increased under shade. However, Abrams (1987) findings, contradict the established ideas of high total chlorophyll for shade tolerant species.

In the present study, reduced irradiance during growth caused increase in chlorophyll a in all species. This is supported by the findings of Sukenik *et al.* (1989), Goldborough and Kemp (1988); Berner *et al.* (1987) and Geider *et al.* (1985). An asymptotic increase in light absorption with increasing chlorophyll a density across the plant kingdom from single celled cyanobacteria to trees has been confirmed by Agusti *et al* (1994). Chlorophyll a concentration of photosynthetic tissue decreased as the tissue become thicker. This resulted in low areal chlorophyll a density, inefficient light absorption and finally low growth rate. An increase in chlorophyll b under shade as observed in this work is in conformity with the reports of Sartoni et al. (1993) and Sondergaard and Bonde (1988), as chlorophyll b can harvest light prevailing in shaded habitats more efficiently than chlorophyll a.

Increase in chlorophyll content under shade condition is generally attributed to

a) chloroplasts with large grana stacks which may contain as many as 100 thylakoids per granum (Anderson *et al.*, 1973; Goodchild *et al.*, 1972; Lichtenthaler *et al.*, 1981) and

b) high proportion of Lamellae forming grana and the ratio of thylakoid membranes to stroma (Boardman *et al.*, 1975; Goodchild *et al.*, 1972) i.e. extensive grana formation. According to Sukenik *et al.* (1989), the cells grown under low light condition were characterised by a large relative volume of chloroplast and high surface density of thylakoid membranes. However, Paulson and Delucia (1993) found that the shade acclimatization of Silphium is accomplished without adjustment to thylakoid membrane structure.

A decrease in chlorophyll a/b ratio under shade as observed in this work is in conformity with the earlier reports of Egle (1960). Many recent reports have also conformed these earlier findings (Adams *et al.*, 1988; Andrew *et al.*, 1984; Lichtenthaler *et al.*, 1981; McKiernan and Baker, 1991; Osunkoya *et al.*, 1994; Scheafer and Schmidt, 1991; Sondergaard and Bonde, 1988 and Wejnar and Gundermann, 1987). However, Poulson and Delucia (1993) reported that shade acclimatization of Silphium is accomplished without adjustment to the chlorophyll a/b ratio.

Chlorophyll b belongs to light harvesting chlorophyll ab protein complex, LH chl (Thornber, 1975) which is primarily associated with photosystem PS II (Butler, 1977). High chlorophyll b or low chlorophyll a/b ratio reflects a difference in the proportion of LH chl complex to the total chlorophyll (Lichtenthaler et al., 1981). So the shade plants have a high ratio of PS II to PS I reaction centres (McKiernan and Baker, 1991). A possible function of an increased PS II/PS II ratio in shade plants is to provide a more balanced energy distribution between the two photosystems in shade habitats such as forest floors which because of the filtering effect of the forest canopy, having a very high proportion of far red light, is effective only in excitation of PS I. Such changes in PS II/PS I ratio could also

explain the tendency of shade plants to have a slightly higher ratio of total chlorophyll to P700.

Chlorophyll per unit leaf volume increased in plants grown at reduced irradiance. This is in agreement with the work of Regnier *et al.* (1988). The increase on a leaf volume or weight basis was offset by reductions in leaf thickness; the net result was a decrease in chlorophyll per unit leaf area. Greater chlorophyll content per unit leaf weight may be a factor in the higher photosynthetic rates (leaf weight basis) exhibited by shade plants when exposed to low light intensities by causing an increased light capture per unit leaf volume. According to calculations by Bjorkman (1981), however, a 50% increase in chlorophyll content results in only a 3% increase in absorption of photosynthetically active radiation. Increased chlorophyll content on a leaf weight or volume basis in response to reduced irradiance has been reported for shade and sun adapted species (Bjorkman and Holmgren, 1963; Patterson et al., 1978). This can also be due to photoinjury in exposed leaves and associated chlorophyll as has been reported by Vijayakumar *et al.* (1985).

5.3.2.2 Carotenoid contents

Comparable to the patterns observed for total chlorophyll, there was a gradual increase in carotenoid content under shade. The increase was accelerated with increasing intensity and duration of shade. This is in conformity with the work of Sukenik et al. (1989). Carotenoids function in the photosynthetic tissues of higher plants mainly in two ways (Cegdell, 1988; Young, 1992). They act as accessory pigments harvesting light for photosynthesis, and as photoprotective agents limiting the damaging effects of high irradiance. The absorption spectra of carotenoids are distinct from those of chlorophylls, enabling plants to harvest light over a wider wavelength range. Carotenoids of leaves are highly conserved,

forming major components of the photosynthetic apparatus. Carotenoids are generally divided into two classes: those that contain oxygen (xanthophylls) and those that do not (carotenoids). Carotenes contain α and β carotene whereas xanthophylls contain lutein and xanthophyll cycle intermediates like zeaxanthin, antheraxanthin and violaxanthin. Johnson *et al.* (1993a, b) found that lutien and xanthophyll cycle intermediates are correlated with ability to grow in shade, with lutien content being high in shade species and xanthophyll cycle intermediates low. The ratio of lutien to xanthophyll cycle carotenoids was strongly correlated to an index of shade tolerance (Johnson *et al.*, 1993a, b). It has previously been observed by Thayer and Bjorkman (1990) that leaves of shade plants often contain significant amounts of α carotene. So an increase in carotenoid contents as observed in the present study may be due to an increased lutein and α carotene.

Chapter 6

SUMMARY AND CONCLUSION

The present study envisages to identify the medicinal plants ideally suited for intercropping in rubber plantations and also to find out the optimum light requirement for the growth of these species. Five species of medicinal plants viz. *Adhatoda beddomei, Adhatoda vasica, Alpinia galanga, Plumbago rosea* and *Strobilanthes heyneanus* were subjected to six treatments including five different shade levels of 30%, 40%, 50%, 60% and 70%, along with open sunlight. Periodic observations on morphological physiological, biochemical, anatomical and growth parameters were carried out.

The different treatments were given to three month old plants and sampling were done on the day of the treatment (zero day) and on 90th, 150th, 210th and 270th day after treatment.

In all the five species studied, the total dry matter (TDM) under various shade levels were found to record significant increase as compared to the open plants. The highest shade level of 70% was found to be the best suited in the case of *Adhatoda vasica* and *Plumbago rosea*, whereas it was 50% for *Alpinia galanga* and *Strobilanthes heyneanus*, particularly towards the later period of sampling. The best treatment level for *Adhatoda beddomei* was 60% shade. In general, the total leaf area per plant increased with shade.

