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SHADE-TOLERANT FLOWERING PLANTS IN THE SOUTHERN

AFRICAN FLORA:

MORPHOLOGY, ADAPTATIONS AND HORTICULTURAL APPLICATION

MSc UP 1998

SHADE-TOLERANT FLOWERING PLANTS IN THE SOUTHERN AFRICAN FLORA :

MORPHOLOGY, ADAPTATIONS AND HORTICULTURAL APPLICATION

by

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SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

MAGISTER SCIENTIAE

IN THE FACULTY OF BIOLOGICAL AND AGRICULTURAL
SCIENCES (DEPARTMENT OF BOTANY)

UNIVERSITY OF PRETORIA

PRETORIA

SUPERVISOR: Prof. Dr. A.E. van Wyk

June 1998

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Pretoria

June 1998

Instead of cursing Israel,

Balaam foretelleth Israel's happiness in Numbers 24:6 ....

As the valleys are they spread forth,
as gardens by the river's side,
as the trees of lign aloes
which the ***Lord*** *hath planted,*
and as cedar trees beside the waters.

I hope that everyone who plants a shade garden,
will enjoy a blessing from it.

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CHAPTER 1

INTRODUCTION

Plants are an important part of our lives. Apart from providing food, fibre, medicine and shelter to man and beast, plants are extremely important contributors to our pleasure, comfort, and well-being. They also help conserve energy, and improve the quality of air, water and soil. The areas around our homes, schools, shopping centers, places of work, along streets and highways, in the central city, parks and other landscaped areas are unthinkable without plants.

Ornamental plants enhance our surroundings in a variety of ways: physical, aesthetic, economical and psychological. Cited most often when the value of landscape plantings is extolled, are their physical attributes: influence on climate, air purification, noise reduction, and erosion control (Harris 1992). The microclimate can be greatly enhanced by plants, (particularly trees) when they are properly selected, placed and maintained.

As far as visual benefits are concerned, the landscape aesthetics of plants are becoming more highly valued in our increasingly artificial world. Our ancestors were hunters and gatherers and very much in touch with nature. However, in modern-day living, ornamental plants can often be the only link providing a basic contact with nature. Plants can keep us emotionally balanced and heighten the pleasure we enjoy in our surroundings. A variety of colour, form, texture and pattern can be provided. Lines are softened, focal points can be accentuated and spaces defined. The monotony of pavements and buildings can be relieved. Enticing play areas, as well as cool, fragrant, settings with serene sounds can be created. In new residential areas, plants create the impression of a well-established place and minimize the raw, unfinished look. Plants can unify and give coherence to visually chaotic scenes, and lastly, plants can emphasize the seasons.

The economical benefit of ornamental plants lies therein that wisely designed landscapes can reduce the heating and cooling costs of buildings. Erosion-control plantings conserve storm water and can prevent or reduce maintenance costs and loss of property. Outdoor landscaping and interior plants have been shown to increase worker productivity and to shorten hospital stays (Harris 1992). The market value of property is greatly increased with the presence of plants, especially trees. The other side of economical benefits lies in the production of the ornamental plants itself. The green industry contributes greatly to the economy of a country and can also be an enormous provider of employment.

A number of studies verify the psychological and health benefits of plants (Harris 1992). Hospitals increasingly include plants in their care and rehabilitation programs to speed up patient well-being. Visual encounters with vegetation may be of greatest benefit for individuals experiencing stress or anxiety. Business and industry have found that attractive buildings and landscapes result in above-average labour productivity, lower absenteeism, and easier recruitment of workers with hard to find skills. Equally important, handsome factories and offices build good community relations (Harris 1992). People have a basic desire for contact with plants, and plants can have a strong positive influence on human behaviour. More studies are needed to verify such relationships and to find out how plants can be used more effectively for human well-being.

For all their importance to our well-being and enjoyment, plants in the landscape have their price. If these plant problems are recognized, it is possible to eliminate or at least minimize them. Plants not only have an initial cost, but they must be maintained throughout their lives. Some plants grow easily from seed and they seem to need little or no care; others require a small fortune to plant and maintain.

As public and private plantings become more common and more expensive to maintain, the people responsible for such plantings are becoming more concerned about the proper selection and care of landscape and ornamental plants. The landscape comprises a palette of plant growth habits: trees, shrubs, vines, grasses, herbaceous flowering and foliage plants, as well as annuals.

In the horticultural industry today, it is well known that shady and low light environments are particularly difficult and problematic areas for which to select suitable plants. All types of shaded areas are considered to be a problem to a greater or lesser extent. Permanent shade is created by buildings or walls or dense overhead tree canopies. Temporary shade is created for part of the day as sun travels from east to west. Dappled shade or partial shade refers to conditions where sunlight is filtered through a thin overhead canopy and plants are never in full sun. There are still more variations in these exposure groups. Furthermore, other climatic factors such as water, temperature and nutrition, must be taken into account for each situation. These problems exist for outdoor as well as indoor plantings.

At present the range of shade plants (sciophytes) used for solving this problem in the horticultural industry in southern Africa is limited and mostly exotic. Few new plants are being introduced to the industry in this sector, with even fewer coming out of the southern African flora.

No comprehensive inventory of shade-tolerant southern African flowering plants has yet been attempted. Neither have their special adaptations for growing in the shade been listed, nor have their horticultural implications been illustrated where possible. Apart from being useful for the horticultural and landscaping industries, such a study could also be of great educational and conservation value. The economical and commercial value of these plants could be enormous. The turnover of the green industry in South Africa is estimated at more than R2000 million per annum. The turnover on potplants alone in South Africa is estimated at approximately R300-R400 million per annum. All these benefits can surely make it worthwhile to look for plants that are adapted to low light conditions out of the rich untapped source of southern African flora.

With this study a dissertation on the subject, with a detailed computer-based information storage system on shade-tolerant plants will be made available. This will facilitate the selection of suitable shade-tolerant plants for potential users such as the horticultural industry, landscape architects and botanists.

OBJECTIVES

The objectives of this study are:

- to identify and discuss the ecological, physiological, anatomical, morphological, architectural and reproductive adaptations found in sciophytes;
- to discuss the relevance of the adaptations found in sciophytes to the horticultural industry;
- to identify shade tolerant southern African species, making specific mention of those with market potential;
- to discuss the horticultural attributes and requirements of southern African sciophytes where possible;
- to compile a computerized database of southern African sciophytes that can be used by the horticultural industry.

The dissertation consists of two parts. The first part contains the scientific review of sciophyte adaptations and characteristics, illustrated where possible with horticultural applications. A whole-plant perspective to sun and shade adaptation is given. Principles for the successful growing of shade plants are described.

The second part contains a selective printout of an electronic database listing the shade plants. Detailed information on each plant is given where available. The complete database is available on computer disc. The fields include the names (scientific, vernacular, family, infraspecific), description (distribution, habit, flower, fruit and leaf description), growth requirements (soil, water, temperature, exposure), uses and decorative value, as well as general comments on the plants. For a detailed description of the fields, see the introduction to Part II.

CHAPTER 2

METHODOLOGY

An in-depth literature survey was made of the ecological, physiological, anatomical, morphological, architectural and reproductive adaptations found in sciophytes. This information is applied to southern African sciophytes and critically examined for its horticultural applications.

A systematic survey of the southern African flora was made to identify shade tolerant species. Many books on indigenous flora was consulted, including popular gardening books and informal pamphlets and articles, as well as scientific literature. My own background in the horticultural industry and more than seven years of experience in this field, was of great value in information retrieval from different sources.

To cover all major climatic regions, countrywide visits to botanical gardens, private and public gardens, herbaria and nurseries were made. More than 20 people were interviewed, including botanists, nurserymen, horticulturists, landscapers, amateur botanists and gardeners, seed merchants and potential end-users of shade plants. These include Johan Kluge, Johan Hurter, Neil Fishwick and Jo Onderstall, all from Nelspruit, Geoff Nichols and Richard Symmonds from Durban, Ernst van Jaarsveld, Anthony Hitchcock and Rob and Rachel Saunders from Cape Town, Karen Behr from Bettys Bay, Noeline Kroon from Sasolburg, Andrea Hepplewhite and Kevin Balkwill from Johannesburg, Danie Dry, Priscilla Swartz, Louis and Erika Meintjies and Peter Seldte from Pretoria.

The shade-tolerant plant species that were growing and often being cultivated in these regions were noted, together with all possible information on the plants that the interview could supply. This included distribution, description of all parts of the plant, reproduction, growth requirements and conditions, ornamental value and uses. Together with the information from several publications, this information was combined in the databases for storage and easy retrieval by the user. Almost any combination of plant characteristics or growth requirements or whatever the user may need, can be printed out from this database.

CHAPTER 3

PERSPECTIVES ON SHADE PLANTS: A REVIEW

3.1 INTRODUCTION

In this chapter a broad overview on shade plants is given. This will explain shade adaptations in a comprehensive way and emphasize advanced adaptations as described in Chapter 4. In these two chapters (3 and 4) the adaptations are described and the applications are discussed immediately following the specific adaptations. The application is printed in bold letters to separate it from the descriptive text.

3.2 HELIOPHYTES AND SCIOPHYTES

Plants may be classified ecologically according to their relative requirements for sunlight and shade. Those that grow best in full sunlight are called heliophytes, and those that grow best at lower light intensities are known as sciophytes. Some heliophytic species can also grow fairly well under shady conditions. Heliophytes that cannot tolerate shady conditions are called obligate heliophytes. Sciophytes likewise can be divided into two groups, depending on their relative ability or inability to tolerate full sunlight. Obligate sciophytes or true shade-plants cannot tolerate full sunlight (Daubenmire 1974).

With most submersed aquatics no difficulty is involved in assessing the importance of the light factor, but in terrestrial habitats other factors, especially temperature and relative humidity, vary concomitantly with light intensity and it is very difficult to evaluate light effects alone (Daubenmire 1974). In fact, investigators have frequently concluded that the failure of seedlings under light intensities that appear to be critically low is really due to shade factors other than light. In assessing the value of the light factor it must not be overlooked that photosynthesis is not the only function requiring light. Not only are there differences in light requirements between plant species, but for some plants light requirements differ during various stages of development. Any explanation of the relative difference in successful heliophytes and sciophytes in sun and shade is therefore complex, resting on the net influence of a galaxy of concomitant variables operating on a series of interdependent plant functions (Daubenmire 1974).

3.3 PLASTICITY AND SHADE TOLERANCE

The major "strategies" employed by plant species to cope with environmental variation have been identified; in these - stress-avoidance and stress-tolerance - plasticity is expressed primarily during vegetative growth (Dengler 1994). The competitive, stress-avoiding strategy is typical of many herbaceous, shrub, and tree species of stable, productive habitats. Here, success depends on the ability to sustain high rates of photosynthesis and mineral nutrient uptake in a continually changing environment. Plant species employing this strategy show the greatest morphological plasticity and more rapid turnover of modular parts. Species that are stress-tolerant occupy habitats of low productivity and limited resources (Dengler 1994). Plant growth is affected by environmental variation in light, temperature, water availability, minerals and other factors. Extreme variation in any of these factors may lead to stress. Shade is one of the most common of these stress factors and thus light conditions are an important determinant of phenotypic plasticity.

The leaves and other organs of shade-growing species are long-lived and exhibit less plasticity in size and shape than non shade-growing species. The degree of plasticity shown by any plant population is regarded as being under genetic control and is, in itself an important adaptive characteristic (Dengler 1994).

Differences in morphology and anatomy of "sun" and "shade" leaves from exposed and shaded portions of the canopy of the same individual are good examples of such plasticity and have been observed and documented over many years. More recent experimental studies of the relationship between the light environment and developmental plasticity have focused primarily on the responses of shade-avoiding competitor species. Shade-tolerant species express less developmental plasticity, but are more likely to show post-developmental cytological and biochemical changes (Dengler 1994). These reversible physiological changes, termed acclimatization, are an important aspect of plasticity.

Application

The most important "tactics" of shade plants for their stress-tolerance strategy are optimum utilization of available energy (light), and the conservation of energy. Each special adaptation of shade-tolerant plants can be related to one of these tactics.

3.4 SUMMARY OF CHARACTERISTICS OF SHADE PLANTS

The amount of light available to a plant as it develops exerts a profound influence on the structure and functions of the organs finally produced. According to Daubenmire (1974), in comparison to plants grown under full sun, individuals developing in the shade usually exhibit the following characteristics:

Morphological features

(a) Thinner stems with not so well-developed xylem and supporting tissues.

(b) Longer internodes.

(c) More leaf area per plant.

(d) Less prolific branching.

(e) Larger cells in leaf blades (in part a result of (d) under Physiologal features, below), which in turn results in:
   (i) leaf blades or blade segments usually larger but thinner;
   (ii) stomata larger and further apart;
   (iii) larger vein islets;
   (iv) less hairs per unit area, leaves of shade plants are normally glabrous (hairless).

(f) Leaves normally not lobed.

(g) Thinner cuticle and cell walls.

(h) More and larger chloroplasts.

(i) Not so well developed palisade, if present.

(j) Better developed sponge mesophyll.

(k) Larger intercellular spaces.

(l) Lower ratio of internal/external leaf surface (largely a result of (e) (iii) above).

(m) Lateral walls of epidermal cells more wavy.

(n) Leaf blades flat, more compound, and orientated at right angles to the path of incident radiation.

(o) Higher ratio of total leaf area to vascular tissue of the supporting stem.

(p) Roots shorter, less numerous and less branched, with a lower root/shoot ratio.

(q) Less fresh weight and dry weight of both roots and shoots. The effect of a unit of light energy becomes more pronounced the nearer the approach to the limit of shade tolerance.

(r) Smaller and less numerous nodules on legume roots, weaker development of ectotrophic micorrhizae.

Physiological features

(a) Usually a higher chlorophyll content with carotenoids consequently less apparent and leaves a dark green.

(a) Low photosynthetic rate per unit surface.

(b) Low respiration rate and consequently low compensation point.

(c) Higher percentage of water on a dry-weight basis.

(d) Less rapid transpiration (related to items (l) and (o) under morphological features).

(e) Lower optimum fertility level.

(f) Lower salt content, sugar content and osmotic pressure. The protoplasts of shade leaves exert so little distending force against their cell walls that they wilt when their water content drops only 1-5%, whereas sun leaves can endure a loss of 20-30% without wilting.

(g) Increase in the acidity of cell sap.

(h) Low carbohydrate/N ratio.

(i) Higher K, Ca and P content than sun leaves.

(j) Lower vigour of flowering and fruiting.

(k) Later appearance of flowers, but earlier maturation of leaves.

(l) Less calories per gram dry weight of seeds.

(m) Less resistance to:
  - (i) temperature injury (related to items (e) under morphological features and (f) under physiological features).
  - (ii) drought (related to (e) and (g) under morphological features and (f) under physiological features).
  - (iii) parasites (related to item (g) under morphological features).

The morphological differences described above not only characterize the same species grown under shade and under bright sunlight, but likewise tend to distinguish *heliophytes* from *sciophytes* when they are brought together in the same habitat. The two phenomena may be distinguished by the terms helioplastic and heliomorphic, respectively. It should, however, be noted that the parallelism between heliophytes and helioplastic modifications does not apply to physiological characteristics to the same extent as it does to morphological attributes. For example, heliophytes are capable of more efficient use of high light intensities than are sciophytes, whereas this relationship is reversed in helioplastic individuals. In a series of individuals of a sciophyte grown under different light intensities, for example, those in the denser shade make more efficient use of light (Daubenmire 1974).

The extent to which any differences in structure(s) and function associated with insulation are really the result of heating and drying influences and can never be determined with certainty. This is because light sources usually emit heat as well as light rays, and because when light is absorbed it is converted into heat. Certainly there is a remarkably close similarity between the helioplastic features enumerated above and xeroplastic features (Daubenmire 1974).

In addition to the usual differences in form between plants grown in sun and in shade, light intensity frequently affects the erectness of plants, but the nature of this influence is entirely unpredictable. In many species individuals grown in full sunlight are prostrate and those receiving shade grow erect (Daubenmire 1974).

A green plant from which light is completely excluded responds somewhat differently to the reactions to suboptimal light discussed above. The stems become extremely long, leaves remain in an immature and unexpanded condition, and the plant loses its green chlorophyll pigments. A plant exhibiting such symptoms is said to be etiolated (Daubenmire 1974).

3.5 ADAPTATION TO SUN AND SHADE: A WHOLE-PLANT PERSPECTIVE

Whole-plant energy capture depends not only on the photosynthetic response of individual leaves, but also on their integration into an effective canopy, as well as the costs of producing and maintaining their photosynthetic capacity. Adaptation to the irradiance level at leaf-level alone does not explain shade-plant behaviour satisfactorily. Characteristics must also be examined at canopy-level and plant-level. Givnish (1988) demonstrated this very well in Table I.

Table 1. Characteristic differences between plants adapted or acclimatized to sunny versus shady extremes in irradiance level (Givnish 1988)

TRAIT	SUN	SHADE
LEAF-LEVEL		
PHOTOSYNTHETIC LIGHT RESPONSE		
Light -saturated rate	High	Low
Compensation irradiance	High	Low
Saturation irradiance	High	Low
BIOCHEMISTRY		
N, rubisco and soluble protein content / mass	High	Slightly lower
Chlorophyll a / chlorophyll b ratio	High	Low
Chlorophyll / soluble protein ratio	Low	High
ANATOMY AND ULTRASTRUCTURE		
Chloroplast size	Small	Large
Thylakoid / grana Ratio	Low	High
MORPHOLOGY		
Leaf mass / area	High	Low
Leaf thickness	High	Low
Stomatal size	Small	Large
Stomatal density	High	Low
Palisade / spongy mesophyll ratio	High	Low
Mesophyll cell surface / leaf area ratio	High	Low
Leaf orientation	Erect	Horizontal
Iridescence, lens-shaped epidermal cells	None	Rare
Reddish leaf undersides	Very rare	Infrequent
CANOPY-LEVEL		
Leaf area index	High to low	Low
Phyllotaxis	Spiral	Distichous
Twig orientation	Erect	Horizontal
Asymmetric leaf bases	Very rare	Infrequent
PLANT-LEVEL		
Fractional allocation to leaves	Low	High
Fractional allocation to roots	High	Low
Reproductive effort	High	Low

3.6 SHADE AND TOTAL PLANT FORM

Both sun and shade plants change their overall form in relation to shade. The response, although almost universal, does, however, vary in extent between different species. The shade plants are distinct in their phenoplasticity. They are able to maintain a constant relative growth rate over a range of light intensity from full sunlight to moderate shade. This plastic response is due to the inverse relationship between dry matter gained per unit of leaf area and the leaf area per unit dry weight of leaf. Thus as the efficiency of the leaf declines in terms of relative productivity per unit of leaf weight, the area of the leaf is altered by the plastic response of the plant to low-light intensity and the productivity of the leaf as a whole is maintained (Crawford 1989).

The net effect of the changes in plant form is to increase the proportion of photosynthetically active leaf material. Thus in most species shading tends to increase the proportion of total dry matter that is present in the leaves. This increase in leaf growth as a result of shading appears in most studies to be at the cost of root growth. In shaded habitats a reduction in root development may not be too harmful due to the buffered conditions of the forest floor. Where nutrients are limiting however, this change may prove unfavourable (Crawford 1989).

Application

Shade plants originating from a forest habitat tend to have shallow root systems and are therefore less resistant to severe drought. Contrary to common garden practice, these plants should be watered more frequently, though with smaller volumes of water at a time.

3.7 ACCLIMATIZATION

To what extent can sun plants (or sun leaves) adapt to shade and shade plants (or shade leaves) adapt to bright sunlight? Mature leaves show very little adaptation to shade or sun, but whole plants of some species adapt very well to either condition during development, especially to shade. Of course there are genetic limits to the extent of adaptation. Some plants seem to be obligate shade plants while others are obligate sun plants. But most are facultative sun or shade plants. Facultative C_3 plants and certain C_4 plants adapt somewhat to shade by producing morphological and photosynthetic characteristics similar to those of shade plants (Björkman 1981). Thus their light compensation points decrease. They photosynthesize much more slowly, mainly because they respire much more and photosynthesis is saturated at lower irradiance levels. They gradually develop the ability to grow in shade, but this growth is slow.

The reverse adaptation from shade to sun conditions is less common Shade plants usually cannot be moved to direct sunlight without photosynthesis being inhibited and the older leaves dying within a few days.

Studies were made by Björkman in 1968 on the differentiation of photosynthetic properties in sun and shade ecotypes of *Solidago virguarea.* The results support the conclusion that the markedly less efficient use of weak light by shaded habitat clones grown in strong as compared with weak light is caused primarily by damage to the photosystems. Measurements of Emerson enhancement and of light-induced absorbance changes provide some evidence that photoreaction II is more affected than photoreaction I.

Enzyme extracts prepared from clones native to an exposed habitat were found to contain considerably higher activities of carboxydismutase (ribulose- 1,5-diphosphate carboxylase) than extracts taken from clones native to shaded habitats (where the plants had previously been grown at a moderately high light intensity). Exposed habitat clones apparently have a genetically determined, higher capacity to produce the carboxylation enzyme than do shaded habitat clones. It is concluded from this and other investigations that differentiation between plants from habitats with contrasting light intensities, whether unrelated species or ecotypes of the same species, probably involves the capacity of several component steps of the photosynthetic process (Björkman 1968).

The photosynthetic acclimatization to changing light environment can be very complicated. A remarkable feature of the photosynthetic apparatus of plants is its adaptability to a wide range of light inputs. The leaves of a tree seedling at the bottom of a tropical forest may receive less than 1% of the light incident at the top. Yet, over it's lifespan, the tree may need to cope with both conditions. Moreover, when a canopy gap forms, seedlings and understorey plants suddenly receive irradiances equal to those in the canopy. The additional light will stimulate extra growth if the plant can utilize it and if new stresses such as photoinhibition of photosynthesis do not offset the extra potential carbon gain. Closure of the gap requires that these plants readjust to the lower available light. Survival in the shaded understorey demands maximization of light capture for photosynthesis concomitant with minimization of losses of energy and carbon in respiration. By contrast, leaves exposed to high light must be able to make efficient use of the available energy while avoiding the possibility of loss of photosynthesis because of photoinhibition or other environmental stresses. The capacity to accomplish these compromises is greatly influenced by changes in other environmental factors, such as nutrient availability and temperature, that often accompany changes in light availability (Pearcy & Sims 1994).

Changes in the light environment experienced by forest plants during their lifetime may range from sunflecks to more sustained changes occurring when gaps are formed or canopies develop. Because acclimatization to a changed light environment involves changes in enzyme and pigment amounts, as well as leaf anatomy and resource allocation as new leaves are produced in the new environment, the time scale over which these processes can occur determines the type of light changes for which acclimatization is important. Sunflecks or even the normal diurnal change in solar radiation occur on too fast a time scale for acclimatization (Pearcy & Sims 1994). Thus regulatory mechanisms such as light activation of enzymes operating on time scales of minutes or less are of primary importance for these short-term light changes. These regulatory mechanisms appear to function to maintain a metabolic balance at existing enzyme levels as the levels of external resources, such as light and carbon dioxide change.

By contrast, the acclimatization changes in the concentrations of enzymes or in leaf anatomy are a redeployment of internal resources (primarily nitrogen and carbon) in a way that either enhances the resistance to stress in the new environment. This redeployment appears to require at the minimum a few days to, in some cases several weeks (Pearcy & Sims 1994). Thus to be beneficial, redeployment should only occur in response to sustained changes lasting for periods longer than these response times.

Application

1. **Since plants need time to "grow" into certain physiological requirements for a specific environment, the acclimatization must be done beforehand by the grower to avoid disappointing the customer.**

2. **If propagation of a specific plant for planting in a shady site is done by cuttings, these cuttings must be taken from the shaded side of the plant which is already acclimatized for shady conditions.**

CHAPTER 4

ADAPTATIONS TO SHADE AND POSSIBLE HORTICULTURAL APPLICATIONS

4.1 INTRODUCTION

In any environment the successful plant populations are those which have evolved the most appropriate physiological, morphological, anatomical, architectural, and reproductive mechanisms. Therefore species occupying diverse habitats are often genetically differentiated in ecologically adapted races (ecotypes) (Björkman & Holmgren 1963). Local climate is of primary importance as a selective factor; light, temperature and humidity show the most remarkable variation from one habitat to another. Photosynthesis is a physiological process most sensitive to variation in these external factors. The photosynthetic apparatus tends to adjust to the specific environment so that the available light energy is utilized most efficiently.

4.2 THE NATURAL LIGHT ENVIRONMENT

4.2.1 Daylight

Daylight is made up of direct sunlight and diffuse skylight. At solar elevations of greater than 10°, the global radiation has a characteristically uniform spectrum between 400 nanometers (nm) and 800 nm. Cloud cover and dust/haze, produce two frequently encountered variations of this typical spectral distribution. Clouds appear to act as non-selective diffusing filters, which reflect a considerable proportion of direct sunlight.

The resulting spectrum shows an increase in the proportion of blue (scattered) light, but very little change at the longer wavelengths (600-800 nm) (Morgan & Smith 1981). The presence of dust or haze in the atmosphere results in a reduction in the proportion of blue light and an increase in the proportion of red light in the daylight spectrum (Morgan & Smith 1981).

4.2.2 Twilight

At solar elevations of less than 10°, that is sunrise and sunset, the variations in spectral distribution are small. Twilight spectra are relatively rich in blue light (from diffuse skylight) and few red light (low attenuated and refracted direct sunlight), and poor in orange-red light. This pattern becomes more exaggerated as the solar elevation decreases and will persist for very different periods of time, depending upon latitude and solar declination. These changes can be detected beneath a forest canopy, but they are sensitive to variation in weather, dust and water content of the horizon sky (Morgan & Smith 1981).

4.2.3 Moonlight and starlight

At night the sole sources of light are moonlight and starlight. Moonlight is the reflection of the direct solar beam. Scattering and refraction by the particles of the lunar surface preferentially attenuate the stouter wavelengths with the result that the moonlight spectrum contains a slightly higher proportion of the larger wavelengths than direct sunlight, to which it is otherwise very similar (Morgan & Smith 1981). The spectral distribution of individual stars depends upon their colour temperature. Global starlight has a spectrum which is similar to moonlight, but with a fluency rate several orders of magnitude lower (Morgan & Smith 1981).

4.2.4 Vegetational shadelight

This is the light encountered within or beneath a vegetation canopy. It has two components: unfiltered daylight (direct sunlight, diffuse skylight, or diffuse light from clouds) which has passed through holes in the canopy, and filtered or attenuated daylight, the spectrum of which has been altered by the canopy by the processes of absorption, reflection and transmission. The spectra for reflection and transmission of green leaves are largely a consequence of absorption by chlorophyll (Morgan & Smith 1981).

A spectrum taken from beneath a broadleaf deciduous canopy on a clear sunny day typically shows troughs in the blue and red, a minor peak in the green, and the major band in the far-red wavelengths. Spectra from beneath coniferous woodland level to have a more uniform distribution of radiation with only a minor peak in the blue, and the proportion of far-red light tends to be lower. Vegetation structure and density have a large effect on the spectral distribution of shadelight. Climatic conditions have only a relatively small effect on the spectrum of vegetational shadelight.

The most striking aspect of all these vegetational shadelight spectra is the large difference in attenuation between the far-red and the visible radiation. For closed vegetational canopies the spectral variations reported in literature are summarized in terms of red/far-red ratio (R:FR). This ratio is generally lower beneath broadleaf deciduous woodland than beneath coniferous woodland. R:FR is always lower in shadelight that in daylight (Morgan & Smith 1981).

4.2.5 Sunflecks

Sunflecks are a special case of vegetational shadelight in which direct sunlight breaks through a gap in the canopy. They are composed of direct sunlight,

sunlight reflected from vegetation, diffuse skylight and vegetation-filtered diffuse skylight. Spectra can vary considerably across a sunfleck. With increasing gap size, the spectral distribution tends towards that of daylight from a clear sky (Morgan & Smith 1981).

4.2.6 Underwater

In water, downwelling radiation is refracted and absorbed. The contrast between diffuse and direct radiation diminishes with depth, and, at depth, weak diffuse upwelling radiation can be a significant proportion of total radiation.

Absorption is wavelength-dependant, and is determined by the degree and type of turbidity. In very clear water, far-red light is rapidly attenuated, and the spectrum of downwelling radiation is predominantly blue. Dissolved organic matter in water selectively and strongly attenuate this blue light. A suspension of algae or other water plants also causes selective attenuation, and this depends upon the cell or colony size, concentration and pigment content. This can vary with the season followed by the spectral changes in downwelling radiation. This effect, especially with seasonal algae bloom, has been observed for both freshwater and sea water (Morgan & Smith 1981).

It appears that aquatic plants show similar adaptations to shade plants because of the low light environment. This can often be seen in leaf shape and red undersurface of leaves. It would be an interesting study to compare adaptations in these two environments.

4.3 ECOLOGY AND CLIMATIC FACTORS

4.3.1 The biome concept

A biome is a broad ecological unit that represents a major life zone extending over a large natural area. A biome contains a relative uniform set of life forms and the biotic component includes both plant and animal forms. Relevant features of biota are closely tied to environmental conditions and are more specifically determined by climate (Rutherford & Westfall 1994).

Nearly all life form systems tacitly assume broad principles in that plants have different ecological amplitudes or relevances, the physiological integration of the total environment is needed for a plant's successful existence and there is often a correlation between morphology and adaptation (Rutherford & Westfall 1994).

Rutherford & Westfall (1994) identified desert, grassland, succulent Karoo, forest, nama Karoo, savanna and fynbos biomes for southern Africa.

The most of our shade plants occur in forest, the fynbos, and savanna biomes which corresponds with the main climatic regions of coastal winter rainfall, coastal summer rainfall and bushveld summer rainfall regions.

In southern Africa we have two entirely distinct floras, viz. the southern fynbos (or sclerophyll) and forest of the winter rainfall area, and the tropical forest, savanna and grassveld of the summer rainfall areas (Acocks 1988). Although entirely different in nature and origin, they are today almost inextricably united, and have cooperated to produce that quite distinct vegetation type the Karoo with all its variations (Acocks 1988).

The succulent habit of many of the Karoo species is not particular to any one vegetation type, but is rather a reaction to habitat, in particular to a permanent

The succulent habit of many of the Karoo species is not particular to any one vegetation type, but is rather a reaction to habitat, in particular to a permanent scarcity of moisture. Succulents are represented in all the veld types of South Africa (Acocks 1988) and form a major component of the southern African shade plants.

4.3.2 Plant communities

Some kinds of plants habitually live together. These communities develop because the various species are able to grow and survive in a similar environment. This is not to say that all plants living in a habitat have precisely the same environment. In fact, it is the modifying effect that plants have on their environment which create different environmental niches within the same habitat (Carpenter & Walker 1990).

Many factors interact in a plant community to enable a particular group of plants to share the same habitat. Competition among plants is a primary factor, particularly when for water, light and nutrition exceeds the supply. In plant communities the plant population adjusts itself, so that the plants that survive can share the available resources among themselves. For example, tall-growing species form an overstorey that controls the community, hence they are called the dominant species. Shorter plants will survive only if they can tolerate the reduction of light resulting from the shade created by the tall species. This relationship among plants is called stratification. For a species to maintain dominance in its community, its plants must be able to reproduce themselves, and this entails competing successfully for all commodities (Carpenter & Walker 1990).

Although competition and stratification among plants act to exclude many plants, they also provide a favourable habitat for others (Crawford 1989). Plants that live on the forest floor for instance, enjoy a habitat that is buffered from extremes of temperature, exposure to wind, and desiccation. In comparison with grassland sites, the forest provides a measure of protection against trampling, heavy grazing and fire. The forest soil, depending on the type of dominant tree and the age of the forest, frequently provides the ground vegetation with a more even supply of water throughout the year (Crawford 1989). By increasing evapotranspiration the tree canopy reduces the tendency of soils in humid areas to become waterlogged and its shade in summer lessens the danger of drought. In addition soil respiration can provide the plants that live near the ground with an enriched source of carbon dioxide, a factor that is generally limiting to plant growth (Crawford 1989). The dependence of one species on another for its survival is equally important in the composition of the plant community.