Specific leaf weight (SLW) of all the species decreased with shade except in the case of *Alpinia galanga* whereas specific leaf area (SLA) of plants increased under

shade in all species, except in *Adhatoda vasica*, where the increase was not significant. Leaf weight ratio (LWR) was also found to increase with shade.

The effect of shade on crop growth rate (CGR) was found to increase with shade intensity only during the initial sampling. CGR either remained the same or showed a decline in comparison with the open plants during the final phases of growth. Relative growth rate (RGR) also followed a similar trend as that of CGR.

The effect of shade on net assimilation rate (NAR) was not significant in the case of *Adhatoda beddomei*, *Adhatoda vasica* and *Plumbago rosea*. NAR decreased during the last sampling corresponding to 301st day of growth, in *Alpinia galanga* in *Strobilanthes heyneamus*.

Leaf area ratio (LAR) invariably increased with shade, the maximum being attained at 70% shade for all the species except *Adhatoda beddomei* in which the optimum level was 60%. Unshaded plants registered minimum LAR in all the five species.

The measurements of leaf thickness showed that the thickness of palisade as well as spongy mesophyll cells showed a decline in the plants given 70% shade as compared to the open plants for all the species. Correspondingly the total leaf thickness of the different species also decreased in the shade plants, except in the case of *Alpinia galanga*. In general, the expression of shade adaptation with respect to cellular dimensions varied considerably within the different species studied. For instance, in the case of *Alpinia galanga*, the epidermis in the shade plants was consistantly two layered whereas in *Adhatoda beddomei*, the shade plants were characterised by a reduction in the number of palisade layers, indicating also a reduction in their cell number. Similar reduction in palisade and spongy cells in shade plants was also exhibited by *Plumbago rosea* and *Strobilanthes heyneamus*.

Under normal sunlight, the peak Pn was observed at 09.00 h for *Adhatoda vasica*, *Alpinia galanga* and *Plumbago rosea* while for *Adhatoda beddomei* and *Strobilanthes heyneanus* it was at 10.0 h. Under shade conditions peak Pn was observed for all the species at 10.00 or 11.00 h and continued for 3 to 4 hours. Lowest Pn was recorded for all the species either in the morning (07.00 h) or in the afternoon (18.00 h).

Maximum Pn under shade was lower than in open sunlight irrespective of species. Between species, the highest rate (7.8 μ mole CO_2 m^{-2} s^{-1}) was recorded for *Adhatoda beddomei* and the lowest rate (6.6 μ mole CO_2 $m^{-2}s^{-1}$) for *Strobilanthes heyneamus* under shade. Maximum Cs value was recorded under shade than under light in all species except *Adhatoda beddomei*. Among the species, *Adhatoda vasica* showed the highest value both under light (0.69) and shade (1.25). Transpiration rate (E) showed a similar trend like Pn and Cs in all the species. Among the species, *Adhatoda vasica* showed the highest E both under light (50.3 m mole $m^{-2}s^{-1}$) and shade (42.9).

On the whole, 30% shade treatment was found to be optimum in the case of *Alpinia galanga* and *Plumbago rosea* and open sunlight in the case of *Adhatoda beddomei* and *Adhatoda vasica*. *Strobilanthes heyneanus* tolerates upto 40% shade. Open condition was slightly injurious in the case of *Plumbago rosea*. The higher levels of 50 to 70% was inhibitory for all the species.

One of the major effect of shade on shade adapted plant is the increase in concentration of chlorophyll pigments in leaves. In the present investigation there was an increase in total chlorophyll and component pigments which was directly proportional to the degree and duration of shade. The leaves of shaded plants had rich chlorophyll than the leaves of unshaded or open plants. Shade, besides increasing the chlorophyll a and b, produced a differential increase. Under shade chlorophyll b increases relative to chlorophyll a leading to a lower chlorophyll a/b ratio. Comparable

to the patterns observed for total chlorophyll, there was a gradual increase in carotenoid content also.

The results revealed the mechanisms of shade adaptation both at the structural and functional level. The study further helped to quantify the optimum shade requirement of five species of medicinal plants. Accordingly, the shade requirement varied for different species–the optimum being 70% shade for *Adhatoda vasica* and *Plumbago rosea*, 60% shade for *Adhatoda beddomei* and 50% shade for *Alpinia galanga* and *Strobilanthes heyneanus*. An evolutionary aspect of different degrees of shade adaptation is also clearly evident.

A species wise analysis of the physiological effect of shade indicated a few major common features, with minor differences in certain components. For instance, total dry matter and total leaf area per plant increased under all the levels of shade irrespective of species. Correspondingly, there was a significant reduction in leaf thickness and specific leaf weight. This could be accomplished due to an alteration in the structural make up, with a reduction in cell number as well as intercellular space. A reduction in palisade cell layer under shade, lowers the shading of chloroplasts, enabling a low light saturated photosynthesis for the shade grown plants. The decrease in photosynthetic rate, observed under shade, could have thus resulted from a reduction in palisade cell layer, which contributes to major part of the photosynthetic machinery, coupled with a reduced surface area for gas exchange. On the contrary, on a per leaf basis, the increased photosynthetic rate due to an increased leaf area, in turn enhanced the dry matter production.

In summary, all the five species of medicinal plants tended to enhance the dry matter production under shade. This happens in spite of a clear reduction in the photosynthesis per unit area of leaf. The main mechanism of adaptation is increase in the total leaf area and leaf and shoot dry weight.

BIBLIOGRAPHY

Abrams, M. D. 1987. Leaf structural and photosynthetic pigment characteristics of three gallery-forest hardwood species in North-east Kansas, USA. *Forest Ecology and Management* **22**(3-4): 261-66.

Abrams, M. D. and Kubiske, M. E. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in Central Wisconsin USA influence of light regime and shade tolerance rank. *Forest Ecology and Management* **31**(4): 245-254.

Adams, W. W. III; Osmond, C. B. and Sharkey, T. D. 1987. Responses of two Cam species to different irradiances during growth and susceptibility to photoinhibition by high light. *Plant Physiology* (Bethesda) **83**(1): 213-18.

Adams, W. W. III; Terashima, I; Brugnoli, E. and Demmig B. 1988. Comparisons of photosynthesis and photoinhibition in the Cam Vine Hoya-Australis and several C-3 vines growing on the coast of Eastern Australia. *Plant Cell and Environment* **11**(3): 173-82.