Plant cover had a profound influence on microclimate. Where there is free air movement, there is no difference between air temperatures in sun and shade. In the absence of wind, however, conditions are quite different Inside a forest, where there is less wind and air movement, the temperature is more stable and warmer than outside it or on the forest edges. Even thin shade strongly reduces the heating of soil by solar radiation while under full shade, soil-surface temperatures remain cooler than air temperatures even during the hottest part of the day. Furthermore, the greater humidity of air under vegetation increases the amount of heat needed to raise its temperature appreciably. For these two reasons forests generally depress maximal air temperatures as well as maximal soil temperatures. At night the rate of loss of heat energy by reradiation is retarded by plant cover, with the result that nocturnal temperatures of both soil and air within vegetation characteristically do not drop as low as those of adjacent open areas (Daubenmire 1974).

Application

1. **These microclimatic differences and requirements can often be imitated easily, enabling plants to be grown outside their normal geographic range. This allows plants with ornamental value to be grown in cultivation and to be available for this purpose far from its natural distribution.**

2. **The mutual interaction of plants with each other and with their environment determines the composition of the plant community. For example, in the dry shade of trees with surface roots, different plants would be used than in the case of moist shade with a south facing wall. Maintenance is facilitated because water requirements are homogenous in a specific landscaped area, and because individual plants grow better and have better survival rates.**

4.3.3 Moisture and temperature conditions

The detrimental effects of high light intensities include their influence in promoting rapid transpiration. Light stimulates the guard cells of stomata to open, as well as increases the permeability of the plasma membranes. The stomata of most plants remain open all day and close at night. It has been shown that transpiration increases rapidly at daybreak and slows to a very low level at sundown, if not earlier, owing to a tissue water-deficit (Daubenmire 1974).

In general, moisture conditions are more favourable under light shade than under dense shade or full sunlight, but as emphasized earlier, shade implies a number of concomitant environmental conditions, and their net effect cannot easily be predicted (Daubenmire 1974).

It is possible that the efficiency of light energy increases with rising temperature. This is one explanation for the fact that in general, the colder the climate, the more intolerant a species of shade. Nevertheless, there is a strong likelihood that the controlling factor here is really the heating, rather than the lighting effects of insulation. It is significant in this connection that at least certain plants exhibit the same structural characteristics when grown in the shade at favourable temperatures as when grown in sun at lower temperatures (Daubenmire 1974).

Some plant species may grow best in sunny situations because they have high heat requirements. Others may escape destruction by fungi only under the low humidities that accompany bright light. Still others may require high light intensities to stimulate flowering, or to open the guard cells in order to obtain sufficient carbon dioxide (Daubenmire 1974).

In dry climates there are many low-growing plants that occur only in the shade of latter ones, under rocks or in crevices and on the shaded slopes of mountains and hills. In southern Africa many of those are succulent. The reason here might be the more favourable temperature and humidity levels encountered in these niches rather than the shade *per se*.

4.3.4 Light relations in plant communities : Spectral composition

The spectral composition of light is also altered in natural shade environments. Chlorophyll within leaves absorbs wavelengths between 400 and 700 nm and transmits a proportionally greater amount of radiation energy beyond 750 nm. This dramatic difference in spectral composition between sunlight and shade is most often expressed in terms of the absorption maximum of the pigment phytochrome: the ratio between the photon flux at 655--665 nm (red) and the photon flux at 725--735 nm (far-red) (R:RF) ratio in full sun is around 1,03--1,22 and in shade varies from 0,09 to 0,77 (Dengler 1994).

4.3.5 Effect of spectral composition

The natural shade of vegetation canopies both reduces irradiance and alters the spectral composition of light, most significantly the R:RF ratio. There is strong evidence that the phytochrome within young, expanded leaves is the photoreceptor of this change in light quality. Light containing red wavelengths (near 660 nm) converts phytochrome to the far-red-absorbing form; upon illumination with far-red light (near 730 nm) or in darkness, the phytochrome is converted back to the red-absorbing form. Depending on the wavelengths of irradiation, and equilibrium between the two forms of phytochrome is rapidly reached. The correlation between measured phytochrome equilibria and plant response obtained by using red to far-red light, supports the direct involvement of phytochrome in the detection of shade (Dengler 1994). To test the effect of spectral composition on plant growth, investigators have compared neutral shade (R:FR alteration) with simulated shade (altered R:FR), or have followed a white light photoperiod by a brief period of far-red treatment that alters the phytochrome equilibrium. The most frequently observed photomorphogenetic effects of shade light are increased internode extension and suppressed lateral branch growth.

The euphotic layer of a forest is the top layer and receives 25--100% of relative illuminance, (figure 1). This layer has dense foliage, may produce flowers and fruit prolifically and is the most productive part of the forest. Lower down, the relative illuminance decreases markedly as the oligophotic layer is reached. Here there is usually less prolific growth of plants, less flowering and fruiting and less animal activity. Below the middle layer the relative illuminance can fall to 1--3%. In the oligophotic layer quite strong competition for light takes place and various adaptations of plants are found (Longman & Jenik 1987).

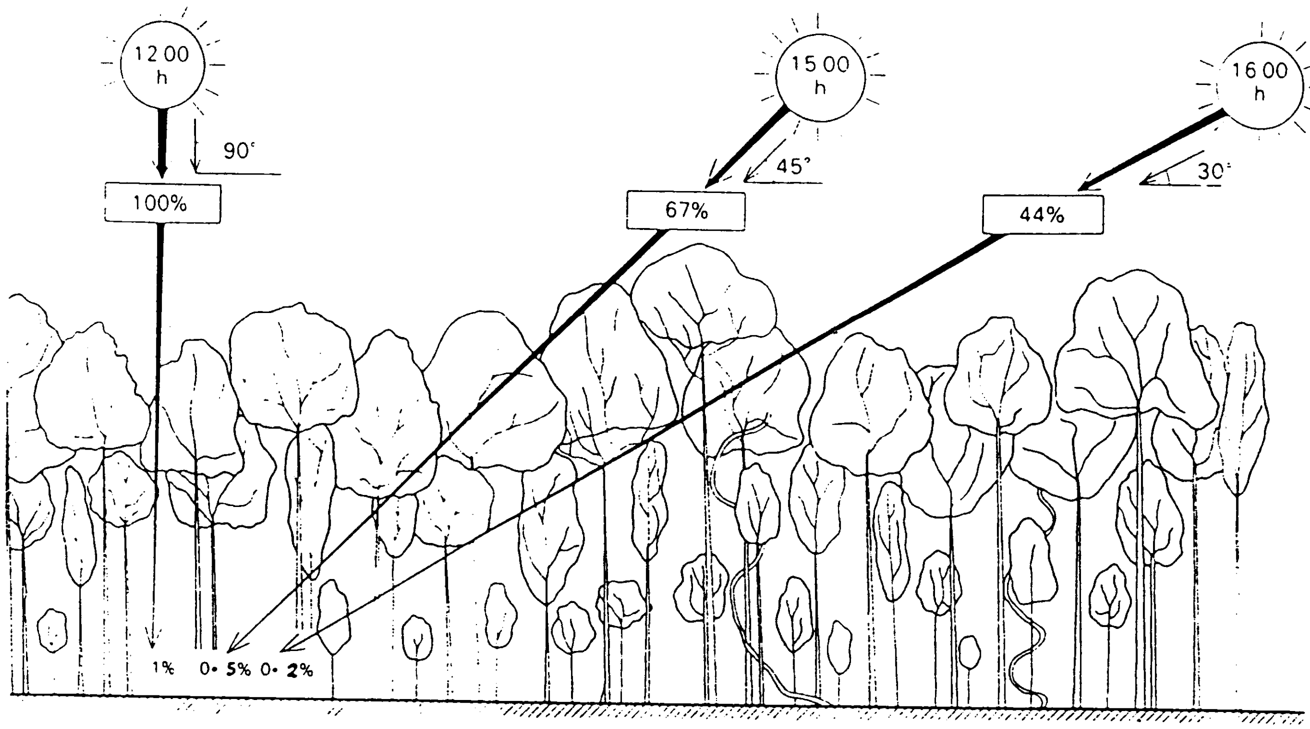

Figure 1. Diagram showing the effect that the structure of tropical forest has upon the penetration of light from different angles. Changes in the relative light intensity above the canopy and at the forest floor, taking as 100% the value above the canopy with the sun overhead at noon (Longman & Jenik 1987)

The quality of the light within the canopy and near the ground in tropical forests is affected by two components: (1) the incidence of unfiltered daylight composed of direct solar irradiation, diffuse skylight and diffuse light reflected from the clouds, and (2) filtered daylight, the spectrum of which has been transformed by the reflection, absorption and transmission processes of the foliage, twigs and stems. Leaves play a major role in the filtering of daylight, for they are effectively opaque in the range of visible wavelengths (400--700 nm), except for a small portion in the green band around 550 nm. Beyond the limits of 700 nm dramatic increase in transparency occurs, and causes a high proportion of far-red wavelengths to penetrate deep into the forest. High representation of far-red radiation is particularly important in relation to the visible near-red band. The low red/far-red ratio occurring within the forest appears to be responsible for numerous morphogenetic processes, notably as a factor maintaining the dormancy of seeds in some colonizing species (Longman & Jenik1987).

The mechanism and ecological significance of the elongation response in plants are presumably similar to that of etiolation, allowing other leaves to grow into better illuminated regions (Fitter & Hay 1981). The situation under a plant canopy, however, has two important characteristics:

a) the alteration in red: far-red ratio is permanent (at least in the leafy season in deciduous forests) and not a 10 min. dawn or dusk effect;

b) the distance from the ground to the unfiltered light may be as much as 100 m, though in temperate woods in southern African conditions 15-30 m is more likely; no etiolation responses will be of value to a herbaceous plant in these conditions, although sustained extension growth might be important for tree seedlings. Weight ratio and petiole length are all characteristically more labile in plants adapted to open conditions than in those found growing in shade.

Another important source of diversity in the illuminance of the forest interior is caused by the small patches of light called 'sunflecks', in which sunlight breaks through a hole in the canopy. Their spectrum and flux density vary considerably over their ever-changing positions, and, remarkably, the red/far-red ratio at their periphery may be lower than in the ambient shade. Moreover, at a certain spot, the photosynthetically active radiation might vary over two orders of magnitude within a few seconds or minutes. Thus the leaves must be adapted to utilizing very low flux densities, but also tolerating and using the high fluxes in sunflecks from direct solar beams (Pearcy 1990, Salisbury & Ross 1992).

The light intensity near the forest floor thus depends partly on the structure of the canopy, but also on the angle at which the sun's rays are striking its surface. The low angle of incidence in the early morning and late afternoon hours increases the path length of the light rays through the canopy. The relative illuminance on the forest floor is considerably diminished, since the oblique rays are obstructed by more leaves, twigs, limbs and trunks, and the number of sunflecks also decreases (Longman & Jenik1987).

4.3.6 Patterns of response to radiant flux density

Flux density or intensity, exerts its primary effect on photosynthesis, acting secondarily on morphogenesis; most morphogenetic responses are to low intensities, but some require greater energy. The ecology of a plant with regard to light intensity is governed by two considerations:

a) placing the leaves in the position that will maximize light interception (architectural). This is above the canopy and in a complex community most of the leaves cannot achieve this. Most leaves will therefore exist at reduced light intensities.

b) maximizing photosynthesis for the energy received, assuming this to be below the light-saturation point for normal photosynthesis, so as to remain in net positive carbon balance (photosynthetic CO_2 fixation greater than the sum of respiration and carbohydrate export). A leaf in negative C-balance will need to import sugars from the rest of the plant and will reduce overall fitness (Dengler 1994).

4.3.7 Temporary light stress

In the northern hemisphere, there is a distinct peak of irradiance in temperate deciduous woods in early spring, and a well-marked group of plants takes advantage of this (Fitter & Hay 1981; Givnish, 1987). Deciduousness in trees in response to seasonal temperature changes (as opposed to variation in water supply) is, however, an adaptive response to avoid frost damage to leaves capable of high productivity, so that the herbs which photosynthesise during this brief seasonal window need to be frost resistant. To take full advantage of the radiation peak they must also have fully expended leaves by April at least, so that leaf growth must take place at very low temperatures in February and March, when photosynthetic activity will be low. This growth therefore requires stored reserves and almost all these species are perennials with underground storage organs, whether bulbs (*Hyacintoides non-scripta, Allium ursinum)* corms (*Cyclamen*), tubers (*Ranunculus ficaria*), or rhizomes (*Anemone nemorosa*). These storage organs are re-charged during the radiation peak (Fitter & Hay 1981).

Occupation of this particular niche, therefore requires the modification of all other parts of the life-cycle. Whereas some species such as *Hyacintoides*, complete their life-cycle during the last phase and remain dormant for the rest of the year, others, such as *Oxalis acetosella*, remain active for a large part of the shade phase. This activity occurs in very dim light and so requires a change in physiology, which is brought about plastically in two distinct ways. *Oxalis* has a photosynthetic system capable of adjustment without morphological change (Fitter & Hay 1981), whereas *Aegopodium podagraria*, a garden weed in northern Europe, but a woodland herb in central Europe, has two leaf types produced by a single plant; thin broad summer leaves, and thicker spring leaves.

Application

In southern Africa, high light intensities, low humidity and relative high day temperatures under deciduous trees during winter and spring days before the first leaves appear, are the norm. Bulbs that flower in late winter and early spring are ideal for this sort of situation. Fast growing ground covers like *Plectranthus* can be planted under these trees for the leafy period. It is a problem however, to plant true shade plants under deciduous trees, and I have seen *Clivia* species planted under *Celtis africana* become severely damaged by winter sun. The protection that the tree canopy gives against very low temperatures is also lost in winter under deciduous trees. Frost sensitive plants can still be grown in colder areas under evergreen trees, but will not survive under deciduous trees.

4.3.8 Effects of topography

The direction and slope of the land surface causes marked variations in the intensity and daily duration of insulation. In general the temperature aspect of this topographic factor is probably more important than the light aspect. On northern slopes temperature and light intensity are higher and humidity is lower. On steep, poleward (southern) slopes, direct sunlight may be completely lacking at noon so that plants must rely heavily on sky light (light scattered by gas molecules and water droplets becomes diffuse light or sky light as contrasted with direct light), which is only about 17% as intense as the light received by a surface level enough to get full direct lighting (Daubenmire 1974).

Application

Select specific eccotypes to match horticultural needs. When hunting for "new" ornamental shade plants, one should try the shaded southern slopes of mountains and hills. Even better, a kloof on the southern slope may produce ecotypes of species that, although they may look identical to their counterparts growing in the sun, might be physiologically different. These shade ecotypes would probably be more suitable for shade gardening.

4.3.9 Mineral nutrition in shaded habitats

Mineral deficiency is a common condition of certain forest soils, notably the podzols (a type of soil characteristic of coniferous forest regions having a greyish-white colour in its upper leached layers) of northern coniferous forests and the laterites (any group of deposits consisting of residual insoluble deposits of ferric and aluminium oxides, formed by weathering of rocks in tropical regions) of tropical rain forests.

In the temperate forests most tree species are infected with ectotropic mycorrhizae. The ground flora also is rich in mycorrhizal associations. Many of the ericaceous genera (e.g. *Erica, Rhododendron*) which are typical of forest floor communities from the northern coniferous forests to the tree covered slopes of the Himalayas, have a particular form of endomycorrhizal association which is characterized by the penetration of the root cortex by septate fungal hyphae forming intercellular hyphal complexes (Moser & Haselwandter,1983).

The many southern African *Erica* species that occur in semi-shade conditions indicate that they are rather facultative than obligate shade plants here. A specialized type of endomycorrhizal association would possibly be also the case for this genus in southern Africa, since they normally occur on nutrient-poor soils.

In early studies on the benefits that accrue to host plants by the development of mycorrhizal associations it was thought that the enhancement of nitrogen uptake played a major role. Although this may sometimes be the case as in ericaceous mycorrhizae, it appears that the greatest influence that the association has on the host plants is to enhance phosphorous uptake from soils with low P availability. The increased uptake appears to come not from using a source of P that is unavailable to the host, but from improved exploitation of greater soil volume by the association (Crawford 1989).

In one study it was concluded that one of the most detrimental aspects of shade environment in forests was the nitrogen deficiency brought about by a very slow rate of decay. Micro organisms responsible for this decomposition also require a lot of nitrogen for the process. The fact that certain plants have much higher nitrogen requirements than others may account for their exclusion from shaded habitats (Daubenmire 1974).

Application

The presence of vesicular arbuscular mycorrhizae (VAM) in the growing medium of ornamental shade plants is very important, especially for forest trees. Plants with coarse roots and few root hairs are dependent on VAM, especially in low-fertility soils and soils with low phosphorous content. The beneficial effects of VAM for the host are that it increases growth nutrient absorption, tolerance against pathogens and also makes the host more resistant to drought (Lombaard 1993).

It is important to recognize that the surge (and subsequent rapid decline) of leaf growth observed in many spring plants of temperate woodlands coincides not only with the "vernal window" of high irradiance, but also with the spring peak of mineral nutrient mobilization from litter decomposition (Grime 1994).

A quite different circumstance of resource supply prevails beneath mature canopies of evergreen trees. Large forest trees that cause deep shade also provide major sinks for mineral nutrients and through intensive mycorrhizal networks, may tightly close and lock up the mineral nutrient cycle, subsequently ground flora are subjected to severe nutrient stress (Grime 1994). On infertile soils in woodland, mineral nutrient constraints preclude the "expensive" development of a temporary canopy during the vernal window and instead favour the slow dynamics, leaf turnover, and conservative use of carbon and mineral nutrients characteristic of many evergreen shade plants (Grime 1994).

The exact opposite may also be true for savanna habitat where a higher amount of nutrients (N, P, K) are available under trees than in the open areas. This is the case in southern Africa with certain *Acacia* species in Sourish Mixed Bushveld where these nutrients stimulate the growth of several grass species. The most important of these grasses is *Panicum maximum*, an important protein rich grazing grass. This phenomenon seems to indicate that the grass-tree association is due to soil enrichment by trees in some way, rather than the shade itself (Bosch & Van Wyk 1970; Smith & Rethman 1989).

The explanation of the superior growth of sciophytes in shade is just as complicated. In the first place sciophytes must have low light requirements The compensation point for heliophytes may be as high as 4 200 L (lux), and as low as 27 L for shade plants. Deep-water algae and mosses that inhabit caves can grow under intensities no greater than that of moonlight (Daubenmire 1974).

Application

Certain observable characteristics in any plant-supporting area suggest a pattern. Analysis of this pattern leads to important conclusions in understanding the ecological relationships and requirements of plants in both natural terrain and managed landscapes.

In the planning and maintenance of landscapes there is a tendency to ignore the ecological relationships of plants and their natural environments. This is unfortunate, because the ultimate performance of a plant or group of plants is dependent on the extent to which the ecological requirements are fulfilled. In addition, the aesthetic qualities of landscape plantings are enhanced when plants of the proper associations are grouped together, just as they are found in natural communities.

4.4 PHYSIOLOGICAL AND PHOTOSYNTHETIC ADAPTATIONS

4.4.1 Introduction

The energy necessary to sustain life on earth is derived from sunlight directly by green plants, or indirectly by other organisms which, except for chemosynthetic bacteria, must eventually depend upon organic compounds synthesized by green plants. Photosynthesis is essentially the only mechanism of energy input into the living world. Through its ability to absorb radiant energy from the sun and convert it into chemical energy contained in simple sugar molecules, chlorophyll provides the essential connecting link between nearly all living organisms and solar energy. In addition light exerts many stimulating effects upon plants, especially upon the differentiation of tissues and organs. In fact, light is rivalled only by water in its influence upon the morphology and anatomy of plants (Daubenmire 1974, Salisbury & Ross 1991). Less evident, but certainly none the less important, are the effects of light on the physiological processes and chemical composition of plants.

4.4.2 Some principles of light absorption by plants

Light has both a wave nature and a particle nature. Light represents only that part of radiant energy with wavelengths that are visible to the human eye, approximately 390 to 760 nm (Figure 2). This is a very narrow region of the electromagnetic spectrum. The particulate nature of light comes in quanta or photons; discrete packets of energy, each having a specific associated wavelength. The energy in each photon is inversely proportional to the wavelength, so the violet and blue wavelengths have more energetic photons than the longer orange and red ones (Salisbury & Ross 1992).

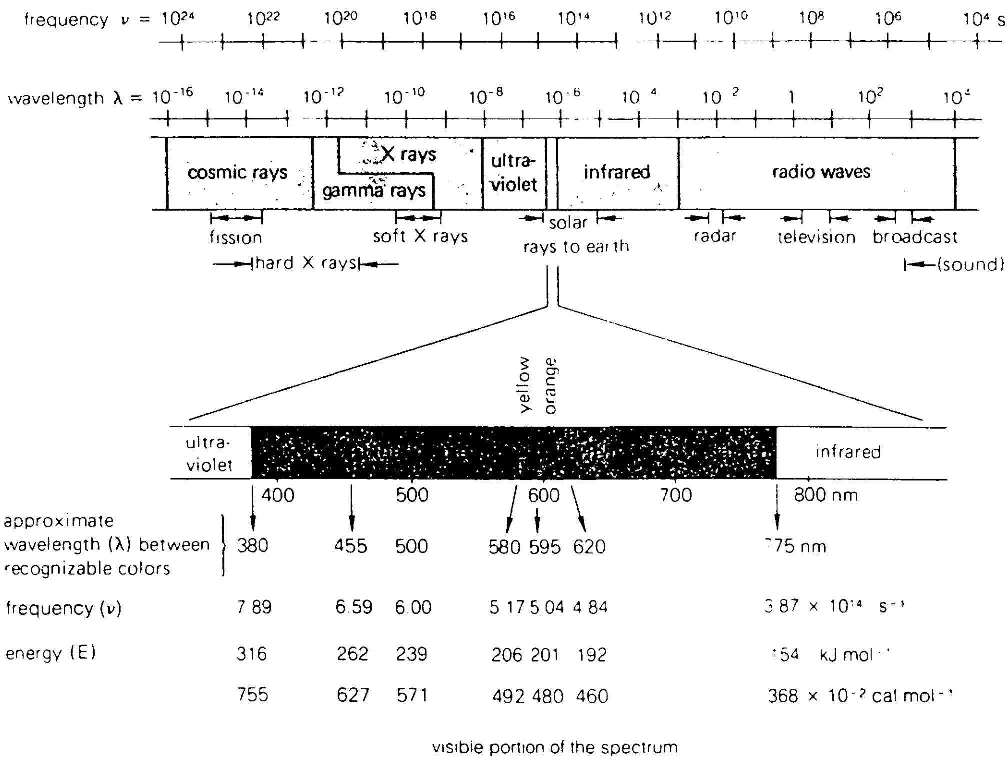

Figure 2. The electromagnetic spectrum, using both frequency (ν) and wavelength (λ) in m. Most of the spectrum is shown, and the visible portion is expanded to depict the region that appears to the human eye to have various colours (Salisbury & Ross 1992).

Thus, the characteristics of light that are most important for plants are irradiance or intensity (measured in foot-candles, lux or photon flux), duration (measured in photoperiods), and quality or spectral composition (measured in wavelengths). The three systems or units for irradiance are: (1) illumination, lumen per square meter - lux (photometric), (2) irradiance, energy in watts per square meter = W/m^2 (radiometric), (3) photon-flux density = quantum per second and square meter (photon radiometry). The flow rate of energy falling on a flat receiving surface (in this case a leaf) per unit time is described as the energy flux or the photon flux (Cathey & Campbell 1980).

Photon units are based on number of photons or quanta which vary in energy with wavelengths. For example, 4 photons at 400 nm have the have the same energy as 7 photons at 700 nm. The following can be defined: *Photosynthetically Active Radiation* (PAR), radiation in the 400 to 700 nm waveband. *Photosynthetic Photon Flux Density* (PPFD), photon flux density of PAR. The number of photons (400 to 700 nm) incident per unit time on a unit surface (suggested units E (einsteins) s^{-1} cm^{2}). *Photosynthetic Irradiance* (PI), radiant energy flux density of PAR. The radiant energy (400 to 700 nm) incident per unit time on a unit surface s/m^{2} (Cathey & Campbell 1980).

Only about 0,2 to 0,3% of the total radiant energy that strikes the earth's surface is actually trapped by plant cells (Hoober 1984). A major factor that contributes to this low yield is that much of the land is arid or otherwise inhospitable to plant life. Yet even in heavily vegetated areas several factors must be taken into account in connection with energy conversion.

Plant pigments only absorb light with wavelengths between 380 and 700 nm (Table 2). Within this range lie the wavelengths of greatest solar intensity, so that nearly one-half of the total spectral energy reaching the earth's surface is available for photosynthesis. Various other losses also occur so that the average practical maximal efficiency of photosynthetic energy conversion is in the order of 5--7%.

Table 2. Photosynthetic efficiency and energy levels (Hoober 1984).

	AVAILABLE LIGHT ENERGY (%)
Total radiant energy at sea level	100
Wavelengths between 400 and 700 nm are photosynthetically usable (50% loss)	50
Reflection, nonproductive absorption, and transmission by leaves(20% loss)	40
Quantum efficiency for CO_2 fixation in 680-nm light (assuming 10 quanta/CO_2 (77% Loss)	9.2
Respiration (40% loss)	5,5
The energy made available through photosynthesis for anabolic processes (constructive metabolism) in plant and animal cells is thus about 5,5% of the total radiant energy.	

The actual efficiency varies among different plants, between geographical locations, and is not uniform throughout the seasons in the year. The surrounding vegetation is probably the most important source of variation in irradiance, and the growth or loss of surrounding plants are the factors most likely to alter the light environment significantly during the development of an individual leaf.

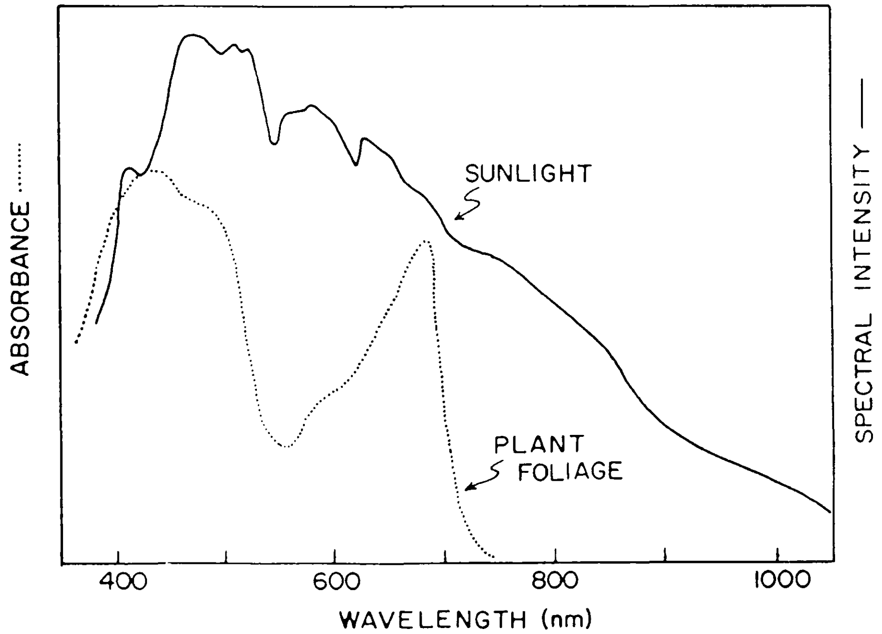

Figure 3. A comparison of the spectrum of sunlight striking the earth's surface with the absorption spectrum of green plant foliage. It is quite apparent that only a portion of the spectrum of light emitted from the sun can be used for photosynthesis by these plants (Hoober 1984).

The least energetic light that performs photosynthesis efficiently in plant cells has a wavelength of about 680 nm, which responds to a peak in the absorption spectrum of chlorophyll *a in vivo*. The efficiency for carbon dioxide fixation in red light is about 30%. Since the same number of quanta is required regardless of the wavelength, the maximal efficiency in blue light, which contains nearly twice the energy per photon as red light, is less.

Leaves of most plant species absorb more than 90% of the violet and blue wavelengths that strike them and almost as high a percentage of the orange and red wavelengths. Almost all of this absorption is by the chloroplast pigments (Salisbury & Ross 1992). In thylakoids, each photon can excite an electron in a carotenoid or chlorophyll. Chlorophylls are green because they absorb green wavelengths ineffectively and instead reflect or transmit them.

Most of the carotenoids (both B-carotene and the xanthopylls) in thylakoids efficiently transfer their excitation energy to the same reaction centres as do chlorophylls and so they contribute to photosynthesis. These pigments absorb only blue and violet wavelengths *in vitro*. They appear yellow or orange to us. The Emerson enhancement effect shows us that two separate groups of pigments or photosystems cooperate in photosynthesis, and for maximum photosynthesis, wavelengths absorbed by both systems must function together. Photosystem I absorbs the long red wavelengths, and photosystem II absorbs the shorter blue wavelengths (Salisbury & Ross 1992).

The use of increasing numbers of plant species in horticulture makes it important to measure light quality and intensity when installing artificial lights. Most "human vision" light sources can be used for regulating and growing of plants. Cathey & Campbell (1980) have described the anticipated growth-regulation performances of various artificial light sources. Using basic information on the use of sensors to measure irradiation, they have suggested conversion factors with which to convert numbers into various systems. Using only these measurements, without a detailed analysis of the variations without the lighted area, can lead to very confusing results. Workers must continue to present the physical measurements of distance and spacing employed for the different types of lamps. Research workers and growers can decide systematically which lamp would be the most energy-efficient system for a specific growing situation.

Application

Lighting to substitute for or supplement the available sunlight can be used to accomplish some goals:

a) Reduce the time required to produce the desired stage of growth.

b) Utilize the lamps as energy sources rather than just for their light - use several criteria for measurement and installation of lamps.

c) Establish the light intensity and duration required for the plant processes to proceed. Overlighting (called "overshoot") wastes energy (visible light and heat).

d) Utilize light properly throughout the growth process so that the plants will not require acclimatization for their successful use by the consumer.

e) Learn how to compare one light source to another to create equally effective lighting systems for growing plants.

f) Develop alternative structures that require lower energy inputs for growing plants.

Plants are widely adapted to growing in highly varied light levels. We seldom see them growing under optimum conditions, however. The technology developed in growth chambers which combines the simultaneous enhancement of light, temperature, water and nutrition is seldom transferred into our traditional growing facilities.

Application

For practical plant lighting, Cathey & Campbell (1980) suggest the following:

a) Display: $0.3W/m^2$. Plants will exist and can be displayed (seen) at this intensity, but little or no significant impact on plants can be expected. The emphasis is directed towards colour rendering and the type of atmosphere created in living spaces. Timing (light-dark durations) and temperature interaction would also not be of concern.

b) Photoperiod: $0.9W/m^2$ Plant growth can be regulated at this intensity and by tradition this intensity has been tagged as the so-called "low light intensity" systems which are triggered by the photo-reversible blue pigment-phytochrome. The range of plant responses (promotion of delay of flowering, promotion of growth) which can be regulated is extensive. It is widely demonstrated and practised by commercial growers. The effectiveness of any lighting system is increased by the use of reflective aluminum soil mulch.

c) Survival: $3.0W/m^2$. Plants can survive at this intensity, by tradition this intensity creates an environment where many green plants can maintain their green colour. Stem lengthening and reduction of leaf size and thickness, however, occur almost immediately following placement of plants under this intensity. In time the overall development of the plant fall behind that of other plants grown under higher intensities. Photoperiod responses do not function well at this intensity since all parts lengthen and seldom develop green foliage. There are, however, strong interactions between this intensity and temperature, watering frequency, and nutrition.

d) Maintenance: 9.0 W/m^2. At his intensity plants can maintain growth over many months. Many indoor gardeners grow their plants at this intensity when starting from seeds, cuttings, or meristems. It has become a convenient base and energy balance, particularly if fluorescent lamps are used as the sole light source for growing plants. During the development of seedlings and the rooting of the cuttings, there appears to be little response to photoperiod. In fact, for most plants during the initial phases of development, continuous light (and heat) should be used to help compensate, in some part, for the limited irradiance. Most plants develop deep green foliage and large leaves, and may accelerate the transfer of nutrients and stored materials from their older to younger, rapidly developing leaves The plants eventually drop or lose an old leaf for each new leaf that develops. Adjustment of the lighting regime to a 12-hour light - 12-hour day cycle, coupled with reduced frequencies of water and fertilization, creates an environment where growth is slowed and few new leaves are formed while most older leaves are retained. Most container grown plants are now "acclimatized" for 4 to 6 weeks under an intensity of 9W/m^2. and are sold to the consumer. An "acclimatized" plant can be readily identified by its slow growth, few if any new leaves, deep green leaves which are broad and flat, and persistent leaves to the soil line.

e) Propagation: 18.0 W/m^2. Plants can be propagated rapidly when exposed to this intensity for a minimum of 6 to 8 hours daily. This is the intensity at which many propagators attempt to shade their greenhouses with one or several layers of neutral filters to restrict the entry of light (and heat) into the propagation area. Cuttings rooted at this intensity maintain a growth rate similar to that of cuttings attached to the stock plant (air layering).

4.4.3 Long-term stress

If a plant is shade resistant and makes no attempt either to place its leaves in unshaded positions, or to restrict their activity to periods of high illumination, selection will act more on the photosynthetic process itself. This is certainly the case for the lower leaves of a plant with a multi-layer canopy, and it follows that both plastic (within a genotype) and genetic (between genotypes) differences must exist in the photosynthetic system (Fitter & Hay 1981).

The problem faced by a shade plant is to maintain a positive carbon balance, and the flux density at which this is reached is the compensation point.

At the compensation point photosynthetic carbon fixation equals respiratory loss. A reduction in respiration will therefore lower the compensation point, but respiration has a purpose and reduction is likely to slow growth down, which could lower the competitive ability of the plant in relation to faster growing species. As a response to low light stress it is therefore only likely to be advantageous in severe shade where growth rates are sufficiently reduced to minimize competitive interactions. It is certainly true that plants capable of growth in deep shade have low relative growth rates (Fitter & Hay 1981).

Application

It is not possible to create instant shade gardens, indoors as well as outdoors, as true shade plants are slow growing. It is a wise idea to use mature plants or plants of the desired size instead of trying to plant small young plants and expect them to grow quickly to this size. Mature plants will naturally cost more as their growers have spent more time, space and effort in cultivating them.

A small reduction in respiratory rate is then a fairly general response to reduced light intensity, but as a major adaptive response it is only of value to severely shaded plants, particularly as a survival mechanism for long-lived plants to persist during periods of temporary stress (Fitter & Hay 1981). This is clearly the value of the near-dormant behaviour of seedlings that are able to survive long periods without growing when under severe competitive stress from older plants, but which can resume normal growth when the stress is removed. This phenomenon is termed initiation. Some woodland plants in the northern hemisphere have been shown to survive in complete darkness for 5 - 6 months. It was also demonstrated that generally small-seeded, pioneer plants, were least resistant to this stress, and that plants grown on nutrient-deficient soils which reduced growth and probably also respiration rates could survive for longer in complete darkness than those grown on fertile soils (Fitter & Hay 1981).

Irradiance affects photosynthesis rates when leaves are exposed to normal air with carbondioxide. There is of course no net CO_2 fixed in darkness (except in CAM plants), and in dim light the respiratory loss of CO_2 exceeds that used in photosynthesis (Figure 4). Above a certain irradiance at a point known as light saturation, increasing light no longer increases photosynthesis. Between darkness and saturation there is an irradiance at which photosynthesis just balances respiration (net CO_2 exchange is zero) known as light compensation point. This point varies between species, with the irradiance during growth, temperature, and CO_2 concentration (Salisbury & Ross 1992).

The photosynthetic light responses of *Tidestromia oblongifolia* shown in Figure 4 are typical of C_4 species native to sunny habitats. Such leaves show no rate saturation up to and even beyond full sunlight and can have maximum rates more than twice those of most C_3 species (at optimum temperatures for each). The responses of *Atriplex hastata* are representative of many irradiances one-fourth to one-half that of full sunlight.

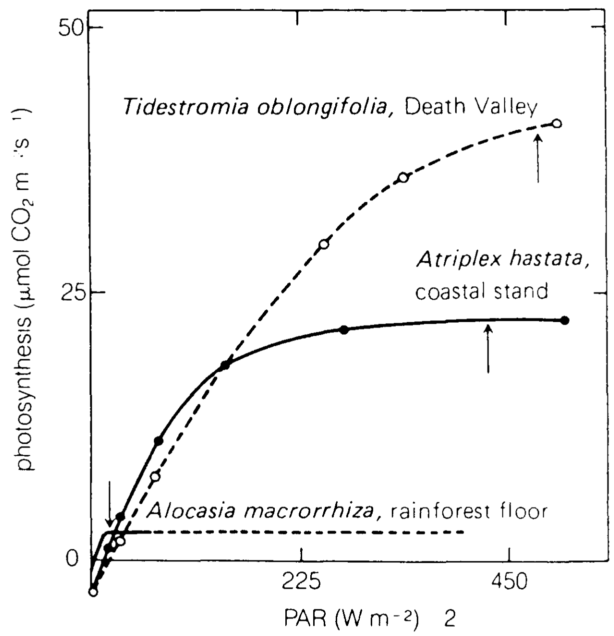

Figure 4. Influence of light on photosynthetic rates in single, attached leaves of three species native to different habitats. Maximum irradiances to which the plants are normally exposes (except for sunflecks that irradiate *Alocasia*) are indicated by arrows. The light compensation points are indicated on the graph where the lines cross the abscissa (Salisbury & Ross 1992).

The responses of members of *Alocasia* species are typical of many species native to shady habitats, including most indoor plants. They exhibit much lower photosynthetic rates under bright sunlight than do heliophytic species grown in open areas. The photosynthetic responses of sciophytes are saturated at much lower irradiances than those of heliophytic species. Under very low irradiance levels sciophytes usually photosynthesize at higher rates than do sun-loving species and their light compensation points are usually low. These characteristics cause them to grow slowly in their natural shady habitats, yet they survive where species with higher light compensation points could not get enough light and would die (Salisbury & Ross 1992). An important complication on the forest floor is the phenomenon of sunflecks that penetrate the tree canopy. The sun and shade leaves of the same species often exhibit up to fivefold difference in photosynthetic capacity (Björkman 1981).

4.4.4 Sunflecks and photosynthetic utilization by understorey plants

An important character of understorey light environments is the high degree of spatial and temporal variability caused by sunflecks (Pearcy 1990). The smearing of sunflecks by penumbra (the fringe region of half shadow resulting from the partial obstruction of light by an opaque object) makes defining sunflecks a difficult exercise (Baldocchi & Collineau 1994). The foliage of tree canopies is clumped both vertically and horizontally, leading to regions of dense cover and other regions with only sparse cover and to canopies of different species, each differing markedly in their architecture and flexibility. The earth's rotation causes sunflecks to move slowly on a daily and seasonal scale, creating low-frequency fluctuations, while canopy movement and leaf flutter in the wind cause much higher frequency variations. Cloud movement can cause additional variation. Consequently the usual diurnal pattern of light in the understorey comprises periods with relatively frequent sunflecks separated by periods with few, or no sunflecks. Records showed that 70% of the sunflecks occurred within 1 minute of the preceding sunfleck while only 5% were preceded by low-light periods of an hour or more (Pearcy 1990).

The light environment in forest understoreys is highly dynamic because the weak light is periodically punctuated by lightflecks, or sunflecks, lasting from a second or less to tens of minutes. Although present for only a small fraction of the day, these sunflecks can contribute more than two-thirds of the photosynthetically active radiation (Pearcy *et al.*1988). Several factors are of importance in determining the capacity of a leaf to utilize sunflecks. Following long low-light periods the induction state of the photosynthetic apparatus is limiting. During induction, 20-60 minutes may be required before maximum assimilation rates are reached, due first to a light activation requirement of ribulose-1,5-biphosphate carboxylase/oxygenase and later to the light-induced stomatal opening. Continuous light is not required and induction occurring during a series of sunflecks results in higher carbon gain for later sunflecks as compared to earlier sunflecks. Post-illumination CO_2 fixation resulting from utilization of metabolite pools built up during the sunfleck can significantly enhance carbon gain during short (5-20 s) sunflecks. The carbon gain of a leaf in response to a sunfleck is a consequence of the limitations imposed by the induction state, plus the enhancement due to post-illumination CO_2 fixation. In the field this will depend on the frequency and duration of the sunflecks and the duration of intervening low-light periods (Pearcy *et al.* 1988).

The decline in assimilation occurring after a sunfleck will be very slow, and most of the CO_2 fixation occurring in response to the sunfleck may actually occur after it has passed. Evidence for the rapid build-up of an assimilatory charge has come from simultaneous measurements of O_2 and CO_2 exchange as shown in Figure 5.

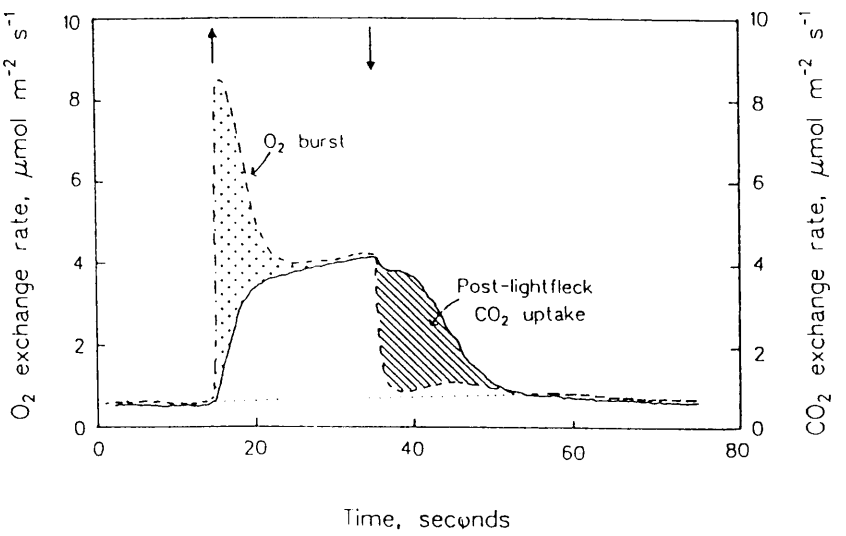

Figure 5. Simultaneous responses of O_2 (dashed line) and CO_2 (solid line) to a 20-s lightfleck showing the transient uncoupling of O_2 evolution and CO_2 uptake. The background PED was 10 μmol photons $m^{-2}s^{-1}$ and the lightfleck was 475 μmol photons $m^{-2}s^{-1}$. The CO_2 and O_2 pressures were 350 and 1780 μbar respectively (Pearcy 1990).

4.4.5 Limitation of the sunfleck use by the photosynthetic induction requirement

When a leaf that has been in low light for an extended time is subjected to a sudden increase in PFD (photosynthetic phlux density), the rate of CO_2 assimilation increases only gradually; 10--30 minutes or more may be required before a steady-state is achieved. This response contrasts with the very rapid increase in assimilation, discussed in the previous section, that occurs in leaves previously illuminated at high PFD but then darkened and reilluminated within a few minutes. The slow increase in assimilation occurring upon the initial in increase in PFD is the well-known induction requirement of photosynthesis, which results from slow light-regulation of photosynthetic enzymes and light-driven stomatal opening. Changes in these factors determine the "readiness" of a leaf to respond to a sudden increase in light and hence are of great importance in determining the utilization of sunflecks. The occurrence of a sunfleck will cause induction to commence and apparently to continue even in the low light between sunflecks. Thus the occurrence of a sunfleck acts in effect to prime the leaf so that it is better able to utilize subsequent sunflecks (Pearcy 1990).

Application

Simulated sunflecks can be created with a lamp and shutter system (as done by Pearcy *et al.*, 1985) and are called lightflecks. With these experiments they confirmed that induction occurred in response to a series of lightflecks for a number of species of diverse types (e.g. shade-adapted tree seedlings as well as soybeans), indicating it is probably a feature for all plants. This method of lighting has never been used for horticultural purposes, however, but it could be useful for indoor container plants. More research on the potential advantages of this application would be informative.

4.4.6 Sunfleck damage to shade-plants

Depending on the type of forest and the time of day, the radiation reaching the ground in a sunfleck can be sufficient to raise the temperature of a leaf of *Impatiens parviflora* in a few minutes by as much as 9 degrees above air temperature. High-temperature damage from sunfleck radiation is also thought to be the explanation for the leaf necrosis that can be seen in some years in Cambridgeshire woods in *Mercurialis perennis* (Rackham 1975).

The shade plant *Oxalis oregana* photosynthesizes in redwood forests at light levels only $^{1}/_{200}$th of full sunlight (Björkman & Poules 1981). Sunflecks penetrate the forest canopy and could damage this delicate species. With only a 10 second lag period after sunlight strikes the leaves, they begin to fold downward, the folding being complete in about six minutes. When shade returns, there is a 10-

minute lag period, but the leaves revert to their horizontal position in about half an hour. Blue wavelengths of light are sensed by a small pulvinus where each leaflet joins the petiole (Björkman & Poules 1981).

4.4.7 C_4 and C_3 photosynthesis

C_4 photosynthesis is experimentally shown to be more efficient than the C_3 version at higher temperatures and higher light intensities. These differences are broadly reflected in world and local geographical distributions and ecological ranges of especially grasses. C_3 families reach maximum diversity in the temperate zone, especially in the northern hemisphere, with major representation elsewhere only at high altitudes and moist habitats. The major C_4 families on the other hand are concentrated in the tropics and subtropics, with C_3 representatives often being aquatic or shade plants. *Oplismenus* is exclusively a C_3 genus (Gibbs Russel *et al.* 1990). A certain variety of *Oplismenus hirtellus*, a perennial grass in mountain forest and deep shade, is grown as a potplant in the U.S.A. (Van Oudtshoorn 1991).

Application

1. **Northern hemisphere C_3 grasses become successful "shade" lawn grasses in southern Africa, such as proven by commercial mixtures of these grasses. "Shade Over" is a good example of this. The lower temperatures in the shade probably allow these grasses to perform better in shade.**

2. **Alpine plants became shade plants in low lying areas, where temperatures are more favourable for their metabolic processes.**

4.5 NON-PHOTOSYNTHETIC RESPONSES TO LIGHT QUALITY

4.5.1 Introduction

In nature, survival is dependant on the sensitivity with which an organism can perceive its environment. As already mentioned, the optimum harvesting of light by photosynthesis is essential for the survival of both the individual organism, and the species.

The non-photosynthetic responses to light quality, namely photomorphogenesis, phototropism and photoperiodism are the physiological manifestations of environmental perception meganisms (Morgan & Smith 1981). The putative photorecepters phytochrome, chlorophyll and the blue-light receptor have been described by Morgan & Smith (1981) as responsible for detecting differences in light quality and quantity.

4.5.2 Seed germination

For many species light-sensitised seed germination has been categorised as being positively photoblastic (germination promoted by white light) or negatively photoblastic (germination inhibited by white light). These two categories can not be applied strictly, however, since they are in reality two different manifestations of the same underlying physiological phenomenon (Morgan & Smith 1981). Light sensitivity appears to ensure that germination will occur only when the seed is either burned or exposed, depending upon the physiological state of the photoreceptor. However, in many cases promotion of germination by light is restricted to a rather limited temperature range (Morgan & Smith 1981).

The seeds of many species show large variability in their germination behaviour of those which require light, some have photoperiodic requirement, whilst others merely require a threshold value of fluency rate. Such variation may clearly have adaptive significance (Morgan & Smith 1981).

Light-sensitive seed germination is not simply an on-/off light-/dark triggered process. When red and far-red are given as admixtures of various proportions, germination is sensitive to R:FR over a wide range. It has been proposed that this is also an ecologically significant phenomenon, since the daytime R:FR of terrestrial light is related to the depth of vegetational shade (Morgan & Smith 1981).

4.5.3 Photomorphogenesis - Red/Far-Red ratio

Stem extension - R:FR of vegetational shade-light can modulate stem extension rate and is proportional to the phytochrome photoequilibrium for the range found in natural shade (Morgan & Smith 1981).

The daytime stem extension response to simulated shade has a systematic relationship to species habitat - species from open habitats react by large increases in stem extension rate, species from woodland/shade habitats react less strongly or not at all (Morgan & Smith 1981). These two classes of response may have ecological significance - species from open habitats may overtop an herbaceous vegetation canopy, whilst woodland herbs cannot overtop their canopy. Indeed, an extreme response by a woodland plant may make it more susceptible to fungal attack (Morgan & Smith 1981).

Apical dominance: Field observations of many species have shown that plants growing in the open branch profusely, whilst shaded plants show complete apical dominance (Morgan & Smith 1981). In the controlled environment R:FR has been found to exert a remarkable degree of control over response. It has been suggested that apical dominance may be another morphological adaptation to vegetational shade light. If axillary bud outgrowth is suppressed by shadelight, the maximum of reserves may be used for rapid stem elongation (Morgan & Smith 1981).

4.5.4 Photropism and turgor movements

There are two types of orientation response-growth eg. curvature resulting from an imbalance in extension growth (phototropism), and movements resulting from turgor changes in specific cells. Orientation of the lamina either towards or away from the largest fluency rate would clearly be advantageous in different situations (Morgan & Smith 1981).

4.5.5 Photoperiodism

This topic has been comprehensively reviewed by several authors and will not be discussed in detail here. Photoperiodic responses occur in light-dark cycles in which the white light must exceed a critical fluency rate. The possible effects of natural variation of light quality - daylight, vegetational shade, twilight - in photoperiodism have been largely unexplored (Morgan & Smith 1981).

4.5.6 Others

Light quality also influences stomatal aperture, chloroplast orientation and nastic (sleep) movements (Morgan & Smith 1981).

Remarks

The evidence suggests that the light quality is of vital importance to plants growing in nature. Natural spectra are in continuous state of flux with large variation determined by factors such as vegetation canopies and solar angle. Plant photoreceptors are most sensitive to precisely those wavelength ranges over which the largest spectral variation occur (Morgan & Smith 1981).

4.6 ANATOMICAL ADAPTATIONS

4.6.1 Anatomy of sun versus shade leaves

Most leaves that develop under conditions of high irradiance (sun leaves) are relatively thick and have a well-developed palisade layer with a high proportion of columnar cells. On the other hand, leaves that develop under low irradiance (shade leaves), such as beneath a plant canopy, have different anatomical and biochemical characteristics (Figure 6). Shade leaves are thinner than sun leaves and have a poorly defined palisade layer and high chlorophyll content per unit leaf volume (Vogelmann & Martin 1993).

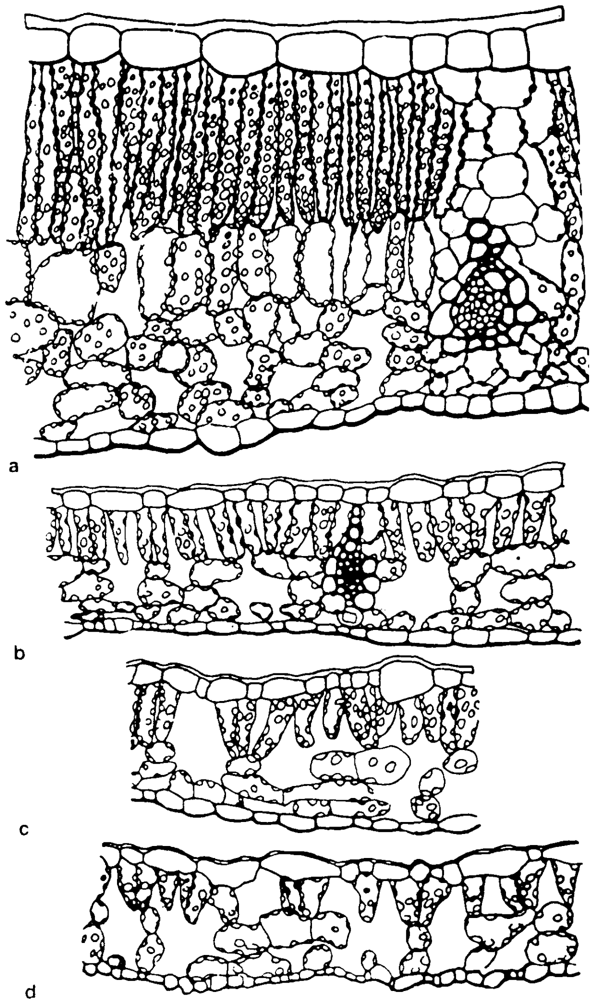

Figure 6. Cross section of leaves of sugar maple (*Acer saccharum*), an unusually shade-tolerant tree, exposed to different light intensities during growth. (a) Sun leaf from south side of isolated tree. Note thick cuticle over the upper epidermis and long palisade parenchyma cells. (b) Shade leaf from centre of crown of an isolated tree. (c,d) Shade leaves from base of two forest trees. All trees were growing near Minneapolis, Minnesota (Salisbury & Ross 1992).

In addition to a possible role in CO_2 assimilation, there have been suggestions that palisade cells may also play a role in the distribution of light within the leaf. Increasing leaf thickness without concomitant changes in the optical properties of the palisade could result in sub-optimal distribution of light to the photosynthetic layers. For example, in a leaf where the mesophyll consisted of spherical cells, the most adaxial cells could receive saturating or even photo-inhibitory amounts of light, whereas cell layers located deeper within the leaf could receive sub-saturating quantities. Because columnar cells may scatter light less than spherical ones, they may facilitate light penetration so that it is distributed more equally throughout the photosynthetic tissues (Vogelmann & Martin 1993).

It is important to keep in mind that the introduction of light into a leaf is determined by several factors. One important factor is such as the angle at which the rays strike the leaf. Thus light in which the rays are parallel to one another (collimated) may penetrate the leaf with a divergence of less than 1 degree. Diffuse light varies within the natural environment and the randomness of the rays depends upon the amount of cloud cover and the amount of light scattering of leaf canopies. The important point is that light gradients within leaves irradiated with equal irradiances of collimated versus diffuse light may be very different from one another. If this is the case, then palisade tissue may have varying levels of functional significance related to the balance between collimated and diffuse light. To examine the interaction between the directional quality of light and leaf tissue, light gradients were measured in two types of leaves irradiated with collimated and diffuse light. One leaf had a well-developed palisade with a high proportion of solumnar cells, whereas the other had spongy mesophyll only (Vogelmann & Martin 1993).

4.6.2 Lens-shaped epidermal cells

The epidermis of the leaves with well-developed palisade was only half the thickness as that of the leaves with only spongy mesophyll. For light introduction into the leaf this cell layer is important because the individual cells act as lenses that focus light in the mesophyll. Columnar palisade cells facilitate the penetration of direct light into the leaves. This may be of special importance within sun leaves which are usually thicker than shade leaves.

In the natural environment, both irradiance and collimation change with time scales of seconds to minutes, causing correspondingly rapid changes in the light gradient within leaves. For example, rapid changes in collimation occur when the sun is obscured by clouds (shadeflecks). It is interesting to note that among alpine plants exposed to intermittent shadeflecks, some showed an immediate depression in photosynthetic rate and stomatal closure when a cloud passed in front of the sun. Part of the altered photosynthetic response may have been caused by changes in the steepness of the light gradient within the leaf as the ambient light changes from collimated to diffuse (Vogelmann & Martin 1993). Enhanced rates of photosynthesis also occur in the leaves of understorey plants when they are exposed to sunlight that passes through the gaps in the leaf canopy (sunflecks). Sunflecks comprise a major fraction of the light that is utilized for photosynthesis by understorey plants, and this light is more collimated than the background diffuse light created by light scattering within the canopy.

In addition to the light gradient, the degree of collimation of ambient light also affects optical phenomena that occur at a finer microscopic scale within the leaf. When leaves are irradiated with collimated light, individual epidermal cells can act as lenses that focus light within the mesophyll. This phenomenon is relatively widespread but is especially prevalent among understorey plants (Vogelmann & Martin 1993).

Application

Leaves exhibiting lens-shaped epidermal cells have a glossy or shiny appearance, which makes them very attractive from an ornamental point of view. So sought after is this quality, that there are even commercial products available to shine the leaves of potplants to give them this "healthy" appearance.

The amount of light intensification within the leaf depends upon the convexity of the epidermal cells and the location of the focal spot within the mesophyll, which attenuates the light by absorption and scattering. Maximum epidermal focal intensification of up to 25 times incident light have been calculated in leaves irradiated with collimated light and intensification of up to 10 times have been measured in replicas of epidermal cells. Focusing is either greatly reduced or eliminated when leaves are irradiated with diffuse light (Vogelmann & Martin 1993).

It seems unlikely that photosynthetic performance of the leaf would be immune to changes in the light gradient or heterogeneity of the internal light microenvironment. There is some evidence that elimination of epidermal focusing decreases light-harvesting.

Leaf anatomy is one level of control for allocation of light to chloroplasts within the leaf. Other controls include altering the number of chloroplasts per cell, the amount of chlorophyll per chloroplast and chloroplast position within the leaf, which can change rapidly. Declining fluency rates within the mesophyll coincide with increasing amounts of chlorophyll, and may reflect changes in the chlorophyll content of individual chloroplasts related to a gradient in sun to shade type chloroplasts within the leaf. Alternatively it could mean that chloroplasts were clustered within the mesophyll. Both patterns were observed in different species (Vogelmann & Martin 1993).

As is the case with many anatomical adaptations, columnar palisade cells might serve several purposes. In addition to facilitating the penetration of light, the tubular shape of the palisade cells may allow for more optimal vertical placement of chloroplasts, which may respond to internal CO_2 concentration within the leaf. Thus optimization of whole leaf photosynthesis could depend upon a balance between internal concentrations of both light and CO_2. This balance could be determined in part by controlling the level of development of palisade and hence the steepness of the light gradient (Vogelmann & Martin 1993).

4.6.3 Chloroplasts: structures and photosynthetic pigments

Chloroplasts of many shapes and sizes are found in various kinds of plants, and with a few exceptions, occur in all members of the Kingdom Plantae as well as in certain algae or algae-like members of the Kingdom Protista.

The pigments present in thylakoid membranes consist largely of two kinds of green chlorophylls, chlorophyll a and chlorophyll b. Also present are yellow to orange pigments classified as carotenoids (Salisbury & Ross 1992).

4.6.4 Chlorophyll content in shade leaves

A common feature of plants that live in deep shade is the dark green colour of the foliage. Experiments to estimate the quantum yield of photosynthesis using leaves with differing chlorophyll contents show that over a wide range there is no appreciable effect on the amount of carbon dioxide fixed per unit of light absorbed. Nevertheless, although sun and shade species do not differ in the efficiency with which they use absorbed quanta, they do differ in their ability to absorb incident light (Crawford 1989). The amount of light needed to attain the light-saturation rate will vary depending on the efficiency with which the photosynthetic pigments absorb light. Thus the higher the chlorophyll content, the greater the amount of light absorbed by a leaf. The high absorbance of chlorophyll in the red and blue regions of the spectrum, however, reduces the gain at these wavelengths with increased chlorophyll content. Thus a three-fold increase in chlorophyll content results in only a 2--3% increase in absorption in these wavebands (Björkman 1981). However, in the far-red and green wavebands there is a much greater increase in absorption. Thus, although an increase in chlorophyll content results in a less than proportional increase in absorption of incident light, this may still be of advantage in areas where the intensity of illumination is low.

Shade plants therefore do not economize in leaf chlorophyll content in the same way as they do in the carbon dioxide fixing enzymes. When grown under deep shade, obligate shade species such as *Cordyline rubra*, contain just as much chlorophyll as sun plants grown at high light intensities (Björkman 1981), the chloroplasts of shade plants can have particularly large stacks of grana with as many as 100 thylakoids per granum (Figure 4). The grana within the chloroplasts are not orientated in one particular direction (as they are in sun plants), presumably due to the non-directional nature of shade-light (Boardman *et al.* 1975). This increase in the amount of light-trapping chlorophyll is also seen in the molecular structure of the chlorophyll itself. Shade plants grown in deep shade show an increase of chlorophyll *b*, with a lower chlorophyll a to chlorophyll b ratio. As chlorophyll *b* is purely a light-harvesting pigment this increase means that there is a higher proportion of light-harvesting chlorophyll in the chloroplasts of shade-tolerant plants (Crawford 1989). It has been suggested that the light-harvesting chlorophyll complex is mainly associated with photosystem II and it appears that shade plants compensate for the greater amount of far-red light relative to red by an increase in photosystem II relative to photosystem I (Butler

1977). In this way the shade plants achieve a more blanched energy distribution between the two photosystems.

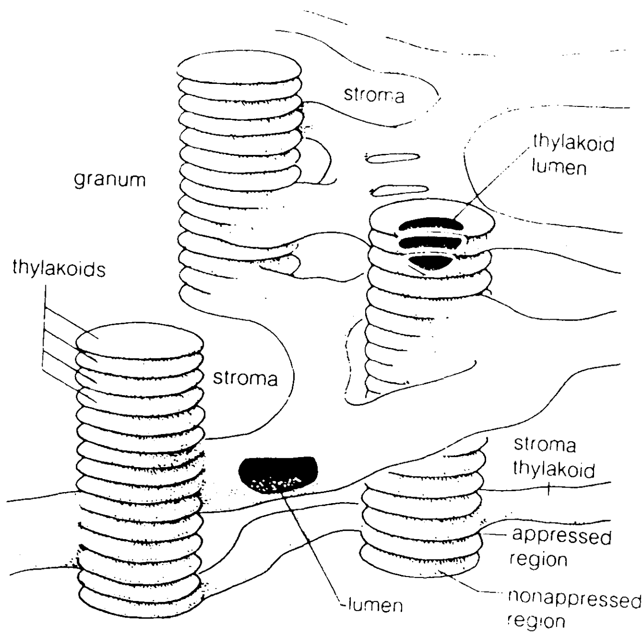

Figure 7. A three-dimensional interpretation of the arrangement of the internal membranes of a chloroplast, emphasizing the relation between stroma thylakoids and grana. Note the lumen in both kinds of thylakoids (Salisbury & Ross 1992).

4.6.5 Effects of light on chloroplast arrangements

When irradiance levels are high, chloroplasts are usually aligned along radial (side) walls of the cells, becoming shaded by each other against light damage. In weak light and often in darkness, chloroplasts are separated into two groups distributed along the walls nearest to (top) and farthest from (bottom) the light source, thereby maximizing light absorption (Figure 8). This movement of plastids, which depends upon the direction of light as well as its irradiance levels, is an example of phototaxis (movement of an entire organism, organ or organelle in response to light) (Seitz 1987).

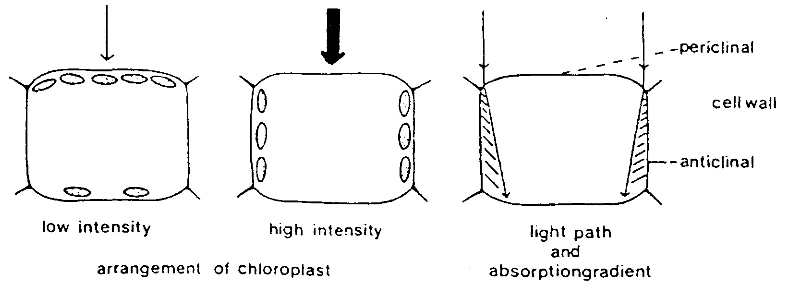

Figure 8. Light dependent intracellular arrangements of chloroplasts and light path with resulting absorption gradient in schematic cross-sections of epidermal cells of *Vallisneria* (Seitz 1987).

In angiosperms phototactic responses to both low and high irradiances are maximal under blue wavelengths, and phytochrome does not participate. Action spectra suggest that cryptochrome is involved (Salisbury & Ross 1992).

In all the species the chloroplast itself does not absorb the light causing its phototaxis; instead, light absorbed elsewhere in the cell causes chloroplast movements through effects on cytoplasmic streaming, which effects result from interactions between microfilaments and microtubules.

Ecologically, chloroplast movements seem important mainly to increase light absorption at low irradiances and to decrease absorption when irradiances are so high that they might cause solarization or other photodestructive effects (Salisbury & Ross 1992). With increasing irradiance, low intensity movement of chloroplasts begins at about the intensity where photosynthetic CO_2 fixation begins and chloroplast orientation changes from low to high intensity arrangement approximately at the saturation intensity of photosynthesis (Seitz 1987).

At high intensities, when photosynthesis is in the range of saturation, a change in the arrangement of chloroplasts does not cause a change in the rate of photosynthesis. The ecological significance of the high-intensity arrangement of chloroplasts thus probably lies more in the fact that light absorption in chloroplasts is reduced in the high-intensity arrangement and thus photochemical damage is less likely to occur. The orientation movement of chloroplasts thus allows the plant to adjust its photosynthetic processes to changes in the environmental light (Seitz 1987).

4.6.6 Adaptations minimizing injury from bright light

The phenomenon known as solarization is a light-dependent inhibition of photosynthesis followed by oxygen-dependent bleaching of chloroplast pigments. A major function of carotenoid pigments is protection against solarization by absorbing excess light energy that is released as heat instead of being transferred to chlorophylls (Salisbury & Ross 1992).