Agata, W; Hakoyama, S. and Kawamitsu, Y. 1985. Influence of light intensity temperature and humidity on photosynthesis and transpiration of *Sasa nipponica* and *Arundinaria pygmaea*. *Botanical Magazine Tokyo* **98**(1050): 125-36.

Agusti, S; Enriquez, S; Frost-Christensen H; Sand-Jensen K and Duarte C. M. 1994. Light harvesting among photosynthetic organisms. *Functional Ecology* **8**(2): 273-79.

Alvim, P. De T. 1960. Physiology of growth and flowering in coffee. *Coffee* **2**: 57-62.

Aminuddin B. M. 1986. Light requirements of *Shorea materialis* seedlings. *Pertanika* **9**(3): 285-90.

Anderson, J. M; Goodchild, D. J. and Boardman, N. K. 1973. Composition of the photosystems and chloroplast structure in extreme shade plants. *Biochimica et Biophysica Acta* **325**: 573-85.

Andrews, M; Box, R; Mcinroy, S. and Raven, J. A. 1984. Growth of *Chara hispida* 2 shade adaptation. *Journal of Ecology* **72**(3): 885-96.

Arnon, D. I. 1949. Copper enzymes in isolated chloroplasts polyphenol oxidase in *Beta vulgaris*. *Plant Physiology* **24**: 1-15.

Asolkar, L. V; Kakkar, K. K. and Chakre, O. J. 1992. *Second supplement to glossary of Indian medicinal plants with active principles* Pt 1 (A-K) (1965-1981). Publication and Information Directorate, New Delhi, pp. 23-24.

Ball, M. C. and Farqhar, G. D. 1984a. Photosynthetic and stomatal responses of two mangroove species *Aegiceras corniclattum* and *Avicennia marina*, to long term salinity and humidity conditions. *Plant Physiology* **74**: 1-6.

Ball, M. C. and Farqhar, G. D. 1984b. Photosynthetic and stomatal responses of the mangroove *Avicennia marina*, to trannient salinity conditions. *Plant Physiology* **74**: 7-11.

Begonia, G. B; Aldrich, R. J. and Nelson, C. J. 1988. Effects of simulated weed shade on soybean photosynthesis, biomass partitioning and axillary bud development *Photosynthetica* **22**(3): 309-19.

Berner, T; Achituv, Y; Dubinsky, Z. and Benayahu, Y. 1987. Pattern of distribution and adaptation to different irradiance levels of zooxanthellae in the soft coral litophyton-*Arobreum octocorallia* alcyonacea. *Symbiosis* **3**(1): 23-40.

Beurlein, J. E. and Pendleton, J. W. 1971. Photosynthetic rates and light saturation curves of individual bean leaves under field conditions. *Crop Science* **11**: 217-19.

Björkman, O; Ludlow, M. M. and Morrow, P. A. 1972a. Photosynthetic performance of two rainforest species in their native habitat and analysis of their gas exchange. *Carnegie Institution of Washington Year Book* **71**: 94-102.

Björkman, O; Boardman, N. K; Anderson, J. M; Thorne, S. W; Goodchild, D. J. and Pyliotis, N. A. 1972b. Effect of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. *Carnegie Institution of Washington Year Book* **71**: 115-35.

Björkman, O. 1968a. Carboxydismutase activity in shade-adapted and sun-adapted species of higher plants. *Physiologia Plantarum* **21**: 1-10.

Björkman, O. 1968b. Further studies on differentiation of photosynthetic properties in sun and shade ecotypes of *Solidago virgaurea* L. *Physiologia Plantarum* **21**: 84-89.

Björkman, O. 1970. Characteristics of the photosynthetic apparatus as revealed by laboratory measurements. In: *Prediction and measurement of photosynthetic productivity*, pp. 267-81. Wageningen Cent. Agric. Publ. Doc.

Björkman, O. 1973. Comparative studies on photosynthesis in higher plants. In: Giese, A. (ed.), Current topics in photobiology, photochemistry and photophysiology, vol. 8, Academic Press, New York, pp. 1-63.

Björkman, O. 1981. Responses to different quantum flux density. *Encyclopaedia of Plant Physiology New Series* **120**: 57-107.

Björkman, O. and Holmgren, P. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. *Physiologia Plantarum* **16**: 889-914.

Björkman, O; Holmgren, P. 1966. Photosynthetic adaptation to light intensity in plants native to shaded and exposed habitats. *Physiologia Plantarum* **19**: 854-89.

Black, J. N. 1955. The interaction of light and temperature in determining the growth rate of subterranean clover (*Trifolium subterraneum* L.). *Australian Journal of Biological Science* **8**: 330-43.

Blackman, G. E. 1960. Responses to environmental factors by plants in the vegetative phase. In: Zarrow, M. S. (ed.), *Growth in living systems*, Basic Books, Inc., New York.

Blackman, G. E. and Black, J. N. 1959. Physiological and ecological studies in the analysis of plant environment. XII. The role of the light factor in limiting growth. *Annals of Botany* **23**: 131-45.

Blackman, G. E. and Wilson, G. L. 1951a. Physiological and ecological studies on the analysis of plant environment. VII. An analysis of the differential effects of light intensity on the net assimilation rate, leaf area ratio and relative growth rate of different species. *Annals of Botany* **15**: 373-408.

Blackman, G. E. and Wilson, G. L. 1951b. Physiological and ecological studies in the analysis of plant environment. VI. The constancy for different species of a logarithmic relationship between net assimilation rate and light intensity and its ecological significance. *Annals of Botany* **15**: 63-94.

Boardman, N. K; Björkman, O; Anderson, J. M; Goodchild, D. J. and Thorne, S. W. 1975. Photosynthetic adaptation of higher plants to light intensity: Relationship between chloroplast structure, composition of the photosystems and photosynthetic rates. In: Avron, A. (ed.), Proceedings of 3rd International Congress on Photosynthesis, Elsevier, Amsterdam, pp. 809-27.

Boardman, N. K. 1977. Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology* **28**: 355-77.

Böhning, R. H; Burnside, C. A. 1956. The effect of light intensity on rate of apparent photosynthesis in leaves of sun and shade plants. *American Journal of Botany* **43**: 557-61.

Bongers, F; Popma, J. and Iriarte-Vivar, S. 1988 Response of *Cordia megalantha* blake seedlings to gap environments in tropical rain forest. *Functional Ecology* **2**(3): 379-90.