Application

a) **One often sees obligate shade plants used incorrectly in full-sun positions in landscaping. Instead of their normal attractive dark-green colour, these plants become yellow and too light in colour as a result of this chlorophyll bleaching. Scorching can also occur and forms necrotic patches on the leaves, or the leaves can burn around the edges. This is often the case with *Philodendron selloum*, *Protasparagus* species, and several fern species.**

b) **In forest tree seedlings, for instance *Podocarpus* species, the protection afforded by solarization is insufficient. Shading the seedlings helps to boost their survival rate.**

Light sensitivity is an important factor in plant succession because unusually sensitive species never become established except in the shade of others. Unusually light sensitive species are often climax species that can reproduce in their own shade.

Application

Young forest trees of many species make very successful indoor container plants because they are adapted to growing at low light intensities.

However, it should not be assumed that merely because shade-tolerant seedlings can live in dense shade, that they will flourish and grow normally. Their shade-tolerating abilities are an adaptation that increases their chances of benefiting from the death of an old tree that would leave a break in the forest canopy. Trees have been known to survive in dense shade without making any diameter growth for as long as 46 years (Daubenmire 1974).

4.6.7 Abaxial anthocyanin layer in leaves of sciophytes: enhancer of light capture in deep shade (Red undersurface of leaves)

Leaves show a wide range of colour combinations and patterning effects. Divergence from a normal uniform green may (especially in forest plants) be grouped into three categories: (1) young leaves of woody plants often have, transiently, intensely cyanic coloration throughout their tissue; (2) many species have permanently patterned leaves in which heavily pigmented, cyanic, chlorotic, or non-pigmented regions occur as spots, bands, margins, or patches; (3) species (nearly always herbaceous) restricted mainly to deeply shaded habitats, often show permanent anthocyanin coloration of the lower (normally abaxial) surface (Lee *et al.* 1979).

Although leaf anthocyanin may be associated with a high-ultraviolet light environment, the light intensity that reaches the forest floor is less than 1% of that in the canopy and there is virtually no damaging UV light present (Lee *et al.* 1979). It is now known unequivocally that light is a limiting factor for growth of forest-floor plants. Not only is the intensity low, but the light is poor in photosynthetically active wavelengths, those available being mainly in the red region. It is thus to be expected that plants in this habitat will show adaptations to enhance utilization of this light.

Another problem concerning the light available for photosynthesis in the forest-floor habitat is the inconstant diurnal distribution of light. Most of the light available that is used for photosynthesis comes in the form of sunflecks. Is it more advantageous for shade-plants to follow a strategy that optimizes the use of sunflecks, or to exploit the lower intensities of the shade which are continuous? The species studied by Lee *et al.* (1979) grew in habitats so deeply shaded, that sunflecks were of relatively less importance than is the case in slightly more open habitats and for plants of the next higher strata within the forest. It should be remembered, however, that sunflecks are not entirely random phenomena, but to a degree are repetitive. In equatorial latitudes, the solar radiation will track over essentially the same path each day of the year. Thus there will be a discrete zone of enhanced net light intensity in some zones relative to others which do not receive these repetitive "fleck-tracks". In habitats where light intensity is very close to the lower limit for plant growth there will be effects caused by this variation in available light, but as it is essentially a non-predictable habitat, there can be no uniform selection pressure.

It is necessary to ask whether the cyanic zone could have any effects in increasing photosynthetic energy capture. The location of the pigment, the known optical properties of anthocyanins, and the absence of any suggestion that absorbed energy can be transferred from the molecule, all indicate that the only possible influence of the cyanic layer on photosynthesis would be to enhance reflectance. Light which would otherwise pass out through the lower surface of the leaf could instead be reflected back through the photosynthetic tissue. Similar physical-optical and biological-ecological aspects exist in red marine algae to enhance photosynthetic performance (Lee *et al.* 1979).

Reflectance measurements with the precise determination of pigment location as reported by Lee *et al.* (1979) show that this is possible. A clearly defined layer of anthocyanin-containing cells on the undersurface of the leaf was found. The layer is one cell thick and located immediately beneath the chlorenchyma and above the lower epidermis which contained no anthocyanin. This cyanic layer functions like a mirror and reflects substantially more light between 600 nm and 750 nm than do green leaf undersurfaces.

Application

1. **Red undersurfaces of leaves can be a good indicator that a plant may thrive under shady conditions.**

2. **The red undersurfaces of leaves have ornamental value and provide extra colour in shady environments where there is normally a shortage of colour, other than green.**

According to Lee *et al.* (1979), these results do not support the hypothesis of leaf temperature modification as there was no significant increase in temperature under field conditions. However, Rackham (1975), has shown that leaf temperature can rise considerably when struck by a sunfleck, causing damage. It is also known that anthocyanin can function as protection against injury from bright light. Where this pigment is located in the superficial layers of the cells, it can act as a reflective screen retarding the penetration of light into the underlying tissue. A simple example is the faster development of the red colour resulting from anthocyanin in apple and other fruits on the sunny side as opposed to the shady side of a tree (Salisbury & Ross 1992, Daubenmire 1974). Red pigment chiefly reflects red rays, and since long rays have greater heating effect, their reflection greatly reduces danger from overheating. The temperature under red spots on fruits has observed to be 22 degrees Celsius lower than under comparable green spots (Daubenmire 1974).

Since adaptations often work in more than one way, it could also be that leaf anthocyanin can have the added benefit of affording protection against sunfleck-overheating, and that it could possibly act as a heat "exchanger". Reflecting ambient red light to aid lower leaves of the same plant in photosynthesis could be another benefit that has not been proven yet, but which seems logical. This would improve the net photosynthesis of the whole plant in these low-light conditions.

Colour polymorphism is seen in many species (Lee *et al.* 1979) where individuals with green leaves as well as individuals with red leaves are common. This colour polymorphism often occurs in *Plectranthus* species and *Crassula* species, and would no doubt be found in more species. This phenomenon also has interesting evolutionary adaptational implications. If the adaptive value of such polymorphism is real, more positive selection for the character might be expected. However, forests are complex, dynamic entities, with a mosaic of canopy phases and natural canopy gaps that appear frequently. It is in the more brightly lit areas below a canopy that net productivity of the forest floor plants will increase, provided they survive the increased temperature and lowered humidity effects. It is reasonable to expect that they will then have greatly increased seed production relative to the members of the same population which remain under deep shade. Thus it seems likely that within an area of forest, seed production will be taking place to a disproportionately large extent in small areas with temporarily increased light intensity; but in such areas, the anthocyanin undersurface is of less effect and thus of less adaptive value. Thus we have the interesting situation where a characteristic has a definite strong adaptive value for the majority of the individuals of the population, yet selection for it is weak (Lee *et al.* 1979). This is because individuals with all-green leaves are, presumably, equally capable of seed production. The genetic elements which produce red leaf undersurface pigmentation in each new generation are therefore probably in a somewhat fluctuating equilibrium with the elements which produce all-green leaves. According to this hypothesis, colour polymorphism is therefore adaptively valuable in itself, as are other instances of polymorphisms (Lee *et al.* 1979).

It is important to bear in mind that there are species which have leaves with red undersurfaces in juvenile, but not in adult, plants. It is a fairly common phenomenon in the juvenile stages of species in which the adults "emerge" out of the understorey into higher strata. This situation seems to be particularly true for plants which become tall shrubs, trees, or high-climbing lianas. Probably the red colour again can be considered as an adaptation that is functional only during the period in which the juvenile occupies a deep-shade habitat (Lee *et al.* 1979). It would be interesting to know if there are any southern African plants showing this adaptation.

Finally it must be noted that some species with red undersurfaces are not confined to low-light habitats. These specific plants might possibly be restricted to the category of spotted, striped, or patterned leaves. In some of these plants the red pigment is in fact not anthocyanin, which may serve as a warning that mere visual observation does not suffice for identification of the adaptation. Because of the complexity of forests, any too facile explanation for a particular observation should automatically be doubted, yet it is reasonable to assume that a modification found widely and almost uniquely in plants of a particular habitat and which is not linked to taxonomic affinity, has adaptive significance (Lee *et al.* 1979).

4.6.8 Significance of iridescence in blue plants of shaded habitats

Many terrestrial plants in lowland tropical rainforests exhibit a conspicuous blue-green iridescence on their leaves. These plants have been observed in Africa, South America and South-East Asia. Species from diverse groups including ferns, mosses and flowering plants on rainforest floors in Malaysia which are "blue" have been observed by Lee & Lowry (1975).

Application

Imagine what a stir it would create were "metallic-blue" plants commercially available. In Malaysia the most spectacular and most common iridescent blue plant is *Selaginella willdenovii*, a moss that is frequently cultivated in greenhouses.

The iridescent blue colour could not be verified by microscopic observation of any granules reflecting blue light, however, and the blue colour disappears when the leaves are immersed in water. The colour must therefore be an optical effect of the leaf surface and not of the internal structure. The two optical phenomena that can provide a physical basis for this effect are diffraction and thin-film interference, both of which have been invoked to explain the iridescent colouring of many animal cuticles. Diffraction effects can be ruled out in the present case because there is no dispersion as the reflected blue colour is constant for white incident light over a wide range of angle of incidence. Furthermore, microscopic examination has revealed no surface features that could function as grating. It has therefore been suggested that the iridescent blue colour is caused by a thin-film quarter wavelength interference filter on the upper cell wall of the epidermis (Lee & Lowry 1975).

When iridescent leaves age or are exposed to sunlight for some time they lose their iridescence and develop an ordinary green appearance. The chlorophyll content of the these two types of leaves was found to be the same. Maximum enhanced reflectance at 405 nm, a null point at 500 nm, and decreased reflectance at longer wavelengths was shown. The effect was obscured above 660 nm by the strong reflective characteristics of all leaves. This corresponds closely with operation of a quarter wavelength interference filter. Electron microscopic analysis would verify the existence of such a structural layer on the wall surface. Solubility experiments suggest that cuticular waxes were not acting as the filter and that the structural basis may well lie in the cellulose orientation at the cell wall surface (Lee & Lowry 1975).

Iridescent blue plants grow exclusively in extremely shady tropical forest environments and no southern African plants with this specific adaptation are known to the writer. The ecological importance of an interference filter in these circumstances is that the increased reflection of photosynthetically less active light (400--500 nm) is accompanied by increased penetration in the most photosynthetically active range (600--680 nm). This would have definite adaptive value (Lee & Lowry 1975).

Furthermore, observations on the leaf anatomy revealed the presence of epidermal cells with egg-shaped or convex outer surfaces that function as lenses (discussed under "anatomical adaptations") as well as chloroplasts in a peculiar position distal to the surface. Thus the analogy of a camera with a coated lens may aid our understanding of the function of the leaf surface in these iridescent plants (Lee & Lowry 1975).

Can it be possible that the blue iridescence associated with these lens-shaped cells serves as protection against sunflecks? Sunflecks consist of much more high-energy blue wavelengths, and the focusing and concentration of these wavelengths could/might be too strong for the cells to absorb (like a magnifying glass that can start a fire), and can start to boil them instead?

4.7 MORPHOLOGY

4.7.1 Introduction

Many investigations of the effects of the light environment on plant growth report characteristics of mature leaves after a period of growth under an experimental treatment. The processes of leaf development are frequently described in terms of leaf number (initiation), leaf shape (morphogenesis), leaf size (expansion), and leaf anatomy (histogenesis). Although these processes are considered individually here, there is extensive temporal overlap among them, and leaf development as a whole is a continuous, integrated process from initiation to senescence and abscission.

The flowering plants are characterized by a striking diversity of leaf size and form. The genetic component of this diversity has yielded characteristics that are taxonomically useful at the level of species, and may additionally characterize taxa at genus, family and higher levels. Such taxonomic variation in leaf morphology and anatomy is a reflection of the interaction between phylogenetic constraints and adaptation for a specific environment (Dengler 1994). Differences among species in effective leaf size (width of the blade or its lobes or leaflets), leaf shape, orientation, thickness, pubescence, anatomy and longevity have been shown to be related to habitat and to be significant for photosynthetic gas exchange. In addition, intraspecific genetic variation in these leaf characteristics typifies some species. For example, Björkman & Holmgren (1963) demonstrated that populations of *Solidago virgaurea* from shaded and exposed habitats showed heritable differences in photosynthetic rates and that these differences were related to leaf structural characters influencing resistance to carbondioxide conductance.

Most studies concerned with the relationship between leaf morphology, anatomy, and photosynthetic rates have found, however, that variations in structural and biochemical characteristics between individual populations are not maintained under uniform environmental conditions. These are rather plastic responses of the genotype to environmental variability (Boardman 1977). Because of the sessile nature of established plants, there is a need for individuals to accommodate continually to a varying environment. Plants do this through a modular pattern of growth in which development of semi-independent units reflect ambient conditions, and coordination among modules may occur primarily by competition for resources.

The relative constancy of leaf weight ratio (LWR) and plasticity of specific leaf area (SLA) imply that the plant has an optimum developmental pattern in terms of dry weight distribution, achieving adaptation to light intensity by changes in leaf morphology. The increased ratio of leaf area to weight must imply important anatomical changes in the mesophyll.

Changes in morphology will certainly influence light interception. In monolayer canopy strategy, plants will tend to have large unlobed leaves to maximize ground coverage with minimum overlap, whereas multilayer species will favour smaller, more dissected leaves (Fitter & Hay 1981).

Leaf morphology affects photosynthesis in four main ways:

a) light interception;
b) temperature regulation;
c) water balance;
d) carbon dioxide diffusion.

Probably the most important are (a) and (b). In all cases the environmental stimulus to which the plant responds is light, whether as flux density, duration, or their product, irradiance.

In dicotyledons, a large proportion of the cell division and cell enlargement associated with leaf surface growth and tissue differentiation occur after the leaf begins to expand from the bud. Thus, these developmental processes are potentially exposed to the direct effects of the environment. In contrast, blade surface growth and tissue differentiation in grasses occur before expansion from the older ensheathing leaves.

Vascular connections with antecendent leaves on a shoot occur early during leaf development, and leaves are net importers of carbohydrates until maturation of photosynthetic tissues. This indicates that photosynthesis of the older leaves on a shoot will strongly influence the early developmental stages in younger dicotyledon leaves as well as most developmental stages in grass leaves.

Plants grown under experimental conditions of low irradiance typically have a reduced rate of leaf production, greater leaf area, reduced leaf thickness, and lower leaf weight. Other changes such as reduced mesophyll tissue (particularly palisade parenchyma) volume, low mesophyll surface ares/unit leaf surface area, reduced stomatal density, and certain biochemical cytological changes are closely correlated with the reduced photosynthetic rates observed under low irradiance.

Experimental evidence indicates that total daily photon flux is more important than instantaneous photon flux for modifying leaf growth. This suggests that irradiance levels are perceived through the effect on photosynthetic rates in expanded leaves and that carbohydrate levels within the shoot will have a significant effect on the development of newly formed leaves. This may explain the acceleration of heteroblastic leaf-shape by high irradiance.

The altered spectral composition of shade light effects internode elongation and apical dominance, although at present there is less evidence to suggest an effect on leaf expansion. Low R:FR ratio's induce larger leaf areas in some shade-intolerant terrestrial species, however, and regulates leaf shape in some aquatic species.

Photoperiod has probably the greatest influence on leaf development through its effect on total daily photon flux Leaf-shape changes have been demonstrated to be associated with the altered phytochrome equilibria induced by day-length. These are probably the heteroblastic changes in leaf form that precede flowering.

Comparative studies on the effect of light on leaf development support the broad categorization of some plant species as *stress-avoiders*, which show the greatest developmental plasticity, and other species as *stress-tolerators*, which exhibit less morphological response, but are still capable of cytological and biochemical adjustments.

Transfer experiments between controlled light conditions indicate that the degree of plasticity of leaf development becomes limited with time and that nutritional conditions experienced by early primordium stages may constrain later ability to respond fully to changing light environment. The developmental pattern of dicotyledon leaves suggest, however, that developmental changes such as tissue differentiation that occur during leaf expansion may respond directly to the immediate photosynthetic environment.

4.7.2 Leaf size

According to Parkhurst & Loucks (1972) and Givnish (1987), the dominant factor controlling the leaf size of plants in different habitats is not considered to be the capture of light, but the optimizing of water-use efficiency. They made this assumption when testing mathematical models for leaf size and found that the predictions that this assumption gave fitted well with observed trends in diverse regions (tropical rain forest, desert, arctic etc.). Their model predicted that only in warm or hot environments with low radiation as in the forest floors of temperate and tropical regions would large leaves be advantageous. Although there is a great deal of variability in leaf size in the herb vegetation of the forest floor, their conclusions are consistent with general trends in leaf size. The variability that does undoubtedly occur is thought to be due to the lack of environmental pressure on leaves on the forest floor. Carbon dioxide is usually not limiting due to soil respiration and low wind speeds (Crawford 1989).

4.7.3 Indumentum

The reflective properties of the leaf are extremely important in relation to the absorption of light. Pubescence can increase reflectance and the desert pubescent form of *Encelia* will absorb only 30% of incident light compared with glabrous leaves of equal chlorophyll content which absorb 84%. In these species the quantum yield for photosynthesis is directly proportional to incident light when radiation is limiting. However, at high-light intensities the light-saturated rate of photosynthesis is the same in the glabrous and pubescent leaves (Ehleringer & Björkman 1978). Shade leaves show very little, if any, pubescence. An optimum usage of available light.

4.7.4 Leaf form

Givnish (1987) has reviewed 23 ecological patterns of leaf form, physiology and leaf arrangements which have been established using comparative studies. Three general sets of energetic trade-off, involving the economics of gas exchange, support, and biotic interactions, appear likely to influence the evolution of leaves and underlie these trends. The following patterns are discussed in these ecological trends:

Effective leaf size (i.e. the width of a leaf or its lobes or leaflets) tends to increase along gradients of increasing rainfall, humidity and/or soil fertility, and to decrease with increasing irradiance. Effective leaf size also tends to decrease with elevation on mountains in regions receiving high rainfall at low elevation and to increase and then decrease with elevation on mountains in regions receiving high rainfall at low elevation and to increase and then decrease with elevation in more arid regions. Finally, even when growing under similar conditions, juvenile trees often bear broader leaves than do mature individuals of the same species.

Leaf thickness tends to increase with decreasing rainfall, humidity and/or soil fertility, and to increase with increasing irradiance and/or leaf lifetime. Leaf thickness tends to increase with elevation on mountains receiving high rainfall.

Light absorbency in the visible spectrum (400--700 nm) tends to decrease, that is, leaves tend to be more highly reflective or glaucous (covered with a whitish or bluish waxy coating, as on the surface of a plum), in sites that are sunnier, more arid or less fertile.

Leaf inclination from the horizontal tends to be greater in sunnier, more arid, or less fertile sites.

Amphistomatous leaves (those with stomata on both surfaces) are frequent in sunny and/or dry sites, whereas hypostomatous leaves (those with stomata only on the lower surface) predominate elsewhere (e.g. shade).

Stomatal conductance generally increases with increasing humidity, soil moisture supply and mesophyll photosynthetic capacity, with the latter being conditioned by irradiance, leaf nitrogen content, leaf water potential and leaf age. Stomatal conductance usually increases with irradiance until heat load and/or leaf water potential become limiting.

Mesophyll photosynthetic capacity (the maximum leaf photosynthetic rate at a given concentration of carbon dioxide in the mesophyll) tends to increase with increasing supplies of light, water and/or nutrients. Photosynthetic capacity per unit leaf mass tends to be greater in deciduous leaves than in evergreen leaves among plants growing in the same area.

Leaves tend to have a higher protein: chlorophyll ratio and a lower chlorophyll a: chlorophyll b ratio in more sunlit environments.

Plants with C_4 or CAM photosynthesis, though less dominant than C_3 plants in most terrestrial habitats, become relatively more common in drier and/or hotter areas or seasons of growth as well as on saline soils.

Evergreen leaves are common in habitats with nutrient-poor soils and/or where there is little seasonal variation in the favourability of conditions for photosynthesis (in seasonal or winter-rainfall climates for example). Plants with deciduous leaves predominate elsewhere, principally in deserts and semi-deserts, seasonal tropical forests, the upper stories of rain forests and temperate forests of eastern Asia, eastern North America and northern Europe.

Application

Deciduousness as well as an annual growth habit in true shade plants are almost non-existent. In shady habitats these strategies are too energy costly, and would be a waste of this hard earned commodity. In horticultural terms, this means that no seasonal aspect in the form of autumn leaf-colour or spring flowers can be expected. This of course has a labour-saving advantage for the gardener, as once the shade garden is established, it will retain its beauty for a long period, with a minimum amount of maintenance.

Leaves with non-entire margins (i.e. toothed or lobed leaves) are most common in dicots of the north temperate zone and forest understoreys everywhere.

Lobed leaves are common only in north temperate zone trees and in tropical trees of early succession.

Leaves with long, acuminate drip tips are common in wet rain forests and cloud forests, particularly among understorey species. In southern Africa, drip tips can be seen in *Eugenia zuluensis*, an understorey tree in mistbelt Afromontane forest.

Leaves with cordate (i.e. heart-shaped) bases are common among vines, forest herbs and aquatic herbs. Sagittate, hastate and auriculate bases are also more common in shade than in sun plants. (Figure 9)

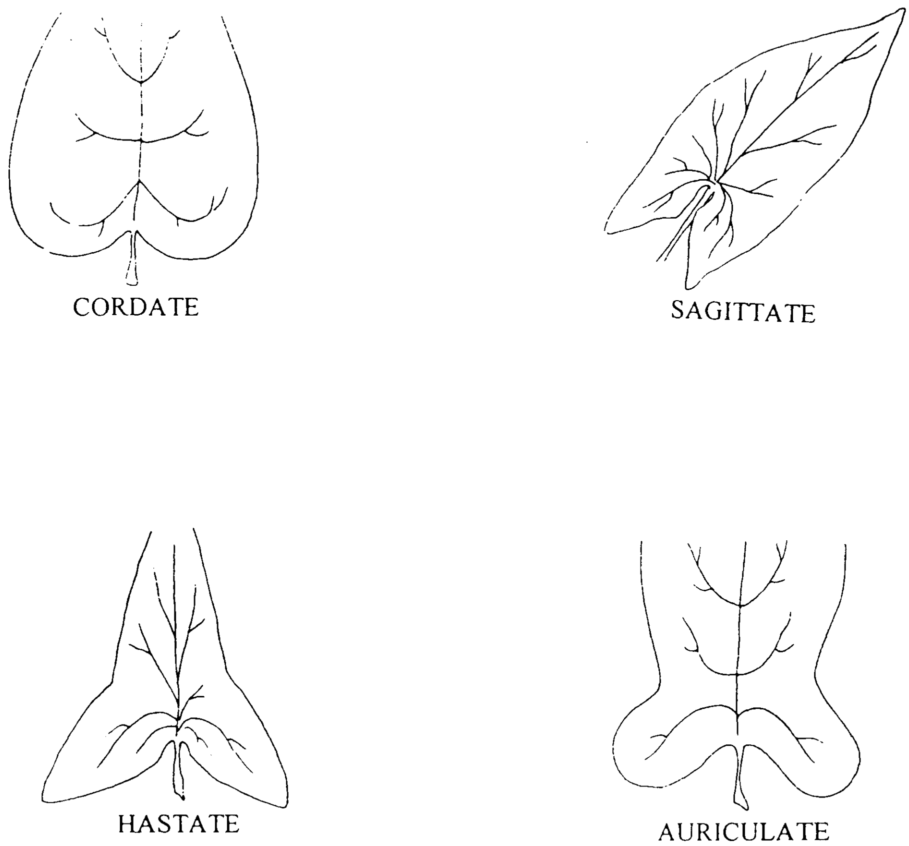

Figure 9. Cordate, saggitate, hastate, auriculate as well as leaves with asymmetric leaf bases are common to groups adapted to shade.

Trees with compound leaves are most common in arid and semi-arid habitats that favour the deciduous habit, at low elevations and in gap-phase succession.

Leaves tend to be borne in a spiral phyllotaxis on erect twigs in sunny environments and in a distichous (in two vertical ranks or rows on opposite sides of an axis) phyllotaxis on horizontal twigs in the shade.

Reddish leaf undersides, lens-shaped epidermal cells and blue iridescence are often associated with the extreme shade of rain forest understoreys. Such conditions are also associated with some rare instances (notably among the Begoniaceae and Gesneriaceae) of stomata arranged in clusters rather than singly.

Asymmetric leaf bases and anisophylly (unequal leaves at each node in species with opposite leaves, especially some *Streptocarpus* species in southern Africa) are also common in rain forest understoreys and other shady habitats.

4.7.5 The significance of grass morphology

Leaf blades of grasses are generally long and narrow, and this shape is significant to the productivity of grass plants (Gibbs-Russel *et al.* 1990) and grasses are normally sun plants. This shape, as well as the leaf arrangement also minimizes self-shading in grasses. Species with short broad blades tend to be annuals or to occur in habitats such as forests or watersides (Gibbs-Russel *et al.* 1990). These broader blades ensure better light absorbtion in low light environments. *Oplismenus hirtellus* and *Setaria megaphylla* are good examples. In *Setaria megaphylla*, a grass that can grow in deep shade, the leaves are plicate (folded lengthwise several times, pleated) and this could serve two purposes. Firstly to enlarge the photosynthetic surface and secondly the folds ensure a surface for optimum angle of sunrays to strike the surface. No matter from what direction the light falls, there is always a surface ready for a 90° light capture, which is the optimum for energy transfer.

4.7.6 Camouflage and defense

The irradiance level, by influencing the potential photosynthetic return from leaf tissue and the optimal allocation of energy to various photosynthetic compounds, affects the likely benefits and opportunity costs associated with different kinds and amounts of defensive measures aimed against folivores (foliage feeders). Angiosperms display an extraordinary range in the kind and amount of chemical, physical and biological defenses they deploy against herbivores.

Shade-adapted species should allocate more to defense than sun-adapted species, because the effective cost of replacing a given amount of leaf tissue is larger in slow-growing shade plants, and because the opportunity cost associated with a given amount of defense is larger in fast-growing sun plants (Coley *et al.* 1985). It is also suggested that sunny conditions should favour carbon-based defensive compounds (e.g. tannins, phenols), whereas shady conditions should favour nitrogen-based defenses (e.g. alkaloids). This is because nitrogen is more likely to limit photosynthesis under sunny conditions, and because fixed carbon is likely to be in less abundant supply under shaded conditions (Givnish 1988).

Assessing the costs associated with visual defenses such as mimicry, aposematic coloration (coloration of certain distasteful or poisonous animals or plants, characterized by bright conspicuous marking which the predator or herbivore recognizes and learns to avoid), or cryptic coloration (tending to conceal by disguising or camouflaging the shape), can be more difficult. Givnish (1988) found that mottled leaves were indeed less heavily attacked than unmottled leaves where they occur at similar frequencies. He presented data showing that at least in the flora of the north-eastern USA, mottled leaves are far more common in herbs of shaded forest understoreys than in any other growth form, and are essentially absent in trees, shrubs, herbs or vines of sunny sites. He presents the hypothesis that mottling serves to camouflage the foliage of certain, particularly vulnerable phenological groups of species (e.g. evergreens, spring ephemerals), by disrupting their outline as perceived by colour-blind vertebrate herbivores in sun-dappled understoreys.

In South Africa this adaptation can quite often be seen in understorey plants in the eastern parts of the country. *Laportia grossa*, the stinging nettle, has white spots on its leaves. *Plectranthus madagascariensis* and *Plectranthus oertendahlii* both have mottled white and green leaves. These plants also have chemical defenses which make them unpalatable. This adaptation has also been noticed by the writer in many exotic garden shade-plants, especially ground-covers in the Lamicaeae family. Instead of lighter spots on leaves, some plants have darker spots or coloration, probably for the same camouflaging purpose. *Drimiopsis maculata* has darker spots on the leaves, will grow in deep shade and has already proved its worth as a potplant. *Zamioculcas zamiifolia* is a member of the Araceae family and a Maputaland endemic with darker stripes, while some of the *Zantedeschia* species have white spots on their leaves. *Sansevieria* species also have white markings on their leaves. Many of the shade plants indeed seem to use both physical and chemical methods of defense and camouflage.

Application

These adaptations are exceptionally attractive and have already proved popular in garden plants. They also provide extra colour for shady spots.

Many of the exotic Araceae members which are well-known potplants also have mottled leaves. *Dieffenbachia* and *Agleonema* are good examples. Other members of the same family, notably *Monstera deliciosa* and *Philodendron selloum*, apparently show another form of mimicry in that they have leave openings, or holes in them. The rationale behind this could be that the leaves appear to folivares to have already been eaten. This family also has raphides (needle-shaped crystals) in their cells which make them unpalatable.

These "holes" in the leaves could possibly have another benefit in that they let sunflecks through to the lower leaves of the plant. Where the Araceae as a family normally show an umbrella-like arrangement with the leaves arranged next to each other, in these two species the leaves overshadow each other. These "holes" would serve perfectly to let sunflecks through to the lower leaves. For shade-plants with an energy crisis, each adaptation has to have more than one function to be economical. These adaptations can often be divergent.

4.8 ARCHITECTURAL ADAPTATIONS

4.8.1 Introduction

Patterns of leaf placement are more complex than a first glance suggests. Two basic architectures for forest trees are suggested -- monolayer and multi-layer (Fitter & Hay 1981). The monolayer is defined as a complete, uniform layer of leaves which lets through little photosynthetically active radiation (PAR) and is low in productivity. The multi-layer species have a broken canopy and rely on the facts that an individual leaf only casts a shadow for a certain distance and that light-saturation for most species occurs at intensities well below full sunlight. Multi-layer species thus permit several layers of leaves to operate at high photosynthetic rates. The multi-layer can therefore grow faster, but since it lets through PAR, it is more open to invasion. Within this basic dichotomy the plant needs to be able to control both leaf production and placement. The morphogenetic responses involved are closely tied to the phytochrome system. Typical responses include stem elongation and leaf orientation.

The support skeleton of a plant - its stems, petioles and analogous structures - play three vital roles in capturing light. It provides the means to arrange, orient and support foliage efficiently, to overtop competitors and invade new space and allows the transport of water, nutrients, sugars and starches to the leaves and other plant organs.

Support, competition, and transport are arguably the most important roles of a plant stem and other support structures, given the fundamental importance of photosynthesis, and the preponderance of leaves versus other organs (such as flowers or fruits) in the biomass borne by the stem (Givnish 1995). The form, growth dynamics and biochemical properties of items have important implications for a plant's rate of growth and competitive ability and play a crucial but often overlooked role in adapting plants for different conditions and influencing their ecological distribution (Givnish 1986).

The primary functions of support and competition impose four principle constraints on stem adaptations for energy capture. These are mechanical stability, mechanical safety, photosynthetic efficiency and whole-plant growth and competitive ability (Givnish 1988).

The requirements for photosynthetic efficiency impose constraints on stem form and branching pattern on the basis of their effect on leaf arrangement and orientation as well as the impact that these have on the rates of photosynthesis and transpiration. Self-shading is likely to reduce both photosynthesis and the costs of transpiration. The resulting decrements to photosynthesis are likely to be especially severe in shady environments: the benefits of reduced transpiration are likely to be particularly great in dry and/or sunny environments (Givnish 1986, 1988).

The requirements for whole-plant growth and competitive ability impose constraints on the maximum rate of net carbon gain by a plant and its ability to overtop other plants. According to Givnish (1995), optimal form, biomechanical properties, and growth dynamics of stems in a particular ecological context are set by five major trade-offs. These trade-offs involve the balance between safety versus growth and competitive ability, growth versus photosynthetic requirements, mechanical versus photosynthetic efficiency, initial versus continuing cost and structural parasitism versus self-support.

4.8.2 Woody and herbaceous plants

The inevitable conflict between stem safety and plant growth in an unproductive environment leads to an ecologically extremely important stem trade-off, that of balancing growth and photosynthetic requirements. As a general principle, taller plants have an advantage in competing for light, but must allocate more to unproductive support tissue. The competitive advantage of increased stature is greatest where coverage is dense, on moist, fertile, infrequently disturbed sites. But the energetic demands of tall plants may exclude them from less productive sites (Givnish 1995).

The lower light requirements of shorter plants (e.g. herbs and shrubs) provide a simple mechanism that permits them to persist under a canopy of taller species, even if all have leaves with the same photosynthetic characteristics. The differing energetic requirements of woody versus herbaceous plants may also help explain the shift from shrub to herb dominance in forest understoreys, often seen in moving from xeric to mesic sites in eastern North America. Being taller than herbs and having stems constructed of costly wood, shrubs should have higher whole-plant compensation points than herbs (Givnish 1988) and may be able to persist mainly on xeric sites, where drought, soil infertility and/or fire maintain a relatively open tree canopy. As shrubs are taller than herbs and root in the same soil horizon, they cast shadows that move little as the sun moves across the sky and may suppress herb growth by competition. On mesic sites, by contrast, the dense tree canopy may lower understorey light levels below the minimum required by shrubs, allowing herbs with shorter, less expensive stems to predominate. This hypothesis has important implications not only for trends in the relation of forest strata to each other, but also for overall forest diversity, given the far greater number of herb species than those of shrubs or trees in most temperate regions (Givnish 1995).

Application

There are not many shrubs to grow in shade, and virtually none for deeply shaded areas. The solution for these difficult areas lie rather in the use of herbaceous perennials, of which there are quite a few to choose from in the southern African flora.

Woody tissue has a higher initial construction cost for stems of a given length or height than mechanically equivalent herbaceous tissue, but only a small fraction of the support structure must be built each year in woody plants (Givnish 1995).

Two predictions that follow directly from this principle are that short plants should be herbaceous, and taller plants should be woody, and herbs should be more shade tolerant than woody plants of the same stature. The proportion of above-ground biomass annually allocated to leaves decreases with plant stature but at different rates in herbs and woody plants, starting higher in shade-adapted herbs before dropping below that in woody plants at about 0,5m. The cross-over point is about 1 m for sun-adapted herbs (Givnish 1995). The reason for the evolutionary ascendance of woody plants is simply that, even though their support tissue is more expensive than that of herbs of the same height, they build only a portion of their stem per year and do not discard previous increments to support the skeleton (Givnish 1988).

4.8.3 Branching patterns

In general we would expect that branching patterns and leaf arrangements that reduce leaf overlap and competition for light often do so at the expense of increased investment in stem tissue, and entail exposure to greater irradiance and transpirational demand (Givnish 1986).

One important prediction based on these considerations involves the fundamental organization of shoots in sun and shade: shade-adapted plants should be plagiotropic (horizontal growth habit), and sun-adapted plants should be orthotropic (vertical growth habit) (Givnish 1986). Plagiotropic shoots are horizontal twigs with leaves arranged distichously in a planar array, and are indeed common in shade-adapted plants; orthotropic shoots are erect, bear spiral leaf arrays, and are generally common in well-lit habitats.

As organs of energy capture, plagiotropic shoots minimize self-shading, and so are well adapted to shady conditions in which light is strongly limiting. Orthotropic shoots self-shade more, but should require less stem tissue to support the same or greater leaf mass. Consequently they may confer an advantage in well-lit situations, in which light less strongly limits photosynthesis and self-shading may reduce water loss (Givnish 1986).

As organs of growth, orthotropic shoots may yield an advantage to sun adapted plants, directing growth upward and helping to prevent overtopping. Plagiotropic growth direct shoots outward and may be favoured in shad-adapted species: increasing total leaf area may be a more certain means of raising whole-plant carbon gain than growing taller for plants that grow far below the canopies of others (Givnish 1988).

Another prediction related to the balance between photosynthetic and mechanical efficiency is that optimal branching angles should minimize both leaf overlap and structural cost, if possible.

4.8.4 Leaf arrangement

For different shoot orientations and branching patterns, selection should favour the phyllotaxis that minimizes self-shading and/or structural costs, at least under relatively moist or shaded conditions (Givnish 1986). In orthotropic shoots, a spiral phyllotaxis with an angle of 137 degrees between successive leaves may be favoured because it minimizes self-shading, or possibly because it results in the most efficient packing for primordia on an expanding shoot apex.

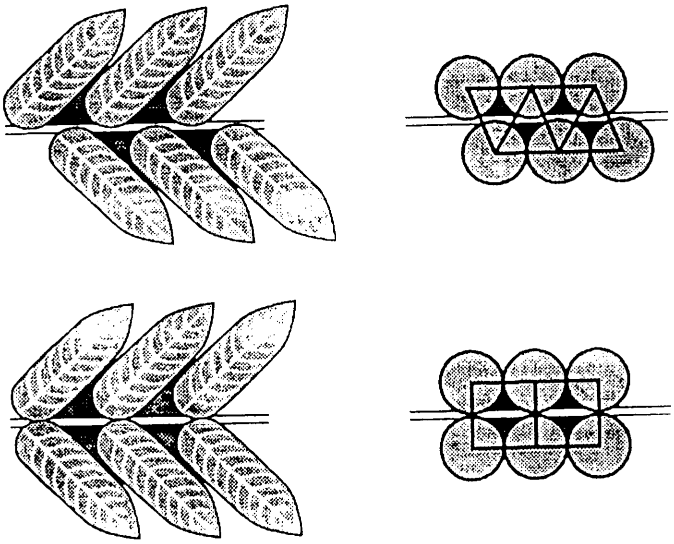

Figure 10. Packing of alternate and opposite leaves in a planar array (left) and packing of disks on triangular vs. rectangular grids (right). Note the smaller amount of uncovered space in the close packing of leaf bases or disks on a triangular (alternate) grid. For circles, alternate packing reduces the area uncovered by 44% (Givnish 1995).

For shade-adapted, plagiotropic shoots, a distichous, alternate leaf arrangement may be best (Figure 10). The tightest packing of convex, bilaterally symmetric leaf bases is possible on a triangular, not square, grid (Givnish 1984). This packing results in fewer uncovered gaps, for which the plant has paid in terms of stem tissue. It should be particularly adaptive in shade-adapted plants that are growing close to their energetic limits. It is interesting to note here that shade-adapted members of some groups that are invariably characterized by opposite leaves (e.g. Gesneriaceae, Melastomataceae) approach the alternative leaf arrangement through anisophylly, in which one leaf is much smaller than the other at a node, with the position of the larger leaf alternating from one side of the twig to the other (Figure 11).

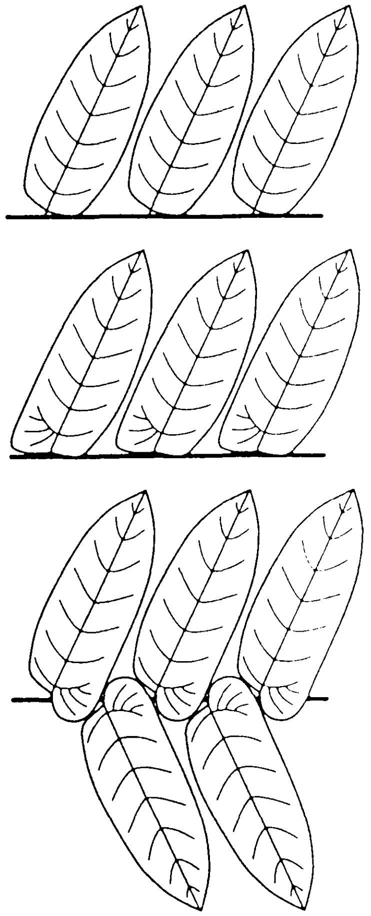

Figure 11. Top: Efficient packing of bilaterally symmetric leaves in a planar array, note gap adjacent to proximal side of leaf base. Middle: Increased efficiency of packing with asymmetric leaf bases in which an additional area is supported by the basal secondary vein on the proximal side. Bottom: Same, but additional area is supported by the distal side of the leaf base (Givnish 1995).

Even an alternate leaf arrangement will leave some space near a branch uncovered if the leaf bases are bilaterally symmetric (Figure 12). Not surprisingly, several shade-adapted groups with plagiotropic shoots (e.g. *Anisophyllea, Begonia, Ulmus*) are characterized by asymmetric leaf bases that appear to provide a final refinement of leaf packing. Such asymmetric leaves seem generally to be restricted to plagiotropic groups adapted to extreme shade (Givnish 1995).

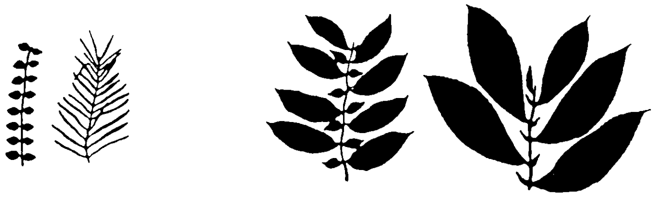

Figure 12. Anisophylly in *Columnea* (Gesneriaceae) sun-adapted species with pendent or erect shoots (e.g. *C.microphylla* and *C.linearis*) are isophyllous; shade-adapted species with horizontal shoots and broader leaves (*C.harrissi* and *C.sanguinea*) are markedly anisophyllous and approach an efficient mosaic of alternative leaves (Givnish 1995).

4.8.5 Grass-architecture

In grasses the plant architecture of the most species (open veld) nearly all have long narrow vertical leaves that are supposedly most efficient in strong light. This leaf configuration makes the best possible use of sunlight by allowing light to penetrate deep inside the leaf canopy of the whole plant (Gibbs-Russel *et al.* 1990). Light therefore, reaches a relatively large total area of leaf surface, and grasses are thus able to produce a large biomass per volume of space occupied.

4.9 REPRODUCTION

Insufficient light represses flowering and fruiting and sometimes holds vascular plants indefinitely in the vegetative condition. Low light intensity favours vegetative development at the expense of flowering and fruiting (Daubenmire 1974). Since the production of these structures is very expensive in terms of the energy budget of a plant, this is one of the most pronounced energy conservation tactics of shade plants.

Application

1. **Crops grown for vegetative parts are favoured by climates with a high percentage of cloudiness, whereas fruits, grains, seeds and flowers are favoured by bright sunlight.**

2. **Very showy and attractive flowers and fruit are seldom found in true shade plants. The ornamental value of these plants lie rather in the often extraordinarily beautiful foliage. This makes it difficult to create a colourful shade garden, though not impossible. Colour can be introduced in the form of plants with coloured leaves and some bulbous plants also provide exciting seasonal flowers. The herbaceous families Lamiaceae, Gesneriaceae and Acanthaceae have valuable shade-flowering representatives. The Rubiaceae and Apocynaceae are valuable for flowering and fruiting shrubs and small trees.**

4.9.1 Plant breeding systems and ecosystems

The long-term survival of an individual plant in a particular habitat depends upon that individual being physiologically and ecologically adapted to the habitat, as well as on successful reproduction within the habitat. Two of the most important processes in plant reproduction are pollination and dispersal. Because plants are stationary, pollination is carried out by various mobile agents, such as insects, water, wind and birds. Dispersal is the process in which seeds are distributed to the new areas, or at least away from the base of the adult plant, so that the offspring do not compete with the parent. For example, on sea-facing dunes on the southern Natal coast, plants that grow close to the sea where there are strong winds are pollinated by wasps, beatles and bees (all strong flying insects), while plants that occur under the canopy of the dune forest (where there is little wind) may be pollinated by moths and butterflies (Balkwill 1996).

All flowers are adapted to mediate the transfer of pollen from anthers to stigmas, whether within a flower (autogamously), or between flowers of the same or different genets (allogamously).

For seed to set in obligately outbred self-incompatible species, there must be adequate pollen transfer between flowers of different genets (genogamously) (Balkwill 1996).

Flowers also harbour the process of fertilisation, embryogenesis and seed production, and develop the fruit within which the seed is dispersed. The diversification of angiosperm flowers has been paralleled by a diversification of flower visitors, and, according to Richards (1986), thus allows the following developments:

a) Many species of plants with biotic and abiotic means of pollen transfer can coexist in a habitat.

b) Energetically efficient means of pollen transfer have evolved.

c) Pollen transfer can occur in environmentally adverse conditions.

d) Speciation of related sympatric congeners into differential adaptive noda has occurred through prepollination reproductive isolation of demes.

e) All habitats are heterogenous and with respect to seed reproduction, they are importantly heterogenous in five variables: time, within a season; height above ground; number of species of potential flower visitors; number of individuals of flower visitors; sites for seedling establishment (Richards 1986).

Thus, for any species of flowering plant, a suite of flower characteristics has evolved which is coadaptive with respect to an equilibrium point of reproductive strategy for a niche based on at least one point amongst each of these variables. Any one species will have its own characteristic flowering time, flower height above ground, means of donating and receiving pollen, seed size, seed number and seed dispersal capability, which allows it to maintain this equilibrium point. Furthermore, the theory of competitive exclusion renders it unlikely that any other species in that habitat will inhabit the same equilibrium point on all five criteria (Richards 1986).

For coexisting species with similar equilibrium points, there will also exist a threshold level of reproductive efficiency. This threshold will be a function of the proportion of the total energy budget of the plant spent in replacing that plant by seed reproduction. Coexisting species in a habitat may have very different equilibrium points of reproductive strategy and will thus be able to coexist with very different levels of reproductive efficiency. For example, a small annual in grass land is likely to flower early, be dwarf, have unspecialized, mostly autogamous flowers, and have large seeds with poor dispersal. More than 50% of its total synthesised energy may be expended on its sole reproductive effort. By contrast, a neighbouring perennial orchid in closed grassland may flower in mid-summer, be taller, attract and reward only one species of pollinator which is scarce in the habitat and which alone can effectively mediate pollination. Thus it may rarely set seed. However, when seeds are set, they are very small and produced in very large quantities. Such species may spend much less than 10% of its total annual energy budget on seed reproduction. Much more of its energy is spent on perennation and vegetative multiplication (Richards 1986).

The question of how many different types of reproductive strategy equilibria can coexist in a habitat will depend, to a great extent, on the total biomass productivity of the habitat. Unfortunately, very little data to support such energetically based models is available and more particularly the knowledge of the allocation of energy budgets in different plants is almost nil. In addition very few studies that compare different habitat types with respect to their pollination syndromes have been done (Richards 1986).

Application

As already mentioned, the reproductive tactics of shade plants would essentially be one of energy conservation. They are often inconspicuous in colour, size of flowers and fruits. The production of many white and cream flowers is another energy conservation method as the plant does not have to reproduce energy-expensive pigments. There must be suitable pollinators in these habitats for the plants. From the different pollination syndromes, it is usually possible to predict what kind of pollinator will transfer pollen in a particular species.

4.9.2 Pollinators

A certain harmony exists between a visitor (pollinator) and a blossom. Lack of this harmony will prevent pollination and may prove fatal to the visitor (Faegri & Van der Pijl 1979). At best, nothing comes out of such a visit. At worst too strong or rapacious visitors may destroy the blossom, while too small visitors may do some damage reaching the nectar or stealing the pollen without effecting pollination. Usually there is some kind of long distance attractant like bright petals or strong scent and there is invariably a reward, such as nectar, pollen or feeding tissue. In some cases mimicry and deceit is used to "trick" the pollinator (Faegris & Van der Pijl 1979).

Observed interdependence between blossoms and pollinators always depends on this harmony, and the absence of a possible pollinator may be due to other factors. The apparent restriction to fly pollination of some plants that occur in shaded, damp places is due to the fact that flies abound in such biotypes, and an insect can only pollinate within its own biotype. However, it should not be forgotten that all such type designations are extremely generalised and flies may be anything from a non-specialized, omnivorous creature like the house-fly, to some of the most specialized pollinator types known, with probosces comparable in length to those of butterflies (Faegri & Van der Pijl 1979).

Where insects are pollinators, it must be remembered that the life of an insect is more or less distinctly divided into two phases: a larval phase during which the insect grows and develops its organs, and an imago phase during which no growth takes place and which is the time of mating. The food requirements of insects differ greatly during these two phases; the larvae need a balanced diet to grow and develop; imagine need energy food to keep their activities going.

Plants form the food of the majority of insects, which may eat any part. The soft, often succulent and sweet, blossom tissues are a favourite food of many species, as garden owners know only too well. Such more or less destructive visits may effect pollination and many insect groups that are mainly looked upon as pests may in reality be of some importance in pollination, for example, hemipters (Faegri & Van der Pijl 1979).

The syndromes of insect pollinated flowers can be very specific. Beetle-pollinated blossoms (cantharophily) pollination units have few visual attractions, no special or definite shape, with no depth effect and no nectar guide, are generally large, flat, cylindric or shallow bowl-shaped, sometimes closed, easy of access (beetles being poor fliers). Colours are dull, frequently greenish or off-white. Odour is strong, fruity, or aminoid. Attractants are open, easily accessible, pollen, food-bodies or nectar. Sexual organs exposed (Faegri & Van der Pijl 1979).

Fly-pollinated blossoms (myophily). The blossoms are regular, simple, with no depth effect. Colours are generally light, but dull. Nectar guides frequently present (some *Streptocarpus* species and members of the Acanthaceae family). Odour is imperceptible. The nectar is open or easily obtainable. The sexual organs are well-exposed (Faegri & Van der Pijl 1979). Many of the shade plants seem to have flowers that fit his category. They have small inconspicuous greenish or yellow green flowers with no detectable scent. Many of our fly species also inhabit shady areas, especially in the savanna and eastern subtropical regions. Some of these flies can often be found under trees, in the shade, sitting and sheltering on the underside of branches.

Besides this series, there is a completely different ecological group of dipters also attracted to blossoms, viz. carrion and dung-flies (there is a corresponding group for beetles). Carrion and dung-flies belong to many different taxa. Some of them are curiously small and may occur in large numbers in one blossom. Some of the facultative shade plants in the drier parts of South Africa that make use of this group of pollinators, for instance many *Stapeliae*. In sapromyophily the basis for the visit is deceit. Foul smelling substances released by the blossoms activate the instincts of the fly for feeding or oviposition, and there is no reward in the form of nectar (Faegri & Van der Pijl 1979).

Butterflies (psychophily) and moths (phalaenophily) are in typical development so different in their relationship to blossoms that they are generally treated apart. However, the fundamental difference is not one of taxonomy, but of ethology. One generally finds that butterflies are diurnal and alighting, while moths are crepuscular or nocturnal and hovering (Faegri & Van der Pijl 1979).

Olfactoric attraction must play a greater part in moth blossoms than in most others, and they can fill the night-air with lovely and even overwhelming fragrances. Sometimes the odour is too strong to be tolerable too close to the house, according to Faegri & Van der Pijl (1979). This is particularly true for *Cestrum nocturnum* and the popular names Dama de noche, or in Sudanese, Sundel malam = night-whore, are apt, it is said, because it is unobtrusive at daytime, agreeable at night and disgusting in the morning. The strong periodicity of odour production can be remarkable. Flowers that fill the air with fragrance at night may be virtually scentless during the day (Faegri & Van der Pijl 1979).

Application

The Dracaenaceae family is well-known for its flowers that open at night. The flowers produce a sweet scent and must be pollinated by moths. Members of this family can grow in deep shade and make indoor container plants par excellence. They would also make good outdoor accent plants in subtropical climates or protected areas. The attractive brightly coloured orange to red fruit is relished by birds and monkeys, who are the natural dispersal agents. Larvae of the skipper butterflies (Hesperidae) breed on this family. The scent and fruit of these plants make them even more attractive as ornamental plants. There are also different forms or varieties of these plants in nature, each of which has specific ornamental value.

In phalaenophilus (moth-pollinated) blossoms not only the periodicity of odour production but also anthesis as a whole shows a correlation with nocturnal visits. If an anthesis lasts for more than one night, the blossom can close (sometimes imitating wilting) during the intervening day(s) so that it loses its visual as well as its olfactoric attraction during the daytime.

Spingids that hover produce a more characteristic syndrome than the Noctuids that usually align or support themselves on the blossom. Spingids are sensitive to strong winds, which make landing impossible. Strong sea-winds, for instance, can imperil pollination (Faegri & Van der Pijl 1979).

Application

There is very little wind and air movement in forests. This makes them ideal for moths and butterflies to live in. There is also a wide selection of food plants in forests for the larvae, species which can be ferocious feeders. Blues butterflies (Lycaenidae) breed on members of the Rubiaceae family.

The families Apocynaceae and Rubiaceae are well-known over the world for their ornamental plants, and are also the families with the most woody representatives for shade or semi-shade.

These two families both have pleasantly scented, mostly white, flowers, often with a narrow tube (*Oxyanthus, Pavetta, Tabernaemontana, Carissa*) for insects with long proboscis.

Many members of both families have attractive red, black or yellow fruits, some of which are eaten by humans. Seed is dispersed by birds and monkeys and provide the added benefit of attracting birds to the garden.

The ornamental value of these plants lie in their dark-green, shiny leaves, flowers, scent and fruit.

That moths see colours in the dark is not evidence against the usefulness of the frequent white and off-white colour found in these blossoms, nor does it prove that there is optical attraction in dull-coloured blossoms (Faegri & Van der Pijl 1979).

4.9.3 Synchronous flowering

Interesting studies have been done by Augsburger (1982) on *Hybanthus prunifolius* (Violaceae), a shrub that occurs commonly in the forest understorey of Barro Colorado Island. These shrubs flower in synchrony in the dry season, a few days after the first rain that is preceded by a drought of sufficient duration and severity. These plants will not flower if they were watered during the dry season and must undergo a period of drought first.

If a single shrub is stimulated to flower out of synchrony, it attracts few pollinators. If a whole clump is stimulated to flower in synchrony, however, it attracts its customary pollinator(s), down from the canopy and achieves normal fruit set. Synchronous flowering leads to synchronous fruiting, and fruiting in synchrony appears to satiate the graniverous caterpillars that should otherwise destroy the seeds before they are dispersed.

Several southern African shade species also flower synchronously in response to dry-season rains. Whether or not they derive the same advantages as *Hybanthus*, is not known. Many of our succulents flower only in response to rain, irrespective of the time of year.

Horticulturists at the University of Maryland have described how to time the flowering of *Amaryllis* bulbs by not watering (Anonymous 1988).

4.9.4 Semelparous flowering

Crawford (1989) divides plants that grow on the forest floor into three groups. The (i) competitors are usually perennial plants with a well-developed capacity for resource capture and high levels of input of resources into new organs. The (ii) stress tolerators, perennials that use captured resources conservatively and have the ability to survive for long periods with little growth or reproduction. The (iii) ruderals are plants with high growth rates and short life-spans and are often capable of prolonging seed dormancy and exploiting irregular occurrences in suitably disturbed habitats.

In the northern hemisphere, the ruderal species include a few annuals and a number of specialized perennials which are able to invade forest clearings. The foxglove *Digitalis purpurea*, typifies a reproductive pattern that is particularly successful in this situation. This species if often referred to a biennial, but should really be considered as a perennial, as it can survive for more than 4 years before dying. More precise terms would be semelparous (single reproducing) and iteroparous (multiple reproducing) perennials. True obligate biennials appear to be rare and semelparous perennials are also not common (Crawford 1989). In certain taxonomic groups, however, semelparous perennials are very frequent. In the Apiaceae, 30% of the European species show this behaviour (Silwertown 1984). The characteristic ability of the foxglove and other species to invade forest clearings, is that of producing large quantities of small seeds which can be widely dispersed. The small seed has the disadvantage that there is an initial lag phase in the development of the seedling and the plant cannot normally flower in the first year of growth. The delay in reproduction is compensated for, however, by the large number of small seeds which can be widely dispersed. The small seed has the disadvantage that there is an initial lag phase in the development of the seedling and the plant cannot normally flower in the first year of growth. The delay in reproduction is compensated for, however, by the large number of seeds that are eventually produced. Semelparous perennials such as foxglove can fill intermittent gaps and when eventually squeezed out by iteroparous perennials can establish new populations due to the efficient dispersal of very large numbers of small seeds (Crawford 1989). The semelparous perennial often has to reach a critical size before it can flower. This ability to queue for reproduction by size rather than age is likely to be a superior strategy in deteriorating environments such as would arise when shade is re-established over a forest clearing (Crawford 1989). In southern Africa this method of reproduction seems to be the case for *Isoglossa woodii*, a member of the Acanthaceae family.

4.9.5 Dispersal

Different parts of a plant may act as the dispersal units (disseminules). In some cases individual seeds are dispersed, while in others, whole fruits may be dispersed (Balkwill 1997). These fruits, may contain one or more seeds.

Dispersal may occur over short (mechanical dispersal) or long distances (wind dispersal). The dispersal distance dramatically affects the kind of variation that can be observed in populations of species. If the dispersal is over short distances, then the offspring of a particular plant will grow close to that plant and are thus likely to be pollinated with pollen from its parents or siblings (Balkwill

1996). As a result, all the plants in an area will be similar to one another, but because they are not exchanging genetic material with other adjacent populations, they are likely to differ from these adjacent populations. This can be seen in a number of members of the Acanthaceae (Balkwill 1996). It can also often be observed in the Lamiaceae, notably the genus *Plectranthus*, where the same species has a few different forms, even within one forest. The genera *Crassula* and *Gasteria* also show many varieties and forms in nature and also hybridise easily. Hybridisation could be a potent factor in the origin of some *Streptocarpus* species and the resultant gene-flow could be a cause of variability and the blurring of specific boundaries (Hilliard & Burtt.1971).

Application

Hand-pollination in the green house can and already has lead to superior ornamental plants of exceptional beauty. Seed of *Streptocarpus* hybrids "Wiesmoor" and "Fiesta F2", is internationally available from commercial seed companies. These hybrids are free-flowering and suitable for pots as well as bedding plants. Not forgetting the original wild forms as ornamental plants, there is potential for many more hybrids.

Different populations of the same species are morphologically quite distinct. If plants from the different populations are transplanted and cultivated under identical conditions, they retain their differences. If they produce seed while grown in close proximity, however, the offspring will be intermediate between the parents and after a few generations it is impossible to determine from what area the parents of the seedling originated. The differences between populations are thus due to the isolation imposed by short distance dispersal (Balkwill 1996).

Application

A specific population may have more ornamental value than other populations of the same species. This makes it easy to select suitable horticultural subjects. It is quite likely, however, that more than one of these ecotypes or populations has ornamental value and because they can still cross-breed, it is essential to propagate these forms vegetatively. A clone of a specific plant will then be produced where all the offspring is identical to the selected mother plant. Many of these forms are described and also have varietal names, often linked to the locality where they were found. If this is not the case, variety names should be given and published.

Plants that display long range dispersal, on the other hand, are often morphologically very constant over the whole of their distribution range because there is a regular exchange of genetic material between populations. The distance over which seeds are dispersed will also determine whether certain species are able to disperse into new habitats or between islands of suitable habitats. This will obviously effect the distribution of the species - those with long-range dispersal will be more likely to be widely distributed, whereas those with short distance dispersal will show local endemism (Balkwill 1996).

A number of different agents may be responsible for the dispersal of various disseminules. From various characteristics of the disseminule, it should be possible to predict what the dispersal agent may be (Balkwill 1996).

The most unspecialised kind of dispersal is that in which the seeds are simply dropped at the base of the parent plant. This would obviously be short-distance dispersal. With mechanical dispersal certain fruits are structured in such a way that when they open, they do so explosively and thereby propel the seed away from the parent plant. Many members of the Acanthaceae display this kind of dispersal, where the capsule splits open either due to wetting or drying (Balkwill 1996). It is this dispersal mechanism of *Julbernadia* and *Brachystegia* that lead to their dominance in the woodland in which they occur (Balkwill 1996).

Some plants are adapted to be dispersed inside animals (endozoochory) and usually have fleshy, edible and digestible layers in their disseminules. Often the flesh or the skin is brightly coloured in order to draw attention to the edible material. These disseminules are dispersed by animals such as monkeys, birds and humans (Balkwill 1996). The families Rubiaceae, Euphorbiaceae and Apocynaceae have such brightly coloured fruits and as in the case of some of the Apocynaceae, although the flesh is edible, the seeds are poisonous.

Application

Apart from being ornamental, members of the families with brightly coloured fruits have the added benefit of attracting birds to the garden, and possibly, if in the right area, monkeys and other small mammals.

CHAPTER 5

SHADE GARDENING

5.1 INTRODUCTION

Shade is often considered to be a problem, but a shaded area is an essential component of a garden in a hot country, and it also provides contrast - a valuable design element in the best gardens. A large number of plants grow in shade in their natural habitats and, in the garden, with a careful choice almost all types of shaded areas can be made interesting and successful.

Shade is an imprecise term, and its effect is closely linked to soil conditions, air circulation, exposure and the nature of the site. There are no hard and fast rules about what plants will grow where and recommendations for one situation are bound to overlap those for another.

Three types of shade are most commonly found in gardens. Permanent shade is created by buildings or walls or dense overhead tree canopies. Temporary shade is created for part of the day as the sun travels from east to west. Dappled or partial shade refers to conditions where sunlight is filtered through a thin overhead canopy and the plants are never in full sun. There are variations within these groups. In temporary shade, the shadows are longer in midwinter than in midsummer (this phenomena is accentuated as distance from equator increases). Where shade is cast by deciduous trees, light penetration is gradually reduced from early spring to midsummer as the leaves expand. Light can be reduced by as much as 52% in summer under deciduous trees. In tropical forests, sunlight does not penetrate to ground level and plants there receive a very low light intensity. Such plants will adapt well when grown at higher levels of light under glass or in temperate countries, or in lighter shade in the open in tropical or subtropical countries. Some forests are virtually shadeless as is the case with *Eucalyptus* forests where the tree leaves are held vertically in strong sunlight. At the other extreme are the dense commercial plantations of conifers which cast such complete shade that no plants will grow beneath them.

The strength of sunlight is another variable factor. Plants which are generally grown in shade in one country or area may flower better in full sun in another country or area. A similar effect is found with some alpine plants which grow in a high light intensity in the mountains but need shade when grown in lowland conditions where temperatures at the equivalent light intensity are too high.

Many woodland plants native to temperate countries, rhododendrons, for example, are well-adapted to growing in relatively low light, and will flower longer and better in shady conditions in the temperate garden than in the open. Woodland gardening, which has developed greatly in the 20th century, has taken advantage of the introduction to cultivation of many plants from the woods of North America and Asia. Many of these woodland gardens are extensive, with a high canopy of well-spaced deciduous trees, and often with a slightly acid but moist and fertile soil.

In southern Africa the closest to this would probably be old established parks and gardens planted with alien deciduous trees. There are no natural deciduous woodlands to compare with these in temperate countries. On a smaller scale, where planting has to be closer to the tree bole, the soil conditions under the shade of trees which are surface-rooting where root competition is strong, making it difficult for other plants to become established. For perpetual, deep, dry shade, great stalwarts are *Protasparagus*, *Crassula* and *Sansevieria.*

Other plants will survive only for a few years in such demanding conditions. Even if a special planting hole is prepared by severing the tree roots and lining the hole with plastic sheeting or geo-textile before filling it with a good soil mixture before planting, the vigorous tree roots will gradually encroach again. Growing plants above ground in containers may be an alternative in these conditions, but they will need extra care in keeping them well watered and flowering may not be so abundant in the shade.

Besides being decorative in their own right, containers are easily replanted and give scope for experimenting with short-lived plants in order to supply a splash of colour where it is most wanted. Most spring-flowering bulbs are excellent and some annuals like *Lobelia* as well as herbaceous perennials like *Begonia, Impatiens, Plectranthus* and members of the Acanthaceae family can also be used to great effect. For more permanent plants a selection can be made from the shade-loving shrubs and young forest trees. There are also some exquisite alpine plants which prefer a cool or partially shaded position.

Dry soil is often a problem in permanent shade as overhead trees or neighbouring buildings may prevent the natural rainfall from reaching the ground. In such soils, the moisture-holding capacity and its nutrient content can be improved by incorporating as much bulky organic material as possible into the topsoil before planting. A 5 cm layer of similar materials spread over the soil as a mulch after planting and topped up annually over damp soil in spring will help to maintain soil moisture and fertility.

In smaller shaded areas with little open sky there are cosmetic devices to give the impression of increased light. These include painting the walls a light colour, laying pale paving or gravel and introducing a mirror or even a pool to reflect overhead light.

Temporary or partial shade caused by overhead trees can be reduced to some extent if necessary, by thinning out the crown or removing some of the lower branches. For most trees this is best done in late winter. An alternative is to turn the source of shade into a feature. A tall deciduous tree can be host to a climber which prefers to have its roots in the shade and reaches up to the sunlight to flower. It is wise to plant climbers in a bottomless box filled with a good soil mixture. The box should be sited at least 90 - 120 cm away from the tree trunk to keep root competition in the early stages of development to a minimum. As the shoots grow they are led towards and eventually tied to the trunk and lower branches of the host tree and guided up into its higher branches.