Bolhar-nordenkampf, H. R. 1982. Shoot morphology and lear anatomy in relation to photosynthetic efficiency. In: *Techniques in bioproductivity and photsynthesis*, eds. J. Coombs and D. O. Hall, Pergamon Press, Oxford.

Bowes, G; Ogren, W. L; Hageman, R. H. 1972. Light saturation photosynthesis rate, RuDP carboxylase activity and specific leaf weight in soybeans grown under different light intensities. *Crop Science* **12**: 77-79.

Butler, W. L. 1977. Chlorophyll fluorescence: A probe for electron transfer and energy transfer. In: Trebst, A and Avron M. (ed.), *Encyclopaedia of Plant Physiology*, New series, vol. 5 (Photosynthesis I), New York, pp. 149-67.

Carter, G. A. and Teramura, A. H. 1988. Vine photosynthesis and relationships to climbing mechanics in a forest understorey. *American Journal of Botany* **75**(7): 1011-18.

Castillo, Z. J. 1961. Ensayo de analysis del erecimiento in cage (Growth analysis study with coffee). *Cenicafe* **12**: 1-16.

Cegdell, R. 1988. The functions of pigments in chloroplasts. In: T. V. Goodwin (ed.), *Plant pigments*, Academic Press, New York, pp. 183-230.

Chabot, B. F. and Chabot, J. F. 1977. Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca*. *Oecologia* **26**: 363-77.

Chabot, B. F; Jurik, T. W. and Chabot J. F. 1979. Influence of instantaneous and integrated light-flux density on leaf anatomy and photosynthesis. *American Journal of Botany* **66**: 940-45.

Chopra, R. N; Nayar, S. L. and Chopra, I. C. 1992. *Glossary of Indian medicinal plants*, CSIR, New Delhi, p. 330.

Cooper, C. S. 1967. Relative growth of alfalfa and birdsfoot trefoil seedlings under low light intensities. *Crop Science* 7: 176-78.

Cowan, I. R. 1986. Stomatal behaviour and the environment. *Advanced Botanical Research* **4**:1176-1227.

Crookston, R. K; Treharne, K. J; Ludford, P. and Ozbun, J. L. 1975. Response of beans to shading. *Crop Science* **15**: 412-16.

de Castro, F; Montenegro, L; Aviles, C; Moreno, M. and Bolanos, M. 1961. Effecto del sombrto en los primeros años de vida de un cafetal. *El Café de El Salvador* **26**(354-355): 317-50.

de Castro, F. S; Moreno, M; Montenegro, L. and Bolanos, M. 1962, Influence of shade, organic matter and planting distances upon growth of coffee seedlings. *Coffee* **4**: 25-35.

Delaney, R. H. and Dobrenz, A. K. 1974a. Morphological and anatomical features of *Alfalfa* leaves as related to CO_2 exchange. *Crop Science* **14**: 444-47.

Delaney, R. H. and Dobrenz, A. K. 1974b. Yield of *Alfalfa* as related to carbon exchange. *Agronomy Journal* **66**: 498-500.

Doley, D. 1978. Effects of shade on gas exchange and growth in seedlings of *Eucalyptus grandis* Mill ex Maiden. *Australian Journal of Plant Physiology* **5**: 723-38.

Ducrey, M. 1992. Variation in leaf morphology and branching pattern of some trophical rain forest species from Guadeloupe French West Indies under semi-controlled light conditions. *Annales des Sciences Forestieres* **49**(6): 553-70.

Ducrey, M. 1994. Influence of shade on photosynthetic gas exchange of 7 tropical rain-forest species from Guadeloupe (French West Indies). *Annales des Sciences Forestieres* **51**(1): 77-94.

Esau, K. 1965. Plant Anatomy, Wiley, New York, pp. 429-30.

Egle, K. 1960. Menge und verhältnis der pigmente. In: Ruhland W. (ed.), *Encyclopaedia of Plant Physiology* 5(1): 452-96, Springer Verlag, Berlin.

Ehleringer, J; Björkman, O. 1978. A comparison of photosynthetic characteristics of *Encelia* species possessing glabrous and pubescent leaves. *Plant Physiology* **62**: 185-90.

Evans, G. D; Hughes, A. P. 1961. Plant growth and the aerial environment. 1. Effects of artificial shading on *Impatiens parviflora*. *New Phytology* **60**: 150-80.

Fahl, J. I; Carelli, M. L. C; Vega, J. and Magalhaes, A. C. 1994. Nitrogen and irradiance levels affecting net photosynthesis and growth of young coffee plants (*Coffea arabica* L.). *Journal of Horticultural Science* **69**(1): 161-69.

Fails, B. S; Lewis, A. J. and Baden, J. A. 1982. Net photosynthesis and transpiration of sun and shade grown *Ficus benjamina* leaves. *Journal of American Society of Horticultural Science* **107**: 758-61.

Foggio, M. N. and Warrington. 1989. Light and vegetative growth in the grasses *Deschampsia flexuosa* L. Trin and *Festuca ovina* L. *Functional Ecology* **3**(4): 439-46.

Frere, H. and Papov, G. F. 1949. *Agrometeorological crop monitoring and forecasting.* FAO, Plant production and protection, paper 17, Rome.

Friend, D. J. C. 1984. Shade adaptation of photosynthesis in *Coffea arabica*. *Photosynthesis Research* **5**(4): 325-334.

Friend, D. J. C; Helson, V. A. and Fisher, J. E. 1962. The rate of dry weight accumulation in Marquis wheat as affected by temperature and light intensity. *Canadian Journal of Botany* **40**: 939-55.

Fukuoka, N; Yoshioka, H; Shimizu, E and Fujiwara, T. 1996. Effect of shading cabbage seedlings on their physiological processes and rooting ability after transplanting to the nursery. *Journal of the Japanese Society for Horticultural Science* **65**(3): 545-51.

Geider, R. J; Osborne, B. A. and Raven, J. A. 1985. Light dependence of growth and photosynthesis in *Phaeodactylum tricornutum* Bacillariophyceae. *Journal of Phycology* **21**(4): 609-19.

Goldsborough, W. J; Kemp, W. M. 1988. Light responses of a submersed macrophyte implications for survival in turbid tidal waters. *Ecology* **69**(6): 1775-86.

Goodall, D. W. 1955. Growth of cocoa seedlings as affected by illumination. *Proc. 14th Int. Hort. Congr.*, pp. 1501-10.

Goodchild, D. J; Björkman, O; Pyliotis, N. A. 1972. Chloroplast ultrastructure, leaf anatomy and content of chlorophyll and soluble protein in rainforest species. *Carnegie Institution of Washington Year Book* 71: 102-07.