Forward planning to prevent troublesome shade when starting or stocking a garden will be amply rewarded. One of the commonest mistakes is to aim for instant effect and to underestimate the speed of growth of a tree or shrub, only to find that shade and invading roots encroach on a once sunny part of the garden. It is always as well to bear this in mind when selecting and positioning such plants.

There is a great difference between the blanketing year-round shade of broad-leafed evergreen trees and the airy summertime shade of *Acacia* species for instance. Deciduous trees themselves show great variation in the kind of shade cast, according to their height and habit and the size and density of their foliage.

Another consideration when choosing shade trees is the timing of leaf development. Under trees like *Celtis africana* that come into leaf early it may be possible to grow only spring-flowering bulbs which bloom in very early spring, whereas *Combretum erythophyllum* does not acquire its full foliage until summer, thus extending the season for growing plants beneath it. On the other hand, tree foliage that does not obscure too much light can be useful in protecting plants from winds and from early and late frosts.

Many of the plants that thrive in dappled shade will perform as well in a south facing border open to the sky, and *vice versa*. Perennials are often interchangeable between the two situations.

5.2 TREES AND SHRUBS

Although two thirds of South Africa is semi-desert with few tree species, the eastern parts of the country are well wooded with almost a thousand tree species occurring in woodland forest or grassland. Of these, many are adapted to grow in shade or filtered sunlight and most are good horticultural subjects. These species vary widely in growth rate, shape size, flower colour and leaf texture, thus providing a great variety to choose from. They can be used individually or as mass plantings, in mixed beds, as accent plants or in containers. Most of these species can be grown in gardens near the coast.

There are several indigenous shrubby semi-herbaceous species with large attractive leaves. *Plectranthus fruticosus* and *P. ecklonii* are shrubs 2--3 m tall which are effective in mass plantings. They bear large spreading leaves and those of *P. fruticosus* are suffused with purple on the lower surface. *Sparrmannia africana* is a shrub 3--4 m tall with large, spreading, hairy leaves and white flowers. It is used throughout the world today. *Indigofera natalensis* is another attractive shrub up to 1,5m tall. *Mitriostigma axillare* is a small shrub up to 1 m tall, with scented white flowers and yellow fruits. *Trichocladus crinitus* is an attractive shrub with large leaves which are glossy above and covered with chocolate brown hairs below.

The woody shrubs are long-lived and slow growing. *Diospyros whyteana* has small, dark-green glossy leaves. *Diospyros natalensis* has attractive horizontal branches and small leaves. The Pondo rose-apple, *Memecylon bachmannii* is a very attractive shrub with rounded shiny leaves and is a must for all shady gardens.

Most of the shade-loving shrubs come from high-rainfall regions, and should be well watered. They will do best in a fertile compost-rich soil. A balanced fertilizer such as 2:3:2 can be applied annually.

Several of the *Cussonia* species (known as cabbage trees), make excellent accent shrubs or small trees. They have erect stems with shiny, compound leaves clustered at the ends of the branches. Height varies from the small 1 m high *Cussonia arenicola* to the tall *C. spaerocephala.* They have succulent roots and are drought resistant. *Dracaena hookeriana* is an erect, single-stemmed plant with an attractive rosette of tapering leaves, which can be used in landscaping to create a tropical effect. Some of the southern African cycads are also suitable for shady areas. *Encephalartos villosus* is the smallest of these and is a species with large leaves up to 2 m tall. The shrubby, caulescent species include *E. paucidentatus, E. transvenosus* and *E. ferox*, all with very ornamental leaves. The Pondo palm *Jubaeopsis caffra*, also thrives in a shady garden and will attain a height of about 10 m. *Strelitzia nicolai* is attractive with its large leaves. It forms a tall, multi-stemmed shrub up to 8 m and gives a lush "tropical" effect. All species mentioned here thrive as container plants.

5.3 HERBACEOUS PLANTS

The biggest group here is probably the *Plectranthus* species. They vary in size and growth form from ground covers to shrubs. It is an easy group to work with, as they are easy to make cuttings from, grow fast and are beautiful in autumn with masses of flowers in shades of purple, mauve, pink, blue and white. The different sizes, shapes, colours, textures and forms of their leaves make them very attractive ground covers, fillers or container plants even when not in flower.

Cineria saxifraga is an evergreen herbaceous perennial with small fan-shaped leaves and bright yellow aster flowers in spring. There are different growth forms of this plant, from flat ground covers to more tuft or clump forming variants up to 10 cm high.

Cliffortia odorata and *C. ferruginea* are both fast growing dense ground covers that belong to the rose family. Their horticultural potential lies in their attractively shaped evergreen leaves rather than in the rather inconspicuous flowers.

Diascia mollis is also a ground cover with pretty pink flowers from spring to autumn. It is especially effective when allowed to grow over the edges of containers or rockeries.

Knowltonia vesicatoria, abundant on the southern slopes of Table Mountain, has very attractive big leaves which makes the plant suitable as focus plant or as a filler. Yellow-green flowers appear on long stems in spring followed by berries that change from green to black as they ripen.

Laportia grossa is a stinging nettle about 30 cm high and grows along the subtropical coast. It has very interesting spotted and hairy leaves that look very attractive when planted in dense groups or between other herbaceous plants.

Pelargonium citronellum has a more shrubby growth form and can reach a height of up to 1 m. The leaves have a delightful citrus aroma. *P. tomentosum* is a ground cover with soft velvety leaves and a strong peppermint aroma.

Helichrysum petiolare "Limelight" is a form particularly attractive for its yellow-green colour of the leaves. The hairy leaves have a faint curry scent when crushed. The ordinary form has grey leaves and can also be used very effectively in half shade.

Phygelius capensis does well next to water and in half shade where it is always moist. In summer it has bright red tubular flowers.

Impatiens hochstetteri subsp. *hochstetteri* is another plant that prefers moist areas. This easy impatiens had soft-pink flowers almost right through the year.

Streptocarpus primulifolius subsp. *primulifolius* is a very striking plant with big leaves and light purple flowers in summer. It can be used to good effect in a sheltered shady area in the garden or as a potplant.

Rhoicissus rhomboidea and *R. tomentosa* are both evergreen with very decorative foliage and special tendrils which enable it to scramble if a support is provided. These species can also make very effective ground covers.

Senecio elegans is an annual that makes a very attractive display in half shade. It grows approximately 50 cm high, with aster-like flowers in shades of purple in spring.

For the cultivation of herbaceous plants, a rich well-drained soil with plenty of water is important. Plants that grow in the shade under trees get little light and have to compete for water and nutrients with the tree roots. Extra care is therefore needed. Prepare the soil very well with compost and bone meal or super phosphate before planting. Nutrients can be replenished every month thereafter during the growth season, alternately one month with 3:2:3 and one month 3:1:5.

5.4 *PROTASPARAGUS* AND *MYRSIPHYLLUM*

Several of our 68 indigenous *Protasparagus (=Asparagus)* and *Myrsiphyllum* species can be cultivated with great success in full to half-shade. Most of them flower in summer and have small sweetly-scented flowers, followed by red, yellow or orange berries with black seeds.

Protasparagus densiflorus has several forms, each differing significantly from the other and each with superb potential as a horticultural subject.

These plants are hardy drought resistant and most versatile. They can be used as ground covers, individual small shrubs, scramblers or in containers outdoors as well as indoors and make excellent subjects for hanging baskets. The foliage can be cut and used in flower arrangements.

Protasparagus usually occur in poor well-drained soil in dry areas, but perform better in soil containing organic material and with regular watering. Liquid fertilizer or 2:3:2 in spring and autumn encourages growth. *Protasparagus* are relatively free of pests and diseases, but can be attacked by stink bugs and pear slugs.

Most species are propagated by seed or division of the fleshy rhizomes.

5.5 BULBOUS PLANTS

A wide variety of shade-loving South African bulbs is very well suited to cultivation, both as garden and container subjects. The family Amaryllidaceae has several outstanding representatives suitable for horticultural use - *Clivia, Nerine, Haemanthus, Amaryllis, Crinum* and *Cyrtanthus.* The families Liliaceae with *Albuca, Bulbine* and Iridaceae with *Dietes, Moraea* and *Tritonia* are also very attractive flowering bulbous plants. Most of these are summer flowering, and some have the added advantage of being evergreen, providing year-round interest in the garden.

Shade-loving bulbs require well-drained soil with plenty of organic matter (well-rotted compost or leaf mould), liberal watering during summer, and as wind-free a situation as possible. During winter they undergo a dormant period when much less water is required. Regular liquid fertilizing during summer is very beneficial, and protection from frost is essential in susceptible areas.

5.6 SUCCULENTS

Many succulents thrive in a shady habitat where they are protected from the hot rays of the sun. There are species with attractive colourful flowers and others with ornamental leaves. The advantages of growing succulent plants are that they are easily propagated, can withstand periodic droughts and grow without much feeding. Succulents are also well suited for windy coastal gardens.

South Africa's great diversity of succulent plants is mainly confined to the Succulent Karoo Biome. Most of the shade-loving succulents, however, originate from the well wooded subtropical eastern parts of the country.

For horticultural purposes, succulents that grow well in the shade can be placed in four categories blanket ground covers, erect herbaceous succulent plants, solitary accent plants and those suitable for containers.

a) The mat-forming ground covers or trailing succulents are the most popular and a valuable asset is they combat soil erosion. They are useful on steep slopes, have very shallow roots and can grow where other plants find it difficult to cope with root competition. Of these the succulent *Plectranthus, Crassula* and *Senecio* species are popular. These are quick growing, rapidly forming a dense cover. *Plectranthus verticillatus* "Barberton", *Crassula spathulata* and *C. expansa* subsp. *fragilis* are excellent for this purpose.

b) The larger, non-trailing herbaceous succulents include species of *Gasteria*, and some of the *Aloe* and *Sansevieria* species with large, erect leaves. These are effective in group plantings.

c) As the term implies, the accent species are used to create focal points. *Gerrardanthus macrorhizus, Petopentia natalansis* and species of *Dioscorea* have huge, succulent caudices that resemble rocks. They can be displayed to striking effect in large containers. *Aloe bainesii* is a large, succulent tree which is a rewarding and valuable accent plant for a large garden.

d) There are many species that thrive in containers on shady stoeps or windowsills. *Ceropegia woodii* and *Senecio rowleyanus* are popular subjects that have trailing stems. *Senecio articulatus* has jointed mottled green stems. The smaller *Haworthia* and *Gasteria* species form dense groups and are easily grown. These dwarf, shade-loving species can also be grouped together to create a miniature, containerized garden.

Succulents do best in a well-drained soil to which ample compost has been added. A balanced fertilizer such as 2:3:2 can be applied annually. The ground covers can be planted *in situ*, the same way as grass is planted. Although they are drought resistant they should be watered regularly for the best results. The soil for containers should be well-drained and consist of two parts sand, one part compost and one part loam.

5.7 INDOOR POTPLANTS

There are a few points to consider for best results with successful indigenous indoor potplants.

When planning mixed container plantings, be sure to group plants with the same cultivation requirements together.

Try using small accent plants in pots as conversation pieces. Use small pots for small accent plants or interesting plants with curiosity value that can serve as conversation pieces. Some of the *Gasteria* species, *Zamioculcas*, bulbous plants in flower, *Bulbine natalensis* with its attractive leaves and *Ornithogalum* bulbs on a shallow tray, can all be used to good effect in this manner.

Some plants make excellent "instant" bonsai specimens, *Begonia dregeii* and *Plectranthus ernstii* with their swollen stems are suitable subjects.

Buxus macowanii, which bears to sets of completely different leaves (juvenile and mature) simultaneously on one plant, makes a very attractive and interesting container plant.

Let bulbous plants come into flower in the nursery or outdoors in a sheltered spot, and then move them indoors as soon as the flowers start to open. They should continue flowering indoors for weeks. *Agapanthus* species and home *Hypoxis* species work well for this purpose. The plants can be taken outdoors again to recover after flowering. *Indigofera frutescens*, a small tree with pink pea flowers, can also be used this way.

Some members of the Lamiaceae and Acanthaceae make good container plants, but should be treated as annuals. Replant them once a year or whenever necessary. These plants are also more subject to pests such as mites, bugs and eelworm when grown indoors. Great care should be taken to ensure that the growing medium and cultivation methods is looked after meticulously.

Encephalartos villosus and *Stangeria eriopus* do well in low light environments and make good container plants. The mat-forming roots on the surface look interesting and form a natural mulch.

Drimiopsis maculata is a plant that fares well in full shade. It likes to be pot-bound and should not be unnecessarily disturbed.

Most of our *Ficus* species make very good container plants. This is not surprising, as many exotic *Ficus* species have been available in the trade for years. We seem to have overlooked our own representatives in the genus. An added advantage is that members of this family have latex which make them more resistant to pests and diseases and therefore healthier potplants. The smaller leafed species look exceptionally good in containers, as they have a fuller, more lush appearance.

The Araliaceae is also a family which has yielded many species that thrive in containers. Australian members of this species, notably *Schefflera* species are very popular potplants worldwide. It is high time that the southern African species also attain international status as container plants.

The Gesneriaceae family is well-known as the family which contains African violets. *Streptocarpus* is another genus in the family with the enormous potential as small potplants. Some hybridization has already been done, though not enough and certainly not in South Africa.

Plectranthus is a genus on which some work has been done, but its potential is still totally underutilized. Some of the indigenous species are even better known in Europe than in South Africa.

Some plants that make good container plants can be "user unfriendly" and care must be taken of the areas in which they are placed All parts of *Acokanthera* *oppositifolia* are poisonous, while members of the Urticaceae (stinging nettles) can cause an unpleasant burning sensation when touched. Thorny plants and leaves with sharp tips like *Encephalartos* species can pierce and tear clothing and skin. Use these plants where people (especially children) will not come into contact with them and ensure that users are well-informed about these properties of the plants.

In theory, all young climbers should make good indoor potplants, e.g. *Bowiea gariepensis, B. volubilis, Dioscorea*. They are specially adapted to grow in full shade for the first part of their life. Don't expect them to flower however, as they only bear flowers when they reach the sunlight is reached in the treetops. *Rhoicussus* species make good container plants and are already used in Europe for this purpose.

Young forest trees are also good container subjects as they are, like climbers, adapted to grow in full shade for the first part of their life. It is unlikely that they will outgrow their containers, as they grow very slowly. Be sure to acquire a plant of desired size, however, as they are unlikely to reach any great height in a short time. Often these plants are more expensive, but remember that this reflects the greater investment of time required to grow them to saleable size. Soil micorrhizae are very important to forest trees. Inoculate potting soil with these organisms, even if this means you have to mix in a handful of forest soil from where the trees occur.

Succulents can make low maintenance potplants. They can survive long periods without water, which means you can go on holiday without having to worry about their watering needs. They also don't get many pests and diseases and are easily propagated. Apart from their attractive foliage, they also may have the added benefit of striking flowers.

Select a good variant or ecotype of plant already as it exists in nature to use as a container plant. A lot of natural selection has already been done and this represents a saving in time and labour and it is also more likely to be a success.

Growth medium for indigenous indoor potplants should consist of:

3 parts potting soil;

1 part compost;

1 part fine sand;

enrich with a slow release fertilizer.

Feed with liquid fertilizer consisting of macro-nutrients as well a micro-elements as soil drench.

More sand in mixture is recommended for succulents (see above).

The most important aspect of pest control is the elimination of ants. Avoid very toxic chemicals indoors such as organophosphates. Dishwashing liquid is effective against pests like aphids and some forms of scale. Oleum, a light mineral oil, is also low in toxicity and can be used with safety.

CHAPTER 6

DISCUSSION

Apart from providing many of the necessities in our lives, plants are major contributors to our pleasure, comfort and well-being. Plants can have a strong positive influence on human behaviour. More sociological and psychological studies are needed to verify such relationships and determine how plants can be used more effectively in this manner. Improvement of employee productivity, shorter convalescence periods for sick people resulting in lower medical expenses, and the rehabilitation of delinquent and disturbed people, are all examples of possible areas of plant influence on people about which very little is known.

The economic and commercial value of ornamental plants can be determined in a more exact manner. There are, however, no exact figures available in the industry. Established gardens increase the value of commercial and private properties, although it is difficult to determine to what extent the landscaping influences the price.

A particularly difficult area in which to establish ornamental plants, are shaded or low light environments. There is a large demand for additional new species of shade-loving plants. One of the objectives of this dissertation has been to identify and discuss the adaptations found in sciophytes. This has been done and where possible the relevance of the adaptations to the horticultural industry has been discussed.

In Chapter 3 a review of shade plants is given. It is interesting to note that the majority of southern African shade plants (more than 80%) are facultative sciophytes. A lot of experimentation can be done to select horticulturally superior subjects, even with plants one would not normally expect to be shade adapted. The important factor here would be the acclimatization aspect. No experimental work has been done, for example, on which side of a plant to take a cutting from. It is not known whether plants propagated from cuttings from the shaded side will prove to be more successful than cuttings taken from the sunny side. This relatively simple kind of experiment could prove to be quite valuable for successful results in the industry.

Where the specific shade adaptations are discussed in Chapter 4, one should always keep in mind the variation in the natural light environment. This involves not only the quality and quantity of light, but also other factors like temperature, humidity and nutrients. Nature must be imitated as closely as possible in all these variables to achieve a successful and satisfactory performance from shade plants.

It is interesting to note how undergrowth in deciduous forests in the Northern hemisphere has adapted to take full advantage of the radiation peak provided by the seasonal window. Nothing is known about the plants in southern Africa occupying this niche and whether the same adaptations occur or not. This kind of shade area is particularly difficult to plant, as light intensities vary from full sun to full shade in one growth season. Filling this niche in a landscaped terrain with plants occuring naturally in similar niches, holds the potential for better results. A field survey of such southern African plants should be carried out.

Mineral nutrition in shaded habitats is another notoriously difficult problem to solve. The importance of beneficial micorrhizae cannot be overemphasized. Inoculants are only starting to become available to the industry. The results of research in this area should be made available and applied.

Much research on the physiology of plants including shade plants has been carried out over the past three decades. Growth regulation performances of various artificial light sources for horticultural purposes have been described in detail and are available for end users.

A very interesting physiological adaptation of shade plants is the utilization of sun flecks. An imitation of this phenomena has not been attempted for horticultural purposes to date. More research on the potential advantages of this application would be informative.

Photoperiodism has been comprehensively reviewed by several authors. However, the possible effects of natural variation of light quality, that is of daylight, vegetational shade light and twilight have largely been unexplored in photoperiodism.

The different anatomical and biochemical characteristics of shade leaves are adaptations that have been comprehensively described by several authors. Many of these adaptations make the plants particularly attractive and ornamental to the human eye. Lens-shaped epidermal cells give leaves a shiny appearance, the red undersurface of leaves, camouflage patterns and the often dark green colour of shade leaves are all features that contribute to their ornamental appeal.

The striking diversity of leaf size and form which characterizes the flowering plants is a reflection of the interaction between phylogenetic constraints and adaptations for a specific environment. Differences between species in effective leaf size, shape, orientation, thickness, pubescence, anatomy and longevity have been shown to be related to habitat and to be significant for photosynthetic gas exchange.

Cordate, sagittate, hastate, asymmetric leaf bases and anisophylly are common leaf shapes in shady habitats. Camouflage in the form of mottled foliage is also far more common in herbs of shaded understoreys than in any other growth form.

It appears that aquatic plants show similar adaptations to shade plants because of the low light environment. This has been observed in leaf shape and red undersides of leaves. It would be an interesting study to compare adaptations in these two environments.

The architecture of the plant support structures and patterns of leaf placement are more complex than a first glance suggests. The primary functions of support and competition impose four principal constraints on stem adaptations for energy capture.

These are mechanical stability, mechanical safety, photosynthetic efficiency as well as whole-plant growth and competitive ability. The different energetic requirements of woody versus herbaceous plants may help explain the shift from shrub to herb dominance in forest understoreys.

Plagiotropic shoots (horizontal twigs with leaves arranged distichously in a planar array), are more common in shade-adapted plants. Orthotropic shoots (erect spiral leaved arrays) are generally common in well-lit habitats. Under shaded conditions, selection favours the phyllotaxis that minimizes self-shading.

As far as reproduction of shade plants is concerned, it should always be kept in mind that low light intensity favours vegetative development at the expense of flowering and fruiting. The total biomass productivity of a habitat will determine how many different types of reproductive strategy equilibria can co-exist. Unfortunately, very little data to support such energetically based models is available. Knowledge of the allocation of energy budgets in different plants is almost nil. In addition, very few studies that compare different habitat types with respect to their pollination syndromes, as well as dispersal methods, have been carried out.

Synchronous flowering is an interesting phenomenon in some species. Several southern African shade species, mainly in the succulent group, flower synchronously in response to dry-season rains. The watering regime of plants in cultivation, should certainly have an influence on the timing, repetition, or even restraint of flowering of certain species. Interesting work has been done on how to time the flowering of *Amaryllis* bulbs by withholding water. Not much information on this behaviour is available however, although it could prove valuable to the horticultural industry. This is also true for temperature differences. Just as some plants must undergo a period of drought first before they flower, others must undergo a period of low temperatures before flowering. This can be seen in *Clivia* species kept as indoor potplants. Temperatures indoors stay constant throughout the year, and these plants will not flower during the next flowering season.

Dispersal of seed and fruit may occur over short or long distances. The dispersal distance dramatically affects the kind of variation that can be observed in populations of species. If the dispersal is over short distances, all the plants in an area will be similar to one another, but because they are not exchanging genetic material with other adjacent populations, they are likely to differ from these adjacent populations. This is often seen in quite a few of the herbaceous perennial and succulent groups. This phenomenon has significant horticultural implications and is discussed under the section conclusions and recommendations in Chapter 7.

Plants that display long range dispersal, on the other hand, are often morphologically very constant over the whole of their distribution range. There is a regular exhange of genetic material between populations. This method is more common in the woody plants. The distance over which seeds are dispersed will also determine whether certain species are able to disperse into new habitats or between islands of suitable habitats. Plants showing long range dispersal will be more likely to be widely distributed, whereas those with short distance dispersal will show local endemism.

The question of how to apply all this information in the everyday practice of horticulture, in this case, shade gardening, has been discussed throughout the dissertation and more specifically in Chapter 5. Here more detail is given on the southern African trees and shrubs, herbaceous plants, bulbous plants, succulents and indoor potplants.

Currently there are approximately 1105 plants in the database. Out of the estimated 24 000 species in the southern African flora, this is only 4,5%. This list only serves as a start, however, and many more plants could be added, possibly even doubling the number of species. This would bring the total percentage, of shade-tolerant plants to approximately 8%, which is still a low percentage, confirming that southern Africa is truly a land of sunshine ! Much more information on each plant should also become available in time and should be included in the database to keep it up to date and complete.

It is interesting to see the percentages of different growth habits represented in the shade tolerant group. Herbaceous perennials and succulents each make up 23% of the group. Woody plants (comprising woody trees, small trees or shrubs and shrubs) make up a large group accounting for 30% of listed species. The fourth largest group of 14% is that of the bulbous plants. The remaining 10% of the shade tolerant plants are made up of several small groups including climbers, orchids, cycads and perennial grasses.

More than 70% of southern African shade plants can be classified as facultative sciophytes and 23% as obligate sciophytes. This latter group represents the true shade plants and need semi-shade to full shade conditions to survive.

Although the database needs much more information and is far from complete, it serves as a useful and workable start. Nothing is available in this field, especially as far as indigenous plants are concerned. This difficult but essential area should rather be seen as a challenge than a problem.

CHAPTER 7

CONCLUSIONS AND RECOMMENDATIONS

PERSPECTIVES ON SHADE PLANTS

- The explanation of the differences between successful heliophytes and successful sciophytes is complex. In terrestrial habitats, other factors, especially humidity, temperature and minerals, vary with light intensity, and it is difficult to evaluate light effects alone.

- Plants cope with environmental stress by avoiding it or tolerating it. Sciophytes can be classified as stress-tolerators. This group occupies habitats where resources, especiallylight, are limited and productivity is low.

- Light conditions are an important determinant of phenotypic plasticity. The leaves and other organs of shade-growing species are long-lived and exhibit less plasticity in size and shape than sun-growing species. Shade plants are more likely to show post-developmental cytological and biochemical changes. The degree of plasticity shown by any plant population is regarded as being under genetic control and is, in itself an important adaptive characteristic. Reversable physiological, anatomical and morphological changes are termed acclimatization and are an important aspect of plasticity.

- Sciophytes practise stress-tolerance by optimum utilization of available energy and by the conservation of energy. Each special adaptation of these plants can be related to one of these tactics.

- To get a whole-plant perspective of adaptation to sun and shade, it should be considered that energy capture by the whole plant does not only depend on the photosynthetic response of individual leaves, but also on their integration into an effective canopy, as well as the costs of producing and maintaining their photosynthetic capacity. Adaptation to the irradiance level at leaf-level alone does not explain shade-plant behaviour satisfactorily. Characteristics must also be examined at canopy-level and plant-level.

- Acclimatization to a changed light environment involves changes in enzyme and pigment amounts, as well as leaf anatomy and resource allocation as new leaves are produced in the new environment. The time scale over which these processes can occur determines the type of light changes for which acclimatization is important. The redeployment of internal resources to enhance resistance to stress in a new environment appears to require at the minimum a few days to, in some cases, several weeks.

Ecology and climate

- Certain observable characteristics in any plant-supporting area suggest a pattern. Analysis of this pattern leads to important conclusions in understanding the ecological relationships and requirements of plants in both natural terrain and managed landscapes.

- In the planning and maintenance of landscapes there is a tendency to ignore the ecological relationships of plants and their natural environments. This is unfortunate, because the ultimate performance of a plant or group of plants is dependent on the extent to which the ecological requirements are fulfilled. In addition, the aesthetic qualities of landscape plantings are enhanced when plants of the proper association are grouped together, just as they are found in natural communities.

- Microclimatic requirements in plant communities can often be imitated easily, enabling plants to grow outside their normal geographic range. This allows plants with ornamental value to be grown in cultivation and to be available for this purpose far from their natural distribution.

- The mutual interactions of plants with each other and with their environment determines the composition of the plant community. For example, in the dry shade of trees with many surface roots, different plants would be used than in the often moist shade of south facing walls. Maintenance is facilitated by selecting suitable plants for each situation. Water requirements should be homogenous in specific landscaped areas. Suitable plants will grow better and should have a higher survival rate, resulting in fewer replacements.

- Always take the deciduousness of trees into account when underplanting. High light intensities, low humidity and relative high day temperatures under deciduous trees during winter and spring days before the first leaves appear, are the norm. Never plant true shade plants under deciduous trees, as they will be severely damaged in winter. The protection that the tree canopy gives against very low temperatures is also lost in winter under deciduous trees. Frost sensitive plants can still be grown in colder areas under evergreen trees, but will not survive under deciduous trees. However, deciduous trees have the benefit of providing a vernal window to the undergrowth and winter and spring flowering bulbs do very well in this situation. During the leafy period the bulbs can be overplanted with fast growing ground covers that thrive in shade.

- Select specific ecotypes to match horticultural needs. Ecotypes that are already adapted are more likely to succeed in cultivation.

- When hunting for "new" ornamental shade plants, one should try the shaded southern slopes of mountains and hills. Even better, a kloof on the southern slope may produce ecotypes of species that, although they may look identical to their counterparts growing in the sun, might be physiologically different. These shade ecotypes would probably be more suitable for shade gardening.

- Mineral deficiency is a common condition of certain forest soils. The presence of vesicular arbuscular mycorrhizae (VAM) in the growing medium of shade plants is very important, especially for forest trees. Plants with coarse roots and few root hairs are dependant on VAM, especially in low-fertility soils and soils with a low phosphorous content. The beneficial effects of VAM for the host are that they increase growth, nutrient absorbtion, tolerance against pathogens, and also make the host more resistant to drought.

- Shade plants originating from a forest habitat tend to have a shallow root system, and are therefore less resistant to severe drought. These plants should be watered more frequently, though with smaller volumes of water at a time.

Physiology and photosynthesis

- The metabolism of true shade plants is slow, which means they are slow growing. It is therefore not possible to create instant shade gardens, either indoors or outdoors. It is a wise idea to use mature plants or plants of desired size for end results, instead of trying to plant small young plants and expect them to grow quickly to this size. Mature plants will naturally cost more as their growers have spent more time, space and effort in cultivating them.

- Plants are widely adapted to growing at highly varied light levels. We seldom see them growing under optimum conditions, however. The technology which has been developed to combine the simultaneous enhancement of light, temperature, water and nutrition is seldom transferred into our traditional growing facilities. For practical plant lighting, Cathey and Campbell (1980) suggested various light levels for plants on display, photoperiod, survival, maintenance, and propagation.

- Lighting to substitute or supplement the available sunlight can be used to accomplish the following:

  a) reduce the time required to produce the desired stage of growth;

  b) utilize lamps as an energy source rather than just for their light - use several criteria for measurement and installation of lamps;

  c) establish the light intensity and duration requirement for the plant processes to proceed. Overlighting wastes energy in the form of visible light and heat;

  d) utilize light properly throughout the growth process so that the plants will not require acclimatization for their successful use by the consumer;

  e) learn how to compare one light source to another to create equally effective lighting systems for growning plants. Any light visible to the human eye contains wavelengths suitable for plants;

  f) develop alternative structures that require lower energy inputs for growing plants.

- Sunflecks are an important source of energy to shade plants in nature. For experimental purposes Pearcy *et al* (1985) simulated sunflecks with a lamp and shutter system. With these experiments they confirmed that induction occurred in response to a series of light flecks for a number of species of diverse types (e.g. shade-adapted tree seedlings as well as soybeans), indicating that it is probably a response common to all plants. This method of lighting has never been used for horticultural purposes, however, it could be useful, especially for indoor container plants.

- C_4 photosynthesis has been shown experimentally to be more efficient than the C_3 version at higher temperatures. Northern hemisphere C_3 grasses become successful shade turf grasses in southern Africa. The lower temperatures in the shade probably allow these grasses to perform better in the shade. The same light-temperature principle can possibly be applied to some alpine plants, which could become shade plants when grown in low lying areas, where the temperatures in full sun is too high for them to survive.

Anatomy

- Many shade plants have lens-shaped epidermal cells to help focus light into the leaf. Leaves exhibiting this characterisic have a glossy or shiny appearance, which makes them very attractive from an ornamental point of view. So sought after is this quality for potplants, that there are even commercial plantcare products available on the market to shine the leaves of indoor plants to give them this "healthy" appearance.

- A common feature of plants that live in deep shade is the dark green colour of the foliage. The higher chlorophyll content allows for a greater amount of light to be absorbed by the leaf. This deep green colour is very attractive in ornamental plants and also gives a "healthy" appearance to potplants especially.

- Solarization is the phenomenon where shade plants are damaged by too much bright light. The carotenoid pigments (yellow) in the leave offer protection against solarization, but where the limits are surpassed, the chorophyll gets destroyed by an excessively high oxygen concentration that has a bleaching effect on chlorophyll. True shade plants are often used incorrectly in full sun positions in landscaping. Instead of their normal attractive dark green colour, these plants become yellow and too light in colour. This is a result of chlorophyll bleaching. Damage can also be severe and irreversible in the form of necrotic patches on leaves.

- Forest tree seedlings are obligate sciophytes in their young stage. Their protection afforded by solarization is insufficient. Shading the seedlings helps boost their survival rate. Young forest trees of many species also make very successful indoor container plants, because they are so well adapted to growing at low light intensities.

- Sciophytes often have an abaxial anthocyanin layer (red undersurface of leaves), which serves as an enhancer of light capture in deep shade. This has two applications. Firstly, one can predict with reasonable certainty that plants with this colouration will be successful in full shade conditions. Secondly, these red or purple undersurface of the leaves are highly decorative and provide extra colour in shady environments where there is normally a shortage of colour, other than green.

- Many plants with a metallic-blue iridescent colour on their leaves have been observed on tropical rainforest floors in South America, South-East Asia and Africa. This could be really exciting in horticultural terms. In Malaysia the most spectacular and most common iridescent blue plant is *Selaginella willdenovii*, a moss that is frequently cultivated in greenhouses. To date, however, no southern African plants are known to exhibit this characteristic.

Morphology

- The dominant factor controlling leaf size of plants in different habitats is not considered to be the capture of light, but the optimizing of water-use efficiency. It is therefore wrong to assume that all shade plants should have large leaves. There is a great deal of variability in leaf size in the herb vegetation of the forest floor. This makes the texture of shade gardens so much more interesting.

- The reflective properties of the leaf are extremely important in relation to the absorption of light. Pubescent (hairy) or waxy coatings can increase reflectance so that as little as only 30% of incident light is absorbed, compared with glabrous leaves of equal chlorophyll content which absorb 84%. This means most shade plants have an attractive smooth, often shiny, surface.

- Evergreen leaves are common in habitats with nutrient-poor soils, and/or where there is little seasonal variation in the favourability of conditions for photosynthesis. Both these factors apply to shade. There are very few if any true shade plants that are deciduous. This is of course an energy conservation method. The seasonal aspect for landscaping purposes cannot be achieved in shade.

- Leaves with cordate (heart-shaped) bases and asymmetric bases as well as anisophylly (unequal leaves at each node in species with opposite leaves) are common in shady habitats. This enlarges the energy capture surface for optimum use of available light. It also makes these plants interesting and attractive from an ornamental point of view.

- It is suggested that shade-adapted species should allocate more energy to defence than sun adapted species, because the effective cost of replacing a given amount of leaf tissue is larger in slow-growing shade plants than in fast growing sun plants. Visual defences such as camouflage are indeed far more common in herbs of shaded forest understoreys than in any other growth form, and are assentially absent in trees, shrubs, herbs or vines of sunny sites. These colourations are aesthetically exceptionally attractive to the human eye and plants with any form of these colouration patterns have proven extremely popular as garden subjects. This also provides extra colour in the shade garden.

Architecture

- The inevitable conflict between stem safety and plant growth in an unproductive environment leads to an ecologically extremely important stem trade-off, that of balancing growth and photosynthetic requirements. The lower light requirements of shorter plants like shrubs and especially herbs, provide a simple mechanism that permits them to persist under a canopy of taller species. The differing energetic requirements of woody versus herbaceous plants may also help explain the shift from shrub to herb dominance in forest understoreys. This means that there are not many shrubs that grow in shade, and virtually none that grow in deeply shaded areas. The solution for these difficult areas lies rather in the use of herbaceous or succulent plants, of which there are quite a few to choose from in the southern African flora.

Reproduction

- Insufficient light represses flowering and fruiting and sometimes holds vascular plants indefintely in the vegetative condition. Low light intensity favours vegetative development at the expense of flowers and fruit as these stuctures are very expensive to produce in terms of the energy budget of a plant and as stress-tolerators, shade plants show great conservation in energy as far as reproductive organs are concerned. This means that crops grown for their vegetative parts, like tobacco, are favoured by climates with a high percentage of cloudiness, whereas fruits, grains, seeds and flowers are favoured by bright sunlight.

- Very showy and attractive flowers and fruit are seldom found in true shade plants. The ornamental value of these plants lie rather in their often extraordinarily beautiful foliage. This makes it difficult, but not impossible to create a colourful shade garden. Colour can be introduced in the form of plants with coloured leaves and bulbous plants may also provide exciting seasonal flowers. The herbaceous families Lamiaceae, Gesneriaceae and Acanthaceae have valuable shade-flowering representatives. The Rubiaceae and Apocynaceae families are valuable for flowering and fruiting shrubs and small trees.

- A great part of the energy budget of shade plants is spent on perennation and vegetative parts. An annual growth habit has not been observed in true shade plants. This fact makes it almost impossible for a seasonal colour display of annuals in the shade garden. However, the fact that, once established, most shade plants are long-lived, means that the well planned shade garden will provide labour saving and almost maintenance free pleasure for many seasons to come.

- The flowers and fruit of shade plants are often small and inconspicuous. It should be considered a "bonus" to have a shade plant with attractive flowers.

- To attract pollinators, many plants have a specific odour. *Dracaena* species, which are pollinated by moths, have a pleasant sweet smell at night. These species make excellent indoor potplants, as well as good outdoor accent plants in subtropical climates or in protected areas. Their fragrance adds to their ornamental value. However, the opposite may also be true. In many members of the *Stapeliae*, foul smelling substances are released by the blossom to attract flies for pollination. It is not recommended that these plants should be used as indoor potplants.

- Synchronous flowering, especially in response to dry-season rains occur in many southern African plants. This phenomenon could be manipulated by giving or withholding water certain plants in order to time the flowering. Unfortunately, not much is known about this pattern of flowering and how to apply it.

- Semelparous (single reproducing) perennials seem to be rare in the southern African flora. These perennials often have to reach a critical size before they can flower. This ability to queue for reproduction by size rather than age is likely to be a superior strategy in deteriorating environments such as would arise when shade is re-established over a forest clearing. In horticultural practice, such species should be treated as annuals. A good example is *Digitalis purpurea,* (foxglove), which is a very popular garden plant from the northern hemisphere.

- Differences between plant populations are often due to the isolation imposed by short distance dispersal. One specific population may have a higher ornamental potential than other populations of the same species. This makes it easy to select suitable horticultural subjects. It is quite likely that more than one of these ecotypes or populations has ornamental value and because they can still cross-breed, it is essential to propagate these forms vegetatively. A clone of a specific plant will then be produced where all the offspring are identical to the selected mother plant.

- Hybridisation can occur easily in some succulents and herbaceous perennials. Hand-pollination in the greenhouse can and already has lead to the breeding of superior ornamental plants. Apart from the many original wild forms already used as ornamental plants, there is potential for many more cultivated hybrids.

Shade gardening

- Shade is an imprecise term, and its effect is closely linked to soil conditions, air circulation, temperature, exposure and the nature of the site. There are no hard and fast rules about what plants will grow where and recommendations for one situation are bound to overlap those for another.

- Three types of shade are most commonly found in gardens. Permanent shade is created by buildings, or walls, or dense overhead tree canopies. Temporary shade is created for part of the day as the sun travels from east to west. Dappled or partial shade refers to conditions where sunlight is filtered through a thin overhead canopy and the plants are never in full sun. There are variations within these groups.

- Dry soil is often a problem in permanent shade as overhead trees or neighbouring buildings may prevent the natural rainfall from reaching the ground. In such soils, the moisture-holding capacity and its nutrient content can be improved by incorporating as much bulky organic material as possible into the topsoil before planting. A thick layer of organic mulch spread over the soil after planting and topped up annually will help to maintain soil moisture and fertility.

- Forward planning to prevent troublesome shade when starting or stocking a garden will be amply rewarded. One of the commonest gardening mistakes is to aim for instant effect and to underestimate the speed of growth of a tree or shrub, only to find that shade and invading roots encroach on a once sunny part of the garden. It is always as well to bear this in mind when selecting and positioning such plants.

- There is an exciting selection of southern African shade plants of all growth habits to choose from. Part II facilitates the selection of trees, shrubs, herbaceous perennials, bulbs and succulents suited for specific situations or purposes.

REFERENCES

Acocks, J.P.H. 1988. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa No. 57, 3rd edn. Botanical Research Institute of South Africa.

Arnold, T.H. & De Wet, B.C. 1993. Plants of southern Africa : names and distribution. Memoirs of the Botanical Survey of South Africa No. 62. National Botanical Institute, Pretoria, South Africa.

Anon. 1988. Accelerate *Amaryllis* blooming by *not* watering. Brooklyn Botanic Garden. *Plants & Gardens News.* 53(3). Anon.

Augsburger, C.K. 1982. A cue for synchronous flowering. In: The ecology of a tropical forest, seasonal rhythms and long-term changes, ed. Leigh, E.G. Jr. *et al.* Smithsonian Institution Press. Washington.

Austin, R.L. 1986. Wild gardening strategies and procedures using native plantings. Simon & Schuster, Inc. New York.

Baldocchi, D. & Collineau, S. 1994. The physical nature of solar radiation in heterogeneous canopies: Spatial and temporal attributes. In: Exploitation of environmental heterogeneity by plants. ed. Caldwell, M.M. & Pearcy, R.W. Academic Press. New York, London.

Balkwill, K. 1996. The "Private Life" of plants. *Parks & Grounds* 91: 45--49.

Berry, J.A. 1975. Adaptation of photosynthetic processes to stress. *Science* 188: 644--645.

Björkman, O. & 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. 1968. Further studies on differentiation of photosynthetic properties in sun and shade ecotypes of *Solidago virgaurea*. *Physiologia Plantarum* 21: 84--99.

Björkman, O. 1981. Responses to different quantum flux densities. In: Encyclopedia of plant physiology. New Series Vol. 12A: 57--107. Springer-Verlag, Berlin.

Björkman, O. & Poules, S.B. 1981. Leaf movement in the shade species *Oxalis oregana.* Response to light level and light quality. Annual report of the Director, Department of Plant Biology, Stanford, California. Carnegie Institution of Washington Year Book 80: 59--62.

Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants. *Ann. Rev. Plant Physiol.* 28 : 355--377.

Boardman, N.K.*et al.* 1975. Photosynthetic adaptation of higher plants to light intensity: Relationship between chloroplast structure, composition of the photosystems and photosynthetic rates. In: Proceedings of 3rd International Congress on Photosynthesis. ed. Avron, A. Elsevier. Amsterdam.

Bosch, O.J.H. & Van Wyk, J.J. 1970. The influende of bushveld trees on the productivity of *Panicum maximum* : A preliminary report. *Hand. Weidingsveren. S.Afr.* 5:69--74.

Bula, R.J. *et al.* 1991. Light emitting diodes as a radiation source for plants. *Hort. Science* 26(2): 203--205

Caldwell, M.M. & Pearcy, R.W. 1994. Exploitation of environmental heterogeneity by plants. Ecophysiological processes above and below ground. Academic Press. New York, London.

Campbell, B.M. & Moll, E.J. 1977. The forest communities of Table Mountain, South Africa. *Vegetatio.* 34(2): 105--115.

Carpenter, P.L. & Walker, T.D. 1990. Plants in the landscape 2nd. edn. W.H. Freeman and Company, New York.

Cathey, H.M. & Campbell, L.E. 1980. Light and lighting systems for horticultural plants. In: Horticultural Reviews, Editorial Board Vol. 2. ed. Dennis, F.G. Jr The AVI Publishing Co. Inc. Connecticut.

Chazdon, R.L. & Pearcy, R.W. 1986. Photosynthetic responses to light variation in rainforest species. II Carbon gain and photosynthetic efficiency during lightflecks. *Oecologia* 69: 524--531.

Codd, L.E. 1985. Lamiaceae. Flora of Southern Africa Vol. 28, Part 4. Botanical Research Institute, South Africa.

Coley *et al.* 1985. Resource availability and plant anti-herbivore defense. *Science* 230: 895.

Corré, W.J. 1983. Growth and morphogenesis of sun and shade plants. 1. The influence of light intensity. *Acta Bot. Neerl.*32 (1/2): 49--62.

Crawford, R.M.M. 1989. Studies in plant survival. Ecological case histories of plant adaptation to adversity. Blackwell Scientific Publications. Oxford.

Daubenmire, R.F. 1974. Plants and environment 3rd.edn. John Wiley & Sons Inc. U.S.A.

Dengler, N.G. 1994. The influence of light on leaf development. In: Growth patterns in vascular plants. ed. Iqbal M. Dioscorides Press, Oregon.

Downs, R.J. & Borthwick, H.A. 1956. Effects of photoperiod on growth of trees. *The Botanical Gazette* 117: 310--326.

Ehleringer, J. & Björkman, O. 1978. A comparison of photosynthetic characteristics of *Encelia* species possessing glabrous and pubescent leaves. *Plant phys.* 62: 185--190.

Ellison, A.M. *et al.* 1993. Seed and seedling ecology of neotropical Melastomataceae *Ecology* 74 (6) 1733--1749.

Faegri, K. & van der Pijl, L. 1979. The principles of pollination ecology. 3rd revised edn. Pergamon Press, Ltd. Oxford.

Fitch, C.M. *et al.* 1987. Indoor gardening. In: *Plants and gardens 43(1):1--87.* ed. Pesch, B.B. *et al.* Brooklyn Botanic Garden.

Fitter, A.H. & Hay, R.K.M. 1981. Environmental physiology of plants. Academic Press, London.

Gibbs-Russel, G.E. *et al.* 1990. Grasses of southern Africa. Memoirs of the Botanical Survey of South Africa. No. 58. National Botanic Gardens. Botanical Research Institute, South Africa.

Givnish, T.J. 1986. Biomechanical constraints on self-thinning in plant populations. *J. theor. Biol* 119: 139--146.

Givnish, T.J. 1987. Comparative studies of leaf form: Assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytol.* 106(Suppl.): 131--160.

Givnish, T.J. 1988. Adaptation to sun and shade: A whole-plant perspective. *Aust. J. Plant Physiol* 15: 63--92.

Givnish, T.J. 1995. Plant stems: Biomechanical adaptation for energy capture and influence on species distributions. In: Plant stems: physiology and functional morphology, ed. Gartner, B.L. Academic Press, New York.

Grime, J.P. 1966. Shade avoidance and shade tolerance in flowering plants. In: Light as ecological Factor. ed. Bainbridge, R.; Evans & G.C. Rackham, O.: 187-207. Blackwell. Oxford.

Grime, J.P. 1994. The role of plasticity in exploiting environmental heterogeneity. In: Exploitation of environment heterogeneity by plants. ed. Caldwell, M.M. & Pearcy, R.W. Academic Press, New York, London.

Hale, M.G. & Orcutt, D.M. 1987. The physiology of plants under stress. John Wiley & Sons, New York.

Harris, J.G. & Harris, M.W. 1994. Plant identification terminology: An illustrated glossary. Spring Lake Publishing, Spring Lake, Utah.

Harris, R.W. 1992. Arboriculture. Integrated management of landscape trees, shrubs and vines. 2nd.edn. Regents, Prentice Hall, New Jersey, U.S.A.

Hilliard, O.M. & Burtt, B.L. 1971. *Streptocarpus.* An African plant study. Hayne & Gibson Ltd., Durban, R.S.A.

Hoober, J.K. 1984. Chloroplasts. Plenum Press, New York, London.

Joffe,P. 1993. Die tuinier se gids tot Suid-Afrikaanse plante. Tafelberg Uitgewers, Kaapstad.

Keever, G.J. & Cobb, G.S. 1986. Temperate zone woody plants for interior environments. J.Environmental Hort 4(1): 16--18.

Kersch, L.A. 1988. Something for nothing. Interior Landscape Industry 5(10): 51--55.

Körner, C. & Diemer, M. 1987. *In situ* photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Functional Ecology* 1:179--194.

Küpers, M. 1994. Canopy gaps: Competitive light interception and economic space filling -- a matter of whole-plant allocation. In: Exploitation of environmental heterogeneity by plants. ed. Caldwell, M.M. & Pearcy, R.W. Academic Press, New York, London.

Kuuluvainen, T. 1992. Three architectures adapted to efficient light utilization: Is there a basis for latitudinal gradients? *Oikos*. 65: 275--284.

Lee, D.W. & Lowry, J.B. 1975. Physical basis and ecological significance of iridescence in blue plants. *Nature*. 254: 50-51.

Lee, D.W. *et al.* 1979. Abaxial anthocyanin layer in leaves of tropical rain forest plants: enhancer of light capture in deep shade. *Biotropica. 11(1): 70--77.*

Lombaard, W. 1993. A survey of vesicular arbuscular mycorrhizae (VAM) with special reference to taxonomy, physiology and economical importance. M.Sc. Thesis. University of Pretoria.

Longman, K.A. & Jenik, J. 1987. Tropical forest and it's environment. 2nd edn. Longman Scientific & Technical, London, Singapore Publishers (PTE) Ltd. Singapore.

McClendon, J.H. & McMillen, G.G. 1982. The control of leaf morphology and the tolerance of shade by woody plants. *Bot. Gaz.* 143(1): 79--83.

Mooney, H.A. *et al.* 1987. plant physiological ecology today. Bio Science 37(1): 18--20.

Morales, D. *et al.* 1991. Morphological and gas exchange response of *Canarina canariensis* (L.) Vatke to sun and shade. *Photosynthetica* 25(4): 481--487.

Morgan, D.C. & Smith, H. 1981. Non-photosynthetic responses to light quality. In: Encyclopedia of plant physiology, ed. Lange, O.L. *et al.* Vol. 12A: 109--130. Springer-Verlag. Berlin.

Moser, M. & Haselwandter, K. 1983. Ecophysiology of mycorrhizal symbioses. In: Encyclopedia of plant physiology, 12c: 392--421. Springer Verlag, Berlin.

Moss, D.N. & Smith, L.H. 1972. A simple classroom demonstration of differences in photosynthetic capacity among species. *Jour. of Agron. Educ.* 1: 16--17.

Osmond, C.B. *et al.* 1980. Physiological processes in plant ecology. Springer-Verlag, Berlin.

Packham, J.R. & Cohn, E.V.J. 1990. Ecology of the woodland field layer. *Arboricultural Jnl.* 14: 357--371.

Parkhurst, D.F. & Loucks, O.L. 1972. Optimal leaf size in relation to environment. *J. Ecol.* 60: 505--537.

Pearcy, R.W. *et al.* 1985. Photosynthetic responses to dynamic light environments by Hawaiian trees. The time course of CO_2 uptake and carbon gain during sunflecks. *Plant Physiol.* 79: 896--902.

Pearcy, R.W. *et al.*1987. Carbon gain by plants in natural environments. Bio Science 37(1):21--29.

Pearcy, R.W. *et al.*1988. Photosynthetic utilization of light flecks by understory plants. *Aust. J. Plant Physiol. 15: 223--238.*

Pearcy, R.W. 1990. Sunflecks and photosynthesis in plant canopies. *Annu. Rev. Plant Mol. Biol.* 41: 421--453.

Pearcy, R.W. 1994. Photosynthetic utilization of sunflecks: A temporally patchy resource on a time scale of seconds to minutes. In: Exploitation of environmental heterogeneity by plants. ed. Caldwell, M.M. & Pearcy, R.W. Academic Press, New York, London.

Pearcy, R.W. & Sims, D.A. 1994. Photosynthetic acclimation to changing light environments: Scaling from the leaf to the whole plant. In: Exploitation of environmental heterogeneity by plants. ed. Caldwell, M.M. & Pearcy R.W. Academic Press, New York, London.

Pienaar, K. 1988. Plant inheems 'n Suid-Afrikaanse gids. C.Struik (Pty) Ltd., Kaapstad.

Pooley, E. 1994. The complete field guide to trees of Natal, Zululand and Transkei. Natal Flora Publications Trust, c/o Natal Herbarium, Durban.

Rackham, O. 1975. Temperatures of plant communities as measured by pyrometric and other methods. In: Light as an ecological factor II. ed. Evans, G.C. *et al.* Blackwell Scientific Publications, Oxford.

Richards, A.J. 1986. Plant breeding systems. George Allen & Unwin, Boston, Sydney.

Roth, I. 1984. Stratification of tropical forests as seen in leaf structure. *Tasks for vegetation science* (6). D.R.W. Junk Publishers, The Hague, Netherlands.

Rutherford, M.C. & Westfall, R.H. 1994. Biomes of Southern Africa: An objective categorization. *Memoirs of the Botanical Survey of South Africa*, No. 63. National Botanical Institute. Pretoria, South Africa.

Salisbury, F.B. & Ross, C.W. 1992. Plant physiology 4th edn. Wadsworth Inc. California, U.S.A.

Scholtz, C.H. & Holm, E. 1985. *Insects of Southern Africa.* University of Pretoria, South Africa.

Seitz, K. 1987. Light-dependent movement of chloroplasts in higher plant cells. *Acta Physiologiae Plantarum.* 9(3): 137--148.

Sheat, W.G. 1989. The A-Z of gardening in South Africa. Struik Publishers, Cape Town.

Sieverding, E. 1991. Vesicular - arbuscular mycorrhiza management in tropical agrosystems. *Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ).* Germany.

Silwertown, J. 1984. Death of the elusive biennial. *Nature* 310: 271.

Smith, G.M. & Rethman, N.F.G. 1989. Implikasies van subhabitat-diversiteit en die rol van bestuur op die voorkoms van 'n aantal grasspesies van die suuragtige-gemengde bosveld. *Tydskrif Weidingsveren S.Afr.* 6(1): 44--50.

Turner, D.L. *et al.* 1987. The effect of light quality and fertility on long term interior maintenance of selected foliage plants. *J. Env. Hort.* 5(2): 76--79.

Van den Berg, E. 1982. Klassifikasie van plantsoorte vir gebruik in landskapontwerp. M.Sc. thesis, Univ. Pretoria.

Van Jaarsveld, E. The Plectranthus handbook. National Botanic Gardens. CTP Book printers, Cape, South Africa.

Van Jaarsveld, E. 1996. Veld gardening in South Africa. *Veld & Flora.* 82(2): 52--56.

Van Oudtshoorn, F.P. 1991. Gids tot grasse van Suid-Afrika. Briza publikasies, Bk. Pretoria.

Van Wyk, A.E. & Malan, S.J. 1988. Veldgids tot die veldblomme van die Witwatersrand & Pretoria gebied. Struik, Kaapstad.

Vogelmann, T.C. & Martin, G. 1993. The functional significance of palisade tissue: penetration of directional versus diffuse light. *Plant, Cell & Env.* 16: 65--72.

ACKNOWLEDGEMENTS

- Johan Kluge,
  Lowveld National Botanical Gardens, Nelspruit

- Johan Hurter,
  Lowveld National Botanical Gardens, Nelspruit

- Neil Fishwick,
  Fishwicks Nursery, Shagen

- Jo Onderstall,
  Nelspruit

- Geoff Nichols,
  Durban

- Richard Symmonds
  Durban Parks Department, Durban

- Ernst van Jaarsveld
  Kirstenbosch National Botanical Gardens, Cape Town

- Anthony Hitchcock,
  Kirstenbosch National Botanical Gardens, Cape Town

- Karen Behr,
  Harold Porter National Botanical Gardens, Betty's Bay

- Rob and Rachel Saunders,
  Silverhill Seeds, Cape Town

- Noeline Kroon,
  Sasolburg

- Andrea Hepplewhite,
  Witkoppen Wild Flower Nursery, Johannesburg

- Kevin Balkwill,
  WITS University, Johannesburg

- Priscilla Schwartz,
  Pretoria National Botanical Gardens, Pretoria

- Peter Seldte
  Malan Seuns Wholesale Nurseries, Pretoria

- Louis and Erika Meintjies
  Bergsig Nursery, Cullinan

- Mike van der Linde
  Information Technology, University of Pretoria

CURRICULUM VITAE

Lorraine Middleton grew up on a farm situated at the foot of the Magaliesberg mountain range in the Rustenburg area and matriculated in 1974 at High School Bergsig, Rustenburg.

Then followed three years' study at the University of Pretoria completing a B.Sc. degree, majoring in Botany and Zoology.

As from 1978, she carried out research at the Onderstepoort Veterinary Research Institute, concentrating on the development of a polivalent vaccine against pneumonia in sheep. Part time studies for an Honours degree in Zoology were completed in 1980 at the Rand Afrikaans University.

She was subsequently involved in research and lecturing in Biology at the Medical University of Southern Africa.

In 1983, she left the scientific world for a career in the sales and marketing various commercial and industrial products and services.

During 1989, she entered the horticultural field building a small endeavour into quite a substantial business enterprise.

Returning for further studies in Botany to the University of Pretoria in 1993, an Honours degree in Botany was completed in 1994.

This dissertation forms part of the requirement for an M.Sc. degree in Botany at the University of Pretoria, completed in 1998.

SUMMARY

SHADE-TOLERANT FLOWERING PLANTS IN THE SOUTHERN AFRICAN FLORA :

MORPHOLOGY, ADAPTATIONS AND HORTICULTURAL APPLICATION

by

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Shade plants (sciophytes) may be regarded as stress-tolerant and are classified either as obligate or facultative. Most southern African sciophytes are facultative.

Two broad adaptive strategies are employed by shade plants. Optimal use is made of available energy and energy is conserved.

Climatic, topographical and ecological factors are inseperable from the presence of shade. Temperature, humidity and nutrient status may even play a more important role in plant adaptation than the presence of shade.

There are 1105 plants listed in the database. As might be expected of forest undergrowth in general, many southern African sciophytes are herbaceous perennials. This group forms 23% of the total number. Equivalent in representententatives, are the xerophytic plants (succulents) also 23%. These two groups together thus forms 43% of the shade plants. The second largest group are the woody plants which in total makes up 30% if the shrubs, trees and climbers are combined. The third largest group are the geophytic (bulbous) plants and forms 14% of the shade plants. All other groups make up less than 5% of the total.

Many of the attributes encountered in sciophytes occurring in tropical rainforests are also found in the drier, southern African climate. The red undersurface of leaves which has hitherto only been described in herbaceous species, is described here in succulent, southern African sciophytes.

The literature relating to anatomical and physiological adaptations of sciophytes is surveyed and discussed. Of particular interest is the phenomenon of sunflecks. Morphological adaptions include heart-shaped leaves, or variations thereof. The arrangements of stems and leaves to maximize the use of available light are architectural adaptations that are also discussed.

Sciophytes practice many conservative reproductive strategies. Small and inconspicuous flowers are the norm. Where flowering in the shade does indeed occur, reproductive structures are adapted to local pollinating agents. Hybridisation of both herbaceous and succulent sciophytes is a common, natural phenomenon.

Throughout the description of the adaptations, the applications thereof in horticultural terms have been highlighted where possible. The application is printed in bold letters directly following the adaptation described in the text. The practical side of shade gardening is discussed, highlighting and describing several southern African plants from different growth groups and situations.

A database has been compiled, listing the southern African shade plants. As much as possible information on each plant concerning the names, distribution, description, uses, growth requirements and other additional general information has been made available in this database. Pre-selected combinations are printed out, for instance plants for specific horticultural uses or certain climatic conditions. Any other selected fields can be retrieved by the user according to his needs and choice directly from the database. The database should also be updated and supplemented with new information on each plant, as well as adding new plants.

OPSOMMING

SKADUPLANTE IN SUIDER-AFRIKA

AANPASSINGS EN TUINBOUKUNDIGE TOEPASSINGS

deur

Lorraine Middleton

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Magister Scientiae

Skaduplante (skiofiete) kan beskou word as stres-verdraagsaam en twee strategieë word gevolg nl. optimum benutting van beskikbare energie en energie besparing. Obligate en fakultatiewe skiofiete word onderskei. Die meeste Suider-Afrikaanse spesies is fakultatiewe skiofiete.

Klimaats-, topografiese en ekologiese faktore is nou verweef met die skadu aspek en gepaardgaande vog, temperatuur en voedingstowwe speel soms 'n groter rol as die skaduwee op sigself.

Daar is 1105 plante gelys in die databasis. Baie Suider-Afrikaanse skiofiete is kruidagtige meerjariges, soos verwag kan word vir ondergroei. Hierdie groep maak 23% van die totaal uit. Gelyk in hoeveelhede is die sukkulente (geofitiese plant). Hierdie twee groepe saam vorm dus 43% van die skaduplante. Die tweede grootste groep is die

houtagtige plante wat in totaal 30% vorm. Dit sluit dan die struike, bome en rankers in. Die derde grootste groep is die geofiete (bolplante), wat 14% van die groep verteenwoordig. Die oorblywende groepe maak minder as 5% van die totaal uit.

Baie van die kenmerke wat skaduplante in tropiese reënwoude vertoon, kom ook by plaaslike verteenwoordigers voor, alhoewel die klimaat baie droër is. Die rooi onderoppervlak van blare wat bv. nog slegs vir kruidagtige spesies beskryf is, kom hier ook by sukkulente voor.

Anatomiese en fisiologiese aanpassings is deur verskeie outeurs ondersoek en beskryf. Een van die mees unieke is die benutting van sonkolle. Morfologies is die blaarvorm dikwels hartvormig of variasies hiervan. Argitektonies is blaar- en stingelrangskikking van so 'n aard dat die beskikbare lig optimaal benut kan word.

By voortplanting is daar aansienlike energie besparingsmetodes by skaduplante. Min en klein onopvallende blomme en vrugte is die reël. Waar daar wel blomme voorkom, is bestuiwing aangepas vir die spesifieke omgewing se bestuiwers. Hibridisasie kom dikwels in die natuur voor by baie van die kruidagtige en sukkulente skaduplante.

Die tuinboukundige toepassings word deurgaans beskryf aan die hand van die beskrywing van die aanpassing. Die toepassings is in vet letters gedruk en volg direk op die aanpassing wat beskryf is in die teks. Toegepaste skadu-tuinbou is bespreek en verskeie Suider-Afrikaanse spesies word uitgelig en beskryf vir verskeie habitatte en groeivorms.

'n Databasis wat die Suider-Afrikaanse skaduplante lys, is opgestel. Soveel inligting as moontlik is versamel vir elke plant. Dit sluit in die name, verspreiding, beskrywing, gebruik, groei vereistes en ander addisionele algemene inligting. Selekteerde eienskappe van skaduplante is uitgedruk, byvoorbeeld plante vir spesifieke tuinboukundige gebruik of sekere klimaatstoestande. Enige ander velde kan deur die tuinboukundige gebruik of sekere klimaatstoestande. Enige ander velde kan deur die gebruiker geraadpleeg word volgens eie behoeftes. Die databasis behoort gereeld op datum gehou en met nuwe inligting aangevul te word.

PART II

THE DATABASE

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PART II

The database is done in Borland®, Paradox for Windows, version 5,0.

The complete database is available on computer disc[#] A printout of selected information on each plant is provided.

FIELDS AND KEYWORDS IN THE DATABASE

Names: Scientific name:

If marked with an asterix (*), it is recommended for horticultural purposes.

*	=	proven successful
**	=	recommended
***	=	highly commendable

Infraspecific names: where applicable

Common names: where available

Family: (-ceae)

Distribution: Natural distribution and habitat:

Description in text and/or region codes

T = Transvaal, N = Natal, O = O.F.S.,

C = Cape, I = Namibia, S = Swaziland,

L = Lesotho, B = Botswana.

[#] Available from the H.G.W.J. Schweickerdt Herbarium, Department of Botany, University of Pretoria.

Climatic zone and/or biome:

1 = coastal summer rainfall,
2 = coastal winter rainfall,
3 = winter rainfall karoo,
4 = summer rainfall karoo/highveld,
5 = bushveld summer rainfall.
Biomes; grassland, savanna, fynbos, succulent karoo, nama karoo, forest.

Description:

Habit : tree, shrub, climber, succulent, herbaceous perennial, annual, orchid, bulbous, restio, perennial grass, annual grass, carnivorous, cycad, palm.

Shape: flat, columnar, round, erect, irregular, scrambling, trailer, clumps, fan-shaped, creeper, compact, multi-stem, arching, stoloniferous rhizomatous, straggling, tufted, v-shaped, rosette cluster, prostrate, climbing, spreading.

Size: height x spread in metres.

Leaves: description in text.

Flowers: description in text.

Flower colour: white, cream, pink, yellow, brown, green, mauve, blue, purple, red, orange, maroon.

Flower season: Sp = spring, Su = summer, Au = Autumn, Wi = winter, All Y = all year.

Flower from: Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec.

Flower to: Jan, Feb, Mar, Apr, May, Jun, Jul, Aug, Sep, Oct, Nov, Dec.

Fruit: description in text, including colour and months.

Growth rate: S = slow, M = moderate, F = fast.

Longevity: in years.

Roots: noninvasive, fibrous, rhizomatous, fleshy, tuber, bulb, woody.

Uses: Edibility and Medicinal: description in text.

Horticultural uses: general (garden), coastal (garden), groundcover container, filler, rockery, indoor potplant, hedge, accent, hanging basket, erosion control, bonsai, windbreak, group plantings, cut flower.

Decorative value: flowers, foliage, aromatic leaves, flower scent, fruit, shape, cones.

Growth requirements: Soil: description in text.

Water : L = low, M = moderate, H = high

Humidity: L = low, M = moderate, H = high

Temperature: L = low, M = moderate, H = high
Frost Tolerance: L = low, M = moderate, H = high
Wind Tolerance: L = low, M = moderate, H = high

Exposure: semi-shade, full shade, full sun.

Propagation: C = cuttings, S = seed, Se = Seperation.

References: K H N = Kirstenbosch Horticultural Notes, K = Kirstenbosch Gardens,
F S A = Flora of southern Africa, volumes and numbers indicated,
P = Pooley, E 1994, The complete field guide to trees of Natal, Zululand Transkei,
vW = Van Wyk, A.E. & Malan S.J. 1988. Veldgids tot die veldblomme van die Witwatersrand en Pretoria gebied,
GN = Geoff Nichols, Durban,
SS = Silverhill Seeds Catalogue, Cape Town
H = Johan Hurter, Nelspruit,
AH = Andrea Hepplewhite, Johannesburg,
FvO = Van Oudshoorn, F.P. 1991. Gids tot die grasse van Suid Afrika,
GR = Gibbs-Russel, G.E. *et al* 1990. Grasses of southern Africa,
O = Jo Onderstall, Nelspruit,
F = Neil Fishwick, Nelspruit,
KB = Kevin Balkwill, Johannesburg.