Grahl, H. and Wild, A. 1973. Lichtinduzierte Veränderungen im Photosynthescapparat von *Sinapis alba. Ber Dtsch. Bot. Ges.* **86**: 341-49.

Groninger, J. W; Seiler, J. R; Peterson, J. A. and Kreh, R. E. 1996. Growth and photosynthetic responses of four Virginia piedmont tree species to shade. *Tree Physiology* **16**(9): 773-78.

Guiscafre, A. J. and Gomez, L. A. 1942. Effect of solar radiation intensity on the vegetative growth and yield of coffee. *Journal of Agriculture* **26**(4): 73-90.

Haberlandt. 1914. *Physiological plant anatomy*, Today and Tomorrow Printers and Publishers, New Delhi.

Hampson, C. R; Azarenko, A. N. and Potter, J. R. 1996. Photosynthetic rate, flowering and yield component alteration in hazelnut in response to different light environments. *Journal of the American Society for Horticultural Science* **121**(6): 1103-11.

Harborne, J. B. 1973. Phytochemical methods, Chapman and Hall, London.

Hariri, M; Prioul, J. L. 1978. Light-induced adaptive responses under greenhouse and controlled conditions in the fern *Pteris cretica var. ouvardii* II. Photosynthetic capacities. *Physiologia Plantarum* **42**: 97-102.

Hesselman, H. 1904. Zur Kenntnis des Pflanzenlebens schwedischer Laubwiesen. Eine physiologisch-biologische and pflanzengeographische Studie. *Beih Bot. Centralbl* **17**: 341-460

Hiroi, T. and Monsi, M. 1963. Physiological and ecological analyses of shade tolerance of plants. 3. Effect of shading on growth attributes of *Helianthus annuus*. *Botanical Magazine* **76**: 121-29.

Holmes, M. G. and Smith, H. 1977a. The function of phytochrome in the natural environment I. Characterization of daylight for studies in photomorphogenesis and photoperiodism. *Photochemistry and Photobiology* **25**: 533-38.

Holmes, M. G. and Smith, H. 1977b. The function of phytochrome in the natural environment II. The influence of vegetation canopies on the spectral energy distribution of natural daylight. *Photochemistry and Photobiology* **25**: 539-45.

Holmes, M. G. and Smith, H. 1977c. The function of phytochrome in the natural environment IV. Light quality and plant development. *Photochemistry and Photobiology* **25** .551-57.

Huang, J. H. and Kuo, S. R. 1996. The morphological changes of Formosan Michelia seedlings grown under different light intensities. *Quarterly Journal of the Experimental Forest of National Taiwan University* **10**(1): 49-65.

Huerta, S. A. 1954. La influence de la intensidad de luz en la efficiencia asimilatoria y el erecimiento de cafeto (The influence of light intensity on the efficiency of assimilation and on growth of coffee). Ph.D. thesis, Inter American Institute of Agricultural Science, Costa Rica.

Hunt, R. 1982. *Plant growth curves-The functional approach to plant growth analysis*, Edward Arnold Publishers Ltd., London.

Huxley, P. A. 1962. Physiological and ecological investigations with coffee seeds and seedlings in Uganda. Ph. D. thesis, University of Reading, Uganda.

Huxley, P. A. 1967. The effects of artificial shading on some growth characteristics of arabica and robusta coffee seedlings 1. The effects of shading on dry weight, leaf area and derived growth data. *Journal of Applied Ecology* **4**: 291-308.

Hughes, A. P. and Cockshull, K. E. 1971. The effects of light intensity and carbon dioxide concentration on the growth of *Chrysanthemum morifolium* cv. Bright golden Anne. *Annals of Botany* **35**: 899-914.

I'ma Neerakkal; Vinoth, T; Vijayakumar, K. R. and Sethuraj, M. R. 1995. Screening for shade tolerance of potential medicinal plants as intercrops in rubber plantations. Presented in International Conference on Current Progress in Medicinal and Aromatic Plant Research, 1995, Calcutta, India.

Indian Rubber Statistics, Rubber Board, Kottayam, vol. 21, 1996.

Johansen, D. A. 1940. *Plant Microtechnique*, Mc Graw Hill, New York.

Johnson, G. N; Scholes, J. D; Horton, P. and Young, A. J. 1993. Relationships between carotenoid composition and growth habit in British plant species. *Plant Cell and Environment* **16**: 681-86.

Johnson, G. N; Young, A. J. Scholes, J. D. and Horton, P. 1993. The dissipation of excess excitation energy in British plant species. *Plant Cell and Environment* **16**: 673-79.

Jones, H. G. 1983. Radiation: In plants and microclimate, pp. 19-20, Press Syndicate of the University of Cambridge, Cambridge.

Joseph, T; George, K. T; Veeraputhran K. and Mohankumar, S. 1995. Are medicinal plants viable as intercrops? *Rubber* **9**(3): 105-10.

Jurik, T. W. 1986. Can species be ranked by SLW relative to shade tolerance? *American Journal of Botany* **73**: 1089-92.

Jurik, T. W; Chabot, J. F. and Chabot, B. F. 1979. Ontogeny of photosynthetic performance in *Fragaria virginiana* under changing light regimes. *Plant Physiology* **63**: 542-47.

Kirk, J. T. O. and Allen, R. L. 1965. Dependence of chloroplast pigment synthesis on protein synthesis: Effect of actidione. *Biochemical and Biophysical Research Communications* **21**: 523-30.

Kirk, J. T. O; Tilney-Bassett, R. A. E. 1967. *The Plastids*. Freeman, San Francisco, 608 p.

Kirtikar, K. R. and Basu, B. D. 1984. *Indian medicinal plants*, 1465-2449.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**(3-4): 419-28.

Kjelgren, R. 1994. Growth and water relations of Kentucky coffee tree in protective shelters during establishment. *Hort Science* **29**(7): 777-80.

Klinka, K; Wang, Q; Kayahara, G. J; Carter, R. E. and Blackwell, B. A. 1992. Light growth response relationship in Pacific silver fir *Abies amabilis* and subalpine fir *Abies lasiocarpa*. *Canadian Journal of Botany* **70**(10): 1919-30.

Kohyama, T. and Hotta, M. 1990. Significance of allometry in tropical saplings. *Functional Ecology* **4**(4): 515-22.

Kramer and Kozlowski. 1979. *Physiology of trees*, Mc Graw Hill Book Co.

Lakshmamma, P. and Rao, I. V. 1996. Response of blackgram (*Vigna mungo* L.) to shade and naphthalene acetic acid. *Indian Journal of Plant Physiology* **1**(1): 63-64.

Ledig, F. T; Borman, F. M. and Wenger, K. F. 1970. The distribution of dry mater growth between shoot and roots in Loblolly pine. *Botanical Gazette* **131**: 349-59.

Lichtenthaler, H. K; Buschmannc, Doll M; Fiebz, H. J; Bach, T; Kozel, U; Meier, D. and Rahmsdorf, U. 1981. Photosynthetic activity, chloroplast ultrastructure and leaf characteristics of high light and low light plants and of sun and shade leaves. *Photosynthesis Research* **2**: 115-41.

Liu, Z; Carpenter, S. B. and Constantin, R. J. 1997. Campthothecin production in *Camptotheca acuminata* seedlings in response to shading and flooding. *Canadian Journal of Botany* **75**(2): 368-73.

Loach, K. 1970. Shade tolerance in tree seedlings II. Growth analysis of plants raised under artificial shade. *New Phytology* **67**: 273-86.

Ludlow, C. J. 1968. Photosynthesis of sun and shade ferns. Ph. D. thesis, Vanderbilt University, Nashville, Tenn., 165 pp.

Ludlow, M. M and Wilson, G. L. 1971. Photosynthesis of tropical pasture plants II. Photosynthesis and illuminance history. *Australian Journal of Biological Sciences* **24**: 1065-75.

Machado, A. 1946. Influencia del sombrio et suelo y los practicas de cultivo en el desarollo del cafeto en sus premeros meses de vida propia; expei mento preliminar (The effect of shade, soil and cultural practices on the early development of the coffee tree). *Bol. Inf. Cent. nac. Invest. Cafe Colombiu* 1-32 (*Horticultural Abstract* **21**: 3009).

Madsen, J. D; Hartleb, C. F. and Boylen, C. W. 1991. Photosynthetic characteristics of *Myriophyllum spicatum* and six submersed aquatic macrophyte species native to lake George New York. *Freshwater Biology* **26**(2): 233-40.

Maestri, M. and Gomez, F. R. 1961. Crescimiento de mudas de cafe (*Coffea arabica* L. var. Bourbor sob differentes de luz. (The growth of transplanted seedlings of coffee under different light intensities). *Revia Ceres* **11**: 265-71.

Maggs, D. E. 1960. The stability of the growth pattern of young apple trees under four levels of illumination. *Annals of Botany* N. S. **24**: 434-50.

Mansfield, T. A. and Jones, M. B. 1976. Photosynthesis: Leaf and whole plant aspects. In: *Plant structure, function and adaptation*, M. A. Hall (ed.), The Mac Millan Press Ltd., London.

Marler, T. E; Schaffer B. and Crane, J. H. 1994. Developmental light level affects growth, morphology and leaf physiology of young carambola trees. *Journal of the American Society for Horticultural Science* **119**(4): 711-18.

Masarovicova, E. and Elias, P. 1985. Seasonal changes in the photosynthetic response of *Mercurialis perennis* plants from different light regime conditions. *Biologia Plantarum* **27**(1): 41-50.

Mathew, M; Potty, S. N; Punnoose, K. I. and George, C. M. 1978. Intercropping in rubber plantations. *Journal of Plantation Crops* 1 (Suppl.), pp. 431-37.

McCarthy, J. J. and Dawson, J. O. 1990. Growth and water use efficiency of *Quercus alba, Quercus bicolor, Quercus imbricaria* and *Quercus palustris* seedlings under conditions of reduced soil water availability and solar irradiance. *Transactions of the Illinois State Academy of Science* **83**(3-4): 128-48.

McClelland, T. B. 1934. Coffee investigations-shading favours coffee development. *Rep. P. Rico fed. agric. Exp. Stn.*, pp. 13-15.

McKendrick, S. L. 1996. The effect of shade on seedlings of *Orchis morio* and *Dactylorhiza fuchsii* in chalk and clay soil. *New Phytologist* **134**(2): 343-52.

McKiernan, M. and Baker, N. R. 1991. Adaptation to shade of the light harvesting apparatus in *Silene dioica*. *Plant Cell Environment* **14**(2): 205-12.

McLaren, J; Smith, H. 1978. Phytochrome control of the growth and development of *Rumex obtusifolia* under simulated canopy light environments. *Plant Cell Environment* **1**: 61-67.

Messier, C; Honer, T. W. and Kimmins, J. P. 1989. Photosynthetic photon flux density red to far-red ratio and minimum light requirement for survival of *Gaultheria shallon* in western red *Cedar western* hemlock stands in Coastal British Columbia Canada. *Canadian Journal of Forest Research* **19**(11): 1470-77.

Midgley, G. F; Rutherford, M. C; Davis, G. W. and Bosenberg, J. D. W. 1992. Photosynthetic responses of *Heliophilous rhus* spp. to environmental modification by invasive shrubs. *Functional Ecology* **6**(3): 334-45.

Mahmoud, A. and Grime, J. P. 1974. A comparison of negative relative growth rates in shaded seedlings. *New Physiology* **73**: 1215-17.

Monselise, S. P. 1951. Growth of citrus seedlings. I. Growth of sweet lime seedlings in dependence upon illumination. *Palestine Journal of Botany Rehovot Ser.* **8**: 54-75

Morgan, D. C. and Smith, H. 1978. The relationship between phytochrome photoequilibrium and development in light grown *Chenopodium album* L. *Planta* **142**: 187-93.

Morgan, D. C. and Smith, H. 1981. Control of development in *Chenopodium album* L. by shadelight. The effect of light quantity (total fluence rate) and light quality (red: far-red ratio). *New Phytology* **88**: 239-48.

Mori, T; Nakashizuka, T; Sumizono, T. and Yap, S. K. 1990. Growth and photosynthetic responses to temperature in several Malaysian tree species. *Journal of Tropical Forest Science* **3**(1): 44-57.

Mulkey, S. S; Smith, A. P. and Wright, S. J. 1991. Comparative life history and physiology of two understory neotropical herbs. *Oecologia* **88**(2): 263-73.

Myerscough, P. J; Whitehead, F. H. 1966. Comparative biology of *Tussilago farfara, Chamaenerion angustifolium, Epilobium montamum* and *Epilobium adenocaulon* L., General biology and germination. *New Phytology* **65**: 192-210.

Nair, G. S; Sudhadevi, P. K. and Alice Kurian. 1991. Introduction of medicinal and aromatic plants as intercrops in coconut plantations. In: S. P. Raychaudhuri (ed.), Recent advances in medicinal, aromatic and spice crops. **1**: 163-65, Today and Tomorrow's Printers and Publishers, New Delhi.

Newell, E. A; McDonald, E. P; Strain, B. R. and Denslow, J. S. 1993. Photosynthetic responses of *Miconia* species to canopy openings in a low land tropical rainforest. *Oecologia* **94**(1): 49-56.

Nilwik, H. J. M. 1981. Growth analysis of sweet pepper (*Capsicum annum* L.) 2. Interacting effects of irradiance, temperature and plant age in controlled conditions. *Annals of Botany* **48**: 137-45.

Njoku, E. 1960. An analysis of plant growth in some West African species. II. The effect of shade. *Journal of the West African Science Association* **6**: 1-17.

Nobel, P. S; Zaragosa, L. J. and Smith, W. K. 1975. Relationship between mesophyll surface area, photosynthetic rate and illumination level during development of leaves of *Plectranthus parviflorus* henekel. *Plant Physiology* **55**: 1067-70.

Nobel, P. S. 1976. Photosynthetic rates of sun versus shade leaves of *Hyptis emoryi* Torr. *Plant Physiology* **58**: 218-23.

Noggle, G. R. and Fritz, G. J. 1977. *Introductory plant physiology*, Prentice Hall of India Pvt. Ltd., New Delhi.

O'Connell, B. M. and Kelty, M. J. 1994. Crown architecture of understory and open-grown white pine (*Pinus strobus* L.) saplings. *Tree physiology* **14**(1): 89-102.

Orlando, C. S. 1963. Influencia de siete intensidades de sombra en almacigos de cafe. (The effects of six shade intensities in coffee nurseries). *Revta cafet. (Guatem.)* **23**: 6-12.

Osunkoya, O. O; Ash, J. E; Hopkins, M. S. and Graham, A. W. 1994. Influence of seed size and seedling ecological attributes on shade tolerance of rain forest tree species in northern Queensland. *Journal of Ecology* **82**(1): 149-63.

Panse, V. G. and Sukhatme, P. V. 1967. *Statistical methods for agricultural workers*, ICAR, New Delhi.

Patterson, D. T. 1979. The effects of shading on the growth and photosynthetic capacity of itchgrass (*Rottboellia exaltata*). *Weed Science* **27**: 549-53.

Patterson, D. T. 1980a. Shading effects on growth and partitioning of plant biomass in cogongrass (*Imperata cylindrica*) from shaded and exposed habitats. *Weed Science* **28**: 735-40.

Patterson, D. T. 1980b. Light and temperature adaptation. In: Hesketh, J. D. and Jones, J. W. (ed.). *Predicting photosynthesis for Ecosystem models*, vol. 1, CRC Press, Boca Raton, pp. 205-35.

Patterson, D. T. 1985. Comparative ecophysiology of weeds and crops. In: Duke S. O. (ed.), *Weed Physiology*, vol. 1, Reproduction and Ecophysiology, CRC Press, Boca Raton, FL.

Patterson, D. T; Longstreth, D. J. and Peet, M. M. 1977. Photosynthetic adaptation to light intensity in Sakhalin knotweed (*Polygonum sachalinense*). *Weed Science* **25**: 319-23.

Patterson, D. T; Bunce, J. A; Alberte, R. S. and Van Volkenburgh, E. 1977. Photosynthesis in relation to leaf characteristics of cotton from controlled and field environments. *Plant Physiology* **59**: 384-87.

Patterson, D. T; S. O. Duke and Hoagland, R. E. 1978. Effects of irradiance during growth on adaptive photosynthetic characteristics of velvet leaf and cotton. *Plant Physiology* **61**: 402-05.

Popma, J. and Bongers, F. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* (Berlin) **75**(4): 625-32.

Paulson, M. E. and Delucia, E. H. 1993. Photosynthetic and structural acclimation to light direction in vertical leaves of *Silphium terebinthinaceum*. *Oecologia* **95**(3): 393-400.

Purvis, M. J; Collier, D. C. and Walls, D. 1966. *Laboratory techniques in Botany*, Butterworths, London.

Rabinowitch, E. I. 1945. *Photosynthesis and related processes*, vol. 1, Interscience, New York, 599 pp.

Radford, P. J. 1967. Growth analysis formulae-Their use and abuse. *Crop Science* **7**: 171-75.

Regnier, E. E. and Harrison, S. K. 1993. Compensatory responses of common cocklebur (*Xanthium strumarium*) and velvet leaf (*Abutilon theophrasti*) to partial shading. *Weed Science* **41**(4): 541-47.

Regnier, E. E; Salvucci, M. E. and Stoller, E. W. 1988. Photosynthesis and growth responses to irradiance in soybean *Glycine max* and three broad leaf weeds. *Weed Science* **36**(4): 487-96.

Regnier, E. E. and Stoller, E. W. 1989. The effects of soybean (*Glycine max*) interference on the canopy architecture of common cocklebur (*Xanthium strumarium*), jimsonweed (*Datura stramonium*) and velvet leaf (*Abutilon theophrasti*). *Weed Science* **37**: 187-95.

Rincon, E. and Huante, P. 1993. Growth responses of tropical deciduous tree seedling to contrasting light conditions. *Trees* 7(4): 202-07.

Rubber Research Institute of India 1990. Annual report 1988-89. RRII, Rubber Board, Kottayam, pp. 58-59.

Sartoni, G; Cinelli, F; Hirata, T; Katayama, N. and Yokohama, Y. 1993. On the lack of green light-harvesting pigments and the extremely high chlorophyll b-a ratio in the deep water green alga, *Palmophyllum crassum* (Chlorosphaerales). *Japanese Journal of Phycology* **41**(4): 327-31.

Satheesan, K. V; Rao, G. G. and Sethuraj, M. R. 1982. Studies on light climate in relation to planting density in fully foliated rubber plantations. *Treephysindia* **82**: 148-52, Kottayam.

Satheesan, K. V; Rao, G. G; Sethuraj, M. R. and Raghavendra, A. S. 1984. Canopy photosynthesis in rubber (*Hevea brasiliensis*). Characteristics of leaves in relation to light interception. In Advances in photosynthesis research, vol. iv, ISBN 90-247-2945-9. Ed. by Sybesma, C. 1984. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague/Boston/Lancaster.

Sathik, M. B; Panikkar, P. K. S; Vijayakumar, K. R. and Sethuraj, M. R. 1995. Intercropping of medicinal plants in mature rubber plantations. Presented in International Conference on Current Progress in Medicinal and Aromatic Plant Research, 1995, Calcutta, India.

Schaefer, C. and Schmidt, E. 1991. Light acclimation potential and xanthophyll cycle pigments in photoautotrophic suspension cells of *Chenopodium rubrum*. *Physiologia Plantarum* **82**(3): 440-48.

Schulze, E. D. and Hall, A. E. 1981. Stomatal response to water loss and CO_2 assimilation rate of plants in contrasting environments 181-231. In: *Encyclopaedia of Plant Physiology* New Series; 12B. Physiological plant ecology.

Shiraishi, S; Hsiung, T. C, Shiraishi, M. and Kitazaki, M. 1996. Changes in the leaf morphology of Vitis grown under different temperature and light conditions. *Science Bulletin of the Faculty of Agriculture*, Kyushu University **51**(2): 25-31.

Shirazi, G. A; Stone, J. F. and Todd, G. W. 1976. Oscillatory transpiration in cotton plant. I Experimental characterization. *Journal of Experimental* Botany **27**: 610-18.

Singh, M; Ogren, W. L. and Widholm, J. M. 1974. Photosynthetic characteristics of several C_3 and C_4 plant species grown under different light intensities. *Crop Science* **14**: 563-66.

Singh, V. P; Dey, S. K. and Murty, K. S. 1988. Diurnal changes in photosynthesis and related characteristics in rice varieties. *Indian Journal of Plant Physiology* **31**: 320-323.

Sivarajan, V. V. and Indira, B. 1995. *Ayurvedic drugs and their plant sources*, Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi.

Sondergaard, M. and Bonde, G. 1988. Photosynthetic characteristics and pigment content and composition in *Littorella uniflora* L. aschers in a depth gradient *Aquatic Botany* **32**(4): 307-20.

Stahl, E. 1883. über den Einfluβ des sonnigen und schattigen Standortes auf die Ausbildung der Laubblätter. *Jena Z Naturwiss* **16**: 162-200.

Stoller, E W. and Myers, R. A. 1989. Response of soybeans *(Glycine max)* and four broad leaf weeds to reduced irradiance. *Weed Science* **37**: 570-74.

Sturdy, D. 1935. Observations on coffee under artificial shade at Selian Coffee Estate, Arusha, *East African Agricultural Journal* **1**: 135-39.

Sukenik, A; Carmeli, Y. and Berner, T. 1989. Regulation of fatty acid composition by irradiance level in the *Eustigmatophyte nannochloropsis* sp. *Journal of Phycology* **25**(4): 686-92.

Sylvain, P. G. 1952. Effect of shade upon growth and differentiation of coffee seedlings as expressed by physical measurement and chemical composition. Mimeographed report, Inter American Institute of Agricultural Sciences, Turrialba, Costa Rica.

Teskey, R. O. and Shrestha, R. B. 1985. A relationship between carbon dioxide photosynthetic efficiency and shade tolerance. *Physiologia Plantarum* **63**(1): 126-32.

Thayer, S. S. and Bjorkman, O. 1990. Leaf xanthophyll content and composition in sun and shade determined by HPLC. *Photosynthesis Research* **23**: 331-43.

Thornber, J. P. 1975. Chlorophyll proteins: Light-harvesting and reaction centre components of plants. *Annual Review of Plant Physiology* **26**: 127-58.

Turner, M. C; Schulze, E. D and Gollan, T. 1985. The response of stomata and leaf gas exchange to vapour pressure deficits and soil/water content in the merophytic herbaceous species, *Helianthus annuus*. *Oecologia* **65**: 348-55.

Turrell, F. M. 1936. The area of the internal exposed surface of dicotyledon leaves. *American Journal of Botany* **23**: 255-64.

Utsunomiya, N. and Higuchi, H. 1996. Effects of irradiance level on the growth and photosynthesis of cherimoya, sugar apple and soursop seedlings. *Environment Control in Biology* **34**(3): 201-07.

Venkataramanan, D. and Govindappa, D. A. 1987. Shade requirement and productivity of coffee. *Journal of Coffee Research* **17**(2): 16-39.

Venkataramanan, D; Vasudeva, N; Raju, K. I; Ratageri, M. C. and Gopal, N. H. 1983. Growth analysis of coffee 1. The relative growth and net assimilation rate of certain cultivars of coffee. *Journal of Coffee Research* **13**(1): 6-13.

Vijayakumar, K. R; Unni, P. N. and Vamadevan, V. K. 1985. Prevention of photoinduced chlorophyll loss by the use of lime reflectant on the leaves of black pepper (*Piper nigrum* L.). *Agricultural and Forest Meteorology* **34**: 17-20.

Watson, D. J. 1952. The physiological basis of variation in yield. *Advances in Agronomy* **4**: 101-45.

Wejnar, R. and Gundermann, U. 1987. Studies on photosynthetic pigments in lemnaceae 1. The pigment content of indigenous lemnaceae. *Limnologica* **18**(2): 405-08.

Whitehead, F. H. 1973. The relationship between light intensity and reproductive capacity. In: Slatyer, R. O. (ed.), *Plant response to climate factors*, UNESCO, Paris, pp. 73-75.

Wilson, D. and Cooper, J. P. 1969a. Assimilation rate and growth of *Lolium* populations in the glass house in contrasting light intensities. *Annals of Botany* **33**: 951-65.

Wilson, D. and Cooper, J. P. 1969b. Effect of light intensity during growth on leaf anatomy and subsequent light-saturated photosynthesis among contrasing *Lolium* genotypes. *New Phytology* **68**: 1125-35.

Wolfe, W. L. and Zissis, G. J. 1978. *The infrared handbook*. Infrared Informations and Analysis Centre, Environmental Research Institute of Michigan.

Wong, S. C; Cowan, I. R. and Farqhar, G. D. 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature* **282**: 424-26.

Wylie, R. B 1951 Principles of foliar organizaiion shown by sun-shade leaves from ten species of deciduous dicotyledonous trees *American Journal of Botany* **38**: 355-61.

Xu, D Q; Li, D. Y; Shen, Y. G. and Liang, G. A. 1984. On midday depression of photosynthesis of wheat leaf under field contion. *Acta Physiological Sinica* **10**: 269-76.

Young, A. J. 1992. The photoprotective role of carotenoids in higher plants. *Physiologia Plantarum* **33**: 702-08