General: Any additional information, discription in text.

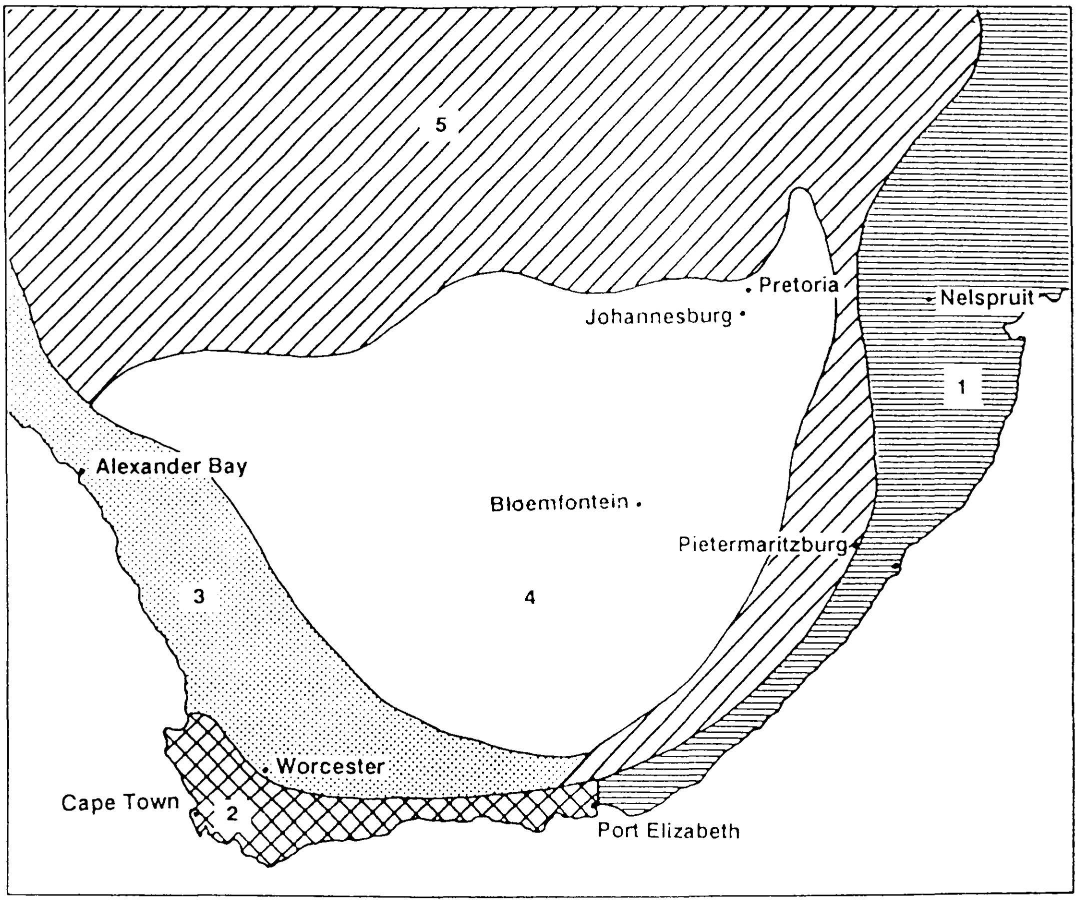


Figure 13. Climatic planting zones for southern Africa. These zones are a guide and exceptions do occur, e.g. isolated frost pockets in zone 1 and frost free areas in zones 4 and 5 do occur. (Kirstenbosch Horticultural Notes 1992.)

Mean monthly minimum temperature for coldest month

Zone 1. Coastal summer rainfall — Frost free — 5° to 10° C

Characterized by the dry, frost-free winters, this area is influenced by the warm Indian Ocean. It includes the coastal towns of Natal, Transkei and eastern Cape, as far south as Port Elizabeth. The southern part is subject to winter rainfall and has cooler conditions. The coastal city of Port Elizabeth and adjacent regions are also subject to strong winds which should be taken into account when selecting plant material.

Zone 2. Coastal winter rainfall — Frost free — 0° to 10° C

This region is virtually frost-free, and when frost occurs it is very light and of short duration. Many subtropical plants grow well here. Close to the coast wind is stronger, especially the prevailing summer southeasterly winds. The soils are generally poor and mainly derived from the Table Mountain group (Cape Supergroup), which also limits the choice of plants in this zone.

Zone 3. Winter rainfall Karoo — Light frost — -5° to 5° C

This region is subject to light frost but in the northern and coastal regions of Namaqualand frost is absent or very light. As the name implies, this region is subject to winter rainfall, however, summer rainfall is also experienced in the eastern parts. The soils are generally rich in minerals and many subtropical plants grow well here provided that they are watered sufficiently and planted in areas where frost is light.

Zone 4. Summer rainfall Karoo / Highveld — Frost — <-5° to 5° C

Situated on the "great escarpment", frost in winter is severe which drastically limits plant choice out of doors. Nevertheless there is a wide choice of frost-resistant plants which can be used very effectively. Rainfall is mainly in summer with dry winters but in the north-western area the rainfall is very low, which should also be taken into account when selecting plant material.

Zone 5. Bushveld summer rainfall — Frost — -5° to 0° C

This region is characterized by its dry winters, however frost may be a problem in certain areas, especially the higher lying regions. The eastern part receives a fair amount of rainfall but toward the north and west it becomes drier. The soils are variable, but generally rich and the choice of plants for this region is great.

WORD LIST FOR DATABASE

Anther	expanded, apical, pollen bearing portion of stamen.
Axil	the point of the upper angle formed between the axis of a stem and any part (usually a leaf) arising from it.
Bract	a reduced leaf or leaf-like structure at the base of a flower or inflorescence.
Calyx	the outer perianth whorl, collective term for all the sepals of a flower.
Canaliculate	with longitudinal channels or grooves.
Cladodes	a stem with the form and function of a leaf.
Compound	with two or more like parts in one organ.
Coppice	a thicket of bushes or small trees.
Corolla	the collective name of all the petals of a flower.
Corona	petal-like or crown-like structures between the petals and stamens in same flowers, a crown.
Cyme	a flat-topped or round-topped determinate inflorescence, paniculate, in which the terminal flower blooms first.
Dentate	toothed along the margin, tooth directed outward rather than forward.
Digitate	lobed, veined, or divided from common point, like the fingers of a hand (palmate).
Fascicle	a tight bundle or cluster.
Glabrous	smooth, hairless.
Glandular	bearing glands.
Inflorescence	the flowering part of a plant, a flower cluster, the arrangement of the flowers on the flowering axis.

Lanceolate	lance-shaped, much longer than wide.
Linear	resembling a line, long and narrow.
Mottled	with coloured spots or blotches.
Oblong	two to four time longer than broad with nearly parallel sides.
Obvate	inversely ovate, with the attachment at the narrower end.
Ovate	egg-shaped in outline and attached at the broad end.
Panicle	a branched, racemose inflorescence with flowers maturing from the bottom upwards.
Pendulous	hanging or drooping downward.
Penduncle	stalk of a solitary flower or of an inflorescence.
Peltate	shield-shaped.
Plicate	plated or folded, as a folding fan.
Pseudo-	(prefix) meaning false.
Pubescent	covered with short soft hairs.
Raceme	an unbranched, elongated inflorescence with pedicellate flowers maturing from the bottom upwards.
Serrated	saw-like, toothed along the margin, the sharp teeth pointing forward.
Sessile	attached directly, without a supporting stalk.
Stoloneferous	bearing stolons, an enlongated, horizontal stem creeping along the ground and rooting at the nodes or at the tip.
Tendril	a slender, twining organ used to grasp support for climbing.
Terete	round in cross section, cylindrical.
Tomentose	with a covering of short, matted or tangled, soft woolly hairs.

Trifoliate	with three leaves or three leaflets.
Tuberoles	a small tuberlike swelling or projection.
Thyrse	a compact cylindrical, or ovate panicle with an indeterminate main axis and cymose sub-axes.
Umbel	a flat-topped or convex inflorescence with the pedicels arising more or less from a common point, like the struts of an umbrella.

Table 3 The major families (abbreviated) of southern African shade plants

Family (-ceae)	Frequency	Percent
Asphodela	87	7.9
Crassula	65	5.9
Gerania	61	5.5
Erica	60	5.4
Acantha	59	5.3
Orchida	53	4.8
Astera	47	4.3
Amaryllida	42	3.8
Lamia	42	3.8
Irida	34	3.1
Rubia	32	2.9
Hyacintha	31	2.8
Gesneria	27	2.4
Mesembryanthema	27	2.4
Euphorbia	21	1.9
Asclepiada	19	1.7
Poa	19	1.7
Ruta	18	1.6
Celastra	16	1.4
Scrophularia	16	1.4
Zamia	16	1.4
Asparaga	15	1.4
Apocyna	12	1.1
Brunia	11	1.0
Other families	275	25.1

Table 4 The major genera of southern African shade plants

Genus	Frequency	Percent
Pelargonium	59	5.3
Erica	58	5.2
Haworthia	36	3.3
Crassula	35	3.2
Plectranthus	30	2.7
Streptocarpus	26	2.4
Aloe	24	2.2
Lachenalia	22	2.0
Encephalartos	16	1.4
Gasteria	16	1.4
Senecio	16	1.4
Tylecodon	15	1.4
Isoglossa	14	1.3
Cyrtanthus	12	1.1
Disa	12	1.1
Gladiolus	12	1.1
Other genera	702	63.5

Table 5 **The habit groups of southern African shade plants**

Habit	Frequency	Percent
woody plants	349	31.6
succulent	239	21.6
herbaceous perennial	237	21.4
bulbous	144	13.0
orchid	53	4.8
climber	29	2.6
cycad	16	1.4
perennial grass	14	1.3
carnivorous	7	0.6
annual	5	0.5
annual grass	5	0.5
restio	5	0.5
palm	2	0.2

Figure 15 Diagram of exposure requirements of southern African shade plants

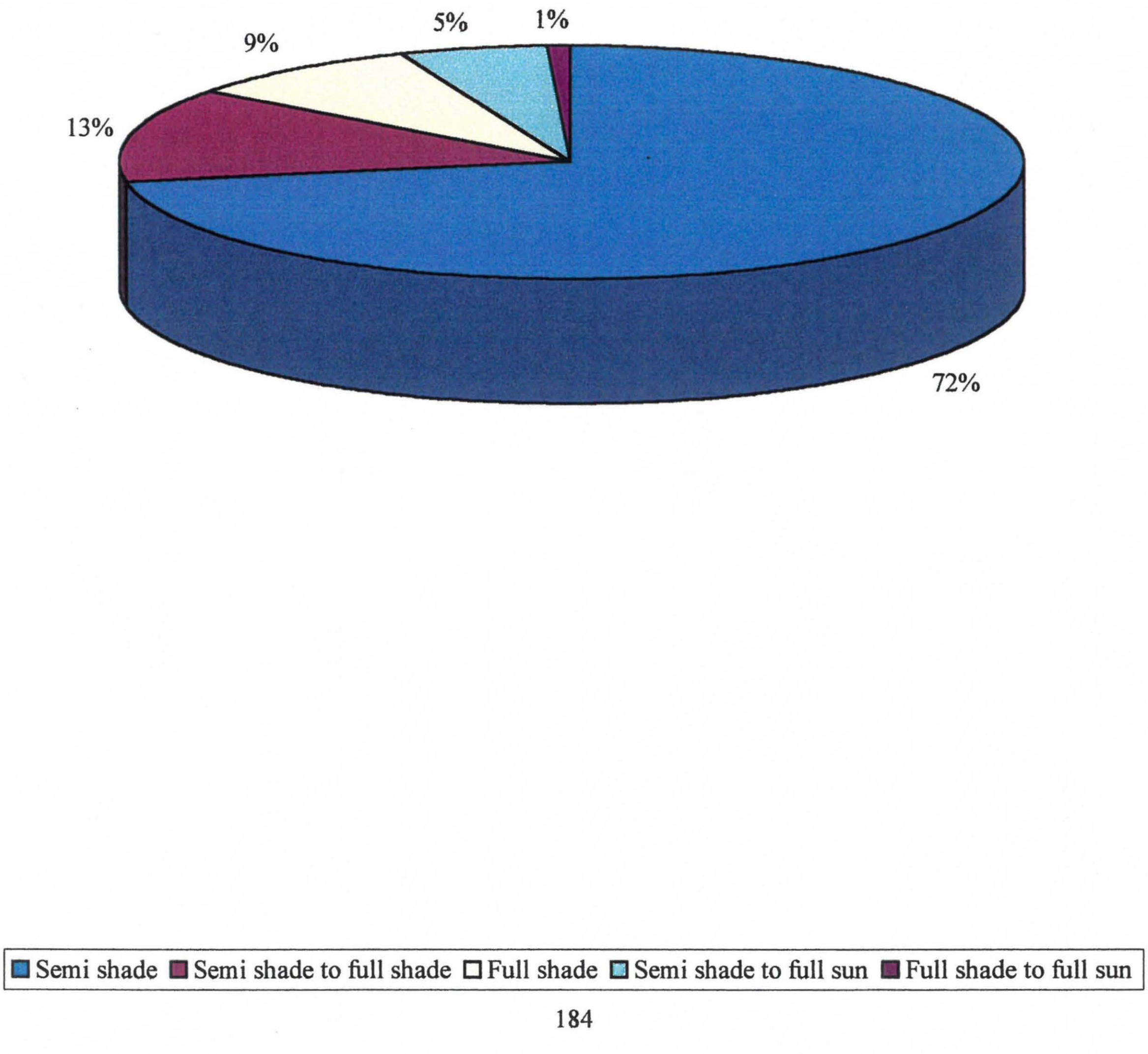
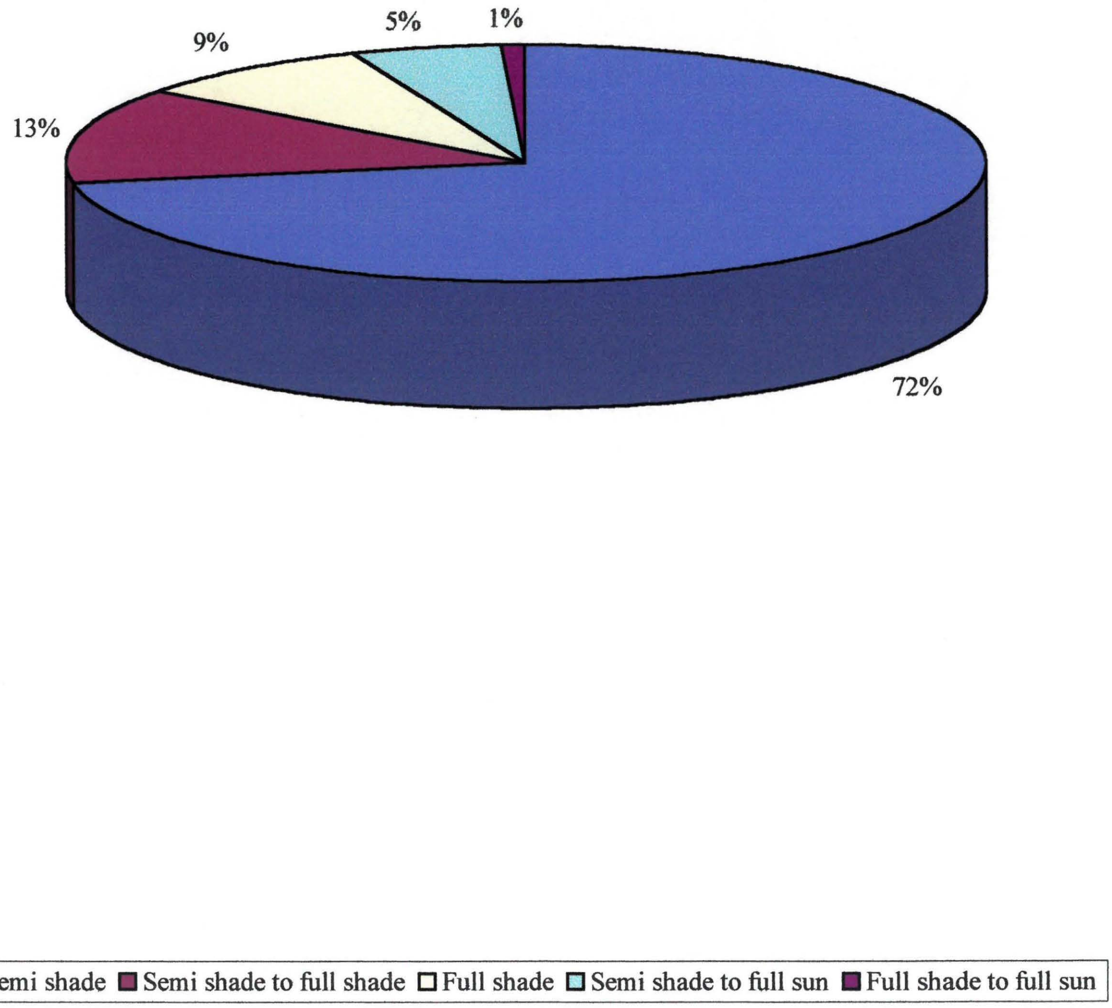


Table 6 Exposure requirements of southern African shade plants

Exposure	Frequency	Percent
semi shade	797	72.1
semi shade to full shade	144	13.0
full shade	97	8.8
semi shade to full sun	59	5.3
full shade to full sun	8	0.7

Figure 15 Diagram of exposure requirements of southern African shade plants



Printout of selected information on each plant (for explanation of abbreviations see pp. 170 – 173)

Name	Family (-ceae)	Habit	Water	Exposure
Acmadenia heterophylla *	Ruta	woody plants	M	semi shade to full sun
Acmadenia obtusata *	Ruta	woody plants	M	semi shade to full sun
Acokanthera oppositifolia ***	Apocyna	woody plants		semi shade to full shade
Acridocarpus natalitius **	Malpighia	woody plants	M-H	semi shade to full sun
Acrolophia micrantha	Orchida	orchid	L-M	semi shade
Adenandra uniflora	Ruta	woody plants	L	semi shade
Adenia digitata	Passiflora	climber		semi shade
Adromischus cristatus	Crassula	succulent	L	semi shade
Adromischus humilis	Crassula	succulent	L	semi shade
Adromischus marianiae	Crassula	succulent	L	semi shade
Adromischus umbraticola	Crassula	succulent		semi shade
Aeollanthus buchnerianus	Lamia	herbaceous perennial		semi shade
Aeollanthus parvifolius	Lamia	succulent		semi shade
Aeollanthus suaveolens	Lamia	annual	L	semi shade
Aerangis mystacidii	Orchida	orchid		semi shade
Aerangis somalensis	Orchida	orchid		semi shade
Agapanthus campanulatus	Allia	bulbous		semi shade
Agapanthus inapertus	Allia	bulbous		semi shade
Agapanthus nutans	Allia	bulbous		semi shade
Agapanthus praecox **	Allia	bulbous		semi shade
Agathosma bisulca	Ruta	woody plants	M	semi shade
Agathosma crenulata *	Ruta	woody plants	M	semi shade to full sun
Agathosma ovata **	Ruta	woody plants	M	semi shade to full sun
Agathosma puberula	Ruta	woody plants	L	semi shade
Agathosma serpyllacea	Ruta	woody plants	L	semi shade
Agathosma tabularis	Ruta	woody plants	M	semi shade
Agathosma venusta	Ruta	woody plants	M	semi shade
Alberta magna ***	Rubia	woody plants	M-H	semi shade to full sun
Albizia adianthifolia *	Mimosa	woody plants	M	semi shade to full sun
Albuca glauca	Lilia	bulbous		semi shade to full shade
Albuca nelsonii *	Lilia	bulbous		semi shade
Alchemilla capensis	Rosa	herbaceous perennial	M	semi shade
Alchornea hirtella *	Euphorbia	woody plants		semi shade to full shade
Alectra orobanchoides	Scrophularia	herbaceous perennial		semi shade
Allophylus dregeanus *	Sapinda	woody plants	M	semi shade
Aloe arborescens	Asphodela	succulent	M	semi shade
Aloe arenicola	Asphodela	succulent	L	semi shade
Aloe aristata	Asphodela	succulent	L	semi shade
Aloe bainesii *	Asphodela	succulent	L	semi shade
Aloe boylei	Asphodela	succulent	L	semi shade
Aloe castanea	Asphodela	succulent	L	semi shade
Aloe ciliaris	Asphodela	succulent		semi shade
Aloe comptonii	Asphodela	succulent	M	full shade
Aloe cryptopoda	Asphodela	succulent	L	semi shade
Aloe fosteri	Asphodela	succulent	L	semi shade
Aloe gracilis	Asphodela	succulent	M	semi shade
Aloe greatheadii	Asphodela	succulent	L	semi shade
Aloe haemanthifolia	Asphodela	succulent	M	semi shade
Aloe humilis	Asphodela	succulent	L	semi shade
Aloe khamiesensis	Asphodela	succulent	L	semi shade
Aloe lutescens	Asphodela	succulent	L	semi shade
Aloe plicatilis	Asphodela	succulent	M	semi shade
Aloe pluridens	Asphodela	succulent	M	semi shade
Aloe succotrina *	Asphodela	succulent	L	semi shade
Aloe tenuior	Asphodela	succulent	L	semi shade
Aloe thompsoniae	Asphodela	succulent		semi shade
Aloe thraskii	Asphodela	succulent	M	semi shade
Aloe vandermerwei	Asphodela	succulent	L	semi shade
Aloe vogtsii	Asphodela	succulent	M	semi shade
Aloinopsis peersii	Mesembryanthema	succulent	L	semi shade
Amaryllis belladonna **	Amaryllida	bulbous	M	semi shade
Anacampseros namaquensis	Portulaca	succulent	L-M	semi shade
Anastrabe integerrima	Scruphularia	woody plants	M-H	semi shade
Anaxeton laeve	Astera	woody plants	M	semi shade
Anchusa capensis *	Boragina	herbaceous perennial		semi shade
Anemone tenuifolia	Ranuncula	herbaceous perennial	M	semi shade

Name	Family	Habit	Water	Exposure
Anginon jaarsveldii	Apia	woody plants	L	semi shade
Angkalanthus transvaalensis	Acantha	herbaceous perennial	L	semi shade
Angraecum cultriforme	Orchida	orchid		semi shade
Angraecum kirkii	Orchida	orchid		semi shade
Angraecum pusillum	Orchida	orchid	M	semi shade
Angraecum sacciferum	Orchida	orchid	L	full shade
Anisotes formosissimus	Acantha	woody plants	L	semi shade
Anomatheca grandiflora	Irida	bulbous		semi shade to full shade
Anomatheca laxa	Irida	bulbous	M	semi shade to full shade
Anomatheca viridis	Irida	bulbous	M	semi shade
Antegibbaeum fissoides	Mesembryanthema	succulent	M	semi shade
Apodolirion lanceolatum	Amaryllida	bulbous	L	semi shade
Apodytes dimidiata	Icacina	woody plants	M	semi shade
Arctotis aspera *	Astera	herbaceous perennial		semi shade
Aristea ecklonii *	Irida	bulbous		semi shade
Artabotrys monteiroae	Annona	climber		semi shade
Astroloba aspera	Aloa	succulent	M	semi shade
Astroloba herrei	Aloa	succulent	L	semi shade
Astroloba robusta	Aloa	succulent	L	semi shade
Astroloba rugosa	Aloa	succulent	L	semi shade
Astroloba spiralis	Aloa	succulent	L	semi shade
Asystasia gangetica *	Acantha	herbaceous perennial		semi shade to full shade
Asystasia varia	Acantha	herbaceous perennial	M	semi shade to full shade
Atalaya natalensis	Sapinda	woody plants	M	semi shade
Athrixia phyliciodes	Astera	woody plants		semi shade
Aodia micrantha	Rubia	woody plants		semi shade
Babiana pygmaea	Irida	bulbous	H	semi shade
Ballota africana	Lamia	herbaceous perennial	L	semi shade
Baphia racemosa	Faba	woody plants	M	semi shade
Barleria gueinzii *	Acantha	herbaceous perennial		semi shade
Barleria lugardii	Acantha	herbaceous perennial	L	semi shade
Barleria obtusa *	Acantha	woody plants		semi shade
Barleria repens	Acantha	herbaceous perennial	L	semi shade to full shade
Bauhinia tomentosa	Caesalpinia	woody plants		semi shade
Begonia dregei *	Begonia	herbaceous perennial	M	full shade
Begonia geranioides	Begonia	herbaceous perennial	M	full shade
Begonia sonderiana *	Begonia	herbaceous perennial		semi shade
Begonia sutherlandii	Begonia	herbaceous perennial	M	semi shade
Behnia reticulata *	Luzuriaga	herbaceous perennial		semi shade to full shade
Berkheya barbata	Astera	woody plants	L	semi shade
Berkheya fruticosa	Astera	woody plants	L	semi shade
Bersama lucens *	Meliantha	woody plants		semi shade to full shade
Bersama swinnyi	Meliantha	woody plants	M	semi shade
Berzelia abrotanoides	Brunia	woody plants	M	semi shade
Berzelia galpinii	Brunia	woody plants	M	semi shade
Berzelia intermedia	Brunia	woody plants	M	semi shade
Blaeria coccinea	Erica	woody plants	M	semi shade
Blaeria ericoides	Erica	woody plants	H	semi shade
Bolusiella maudiae	Orchida	orchid		semi shade
Bonatea speciosa	Orchida	orchid	M	semi shade
Bowiea gariepensis	Hyacintha	succulent	L	semi shade
Bowiea volubilis	Hyacintha	climber	L	semi shade
Bowkeria citrina *	Scrophularia	woody plants		semi shade
Bowkeria cymosa *	Scrophularia	woody plants		semi shade
Bowkeria verticillata *	Scrophularia	woody plants		semi shade
Brachylaena uniflora	Astera	woody plants	M	semi shade
Brunia nodiflora	Brunia	woody plants	M	semi shade
Brunsvigia pulchra	Amaryllida	bulbous		full shade
Buddleja auriculata *	Logania	woody plants		semi shade
Buddleja dysophylla	Logania	woody plants	M	semi shade
Buddleja saligna	Logania	woody plants		semi shade
Buddleja salviifolia	Logania	woody plants		semi shade
Bulbine abyssinica	Asphodela	succulent	M	full shade
Bulbine frutescens	Asphodela	succulent	L	semi shade
Bulbine latifolia	Asphodela	succulent	M	full shade
Bulbine tuberosa	Asphodela	succulent	L	semi shade
Bulbophyllum scaberulum	Orchida	orchid	M	semi shade
Burchellia bubalina **	Rubia	woody plants	M-H	full shade to full sun
Buxus macowanii **	Buxa	woody plants		semi shade to full shade

Name	Family	Habit	Water	Exposure
Buxus natalensis **	Buxa	woody plants		semi shade
Calliandra redacta	Faba	woody plants	L	semi shade
Calodendrum capense	Ruta	woody plants	L	semi shade
Cannomois virgata	Restiona	restio	L	semi shade
Canthium gilfillanii	Rubia	climber	M	semi shade
Caralluma intermedia	Asclepiadaceae	succulent		semi shade
Carissa bispinosa *	Apocyna	woody plants	M	semi shade to full shade
Carissa edulis *	Apocyna	woody plants		semi shade
Carissa haematocarpa	Apocyna	woody plants	L	semi shade
Carissa macrocarpa *	Apocyna	woody plants		semi shade
Carissa tetramera *	Apocyna	woody plants		semi shade
Carissa wyliei *	Apocyna	woody plants	M	semi shade
Cassine reticulata	Celastra	woody plants	L	semi shade
Cassine tetragona *	Celastra	woody plants		semi shade
Cassine transvaalensis	Celastra	woody plants		semi shade
Cassipourea flanaganii	Rhizophora	woody plants		semi shade
Cassipourea gerrardii	Rhizophora	woody plants		semi shade
Catha abbottii *	Celastra	woody plants		semi shade to full shade
Catha edulis *	Celastra	woody plants		semi shade to full shade
Cavacoa aurea *	Euphorbia	woody plants		semi shade to full shade
Celtis africana	Ulma	woody plants		full shade
Celtis mildbraedii	Ulma	woody plants	M	full shade
Centella coriacea	Apia	herbaceous perennial	M	semi shade
Centella eriantha	Apia	herbaceous perennial	M	semi shade
Cephalanthus natalensis	Rubia	woody plants		semi shade
Ceropegia distincta	Asclepiada	succulent	L	semi shade
Ceropegia rendalii	Asclepiada	herbaceous perennial		semi shade
Ceropegia woodii **	Asclepiada	succulent		semi shade to full shade
Charadrophila capensis	Gesneria	herbaceous perennial	H	full shade
Chasmanthe aethiopica *	Irida	bulbous	L	semi shade to full shade
Chasmanthe floribunda	Irida	bulbous		semi shade to full sun
Cheiridopsis brownii	Mesembryanthema	succulent	M	semi shade
Chionanthus battiscombei	Olea	woody plants	M	semi shade
Chironia laxa	Gentiana	herbaceous perennial	L	semi shade
Chlorophytum bowkeri *	Asphodela	bulbous		semi shade to full shade
Chlorophytum comosum **	Asphodela	bulbous		full shade
Chlorophytum undulatum **	Asphodela	bulbous		semi shade to full shade
Chrysophyllum viridifolium	Sapota	woody plants	M	full shade
Cineraria mollis	Astera	herbaceous perennial	M	semi shade
Cineraria saxifraga *	Astera	herbaceous perennial		semi shade
Cirrhopetalum umbellatum	Orchida	orchid		semi shade
Cissus quadrangularis *	Vita	succulent		semi shade
Cliffortia ferruginea *	Rosa	herbaceous perennial		semi shade
Cliffortia odorata *	Rosa	herbaceous perennial		semi shade
Clivia caulescens *	Amaryllida	bulbous	M	full shade
Clivia gardenii *	Amaryllida	bulbous	M	full shade
Clivia miniata ***	Amaryllida	bulbous	M	full shade
Clivia nobilis **	Amaryllida	bulbous	M-H	semi shade to full shade
Clutia pulchella	Euphorbia	woody plants	H	full shade
Coddia rudis *	Rubia	woody plants		semi shade
Coleotrype natalensis	Commelina	herbaceous perennial	M	semi shade
Colubrina nicholsonii	Rhamna	woody plants	L	full shade
Combretum edwardsii	Combreta	woody plants	M	semi shade
Combretum kraussii	Combreta	woody plants	M	full shade
Combretum mossambicense	Combreta	woody plants	L	semi shade
Conophytum bilobum	Mesembryanthema	succulent	L	semi shade
Conophytum breve	Mesembryanthema	succulent	L	semi shade
Conophytum ectypum	Mesembryanthema	succulent	L	semi shade
Conophytum ficiforme	Mesembryanthema	succulent	L	semi shade
Conophytum loeschianum	Mesembryanthema	succulent	L	semi shade
Conophytum marginatum	Mesembryanthema	succulent	L	semi shade
Conophytum obcordellum	Mesembryanthema	succulent	L	semi shade
Conophytum quaesitum	Mesembryanthema	succulent	L	semi shade
Conophytum saxetanum	Mesembryanthema	succulent	L	semi shade
Conophytum truncatum	Mesembryanthema	succulent	L	semi shade
Convolvulus farinosus	Convolvula	climber		semi shade
Cotyledon adscendens	Crassula	succulent	L	semi shade
Cotyledon barbeyi	Crassula	succulent	L	semi shade
Cotyledon orbiculata	Crassula	succulent	L	semi shade to full shade

Name	Family	Habit	Water	Exposure
Cotyledon papillaris	Crassula	succulent	L	semi shade
Cotyledon tomentosa	Crassula	succulent	L	semi shade
Cotyledon velutina	Crassula	succulent	L	semi shade
Cotyledon woodii	Crassula	succulent	L	semi shade
Craibia zimmermannii	Faba	woody plants	L	semi shade
Crassula biplanata	Crassula	succulent	L	semi shade
Crassula capitella	Crassula	succulent	L	semi shade
Crassula coccinea	Crassula	succulent		semi shade
Crassula cotyledonis	Crassula	succulent		semi shade
Crassula cultrata	Crassula	succulent	L	semi shade
Crassula ericoides	Crassula	succulent	M	semi shade
Crassula exilis	Crassula	succulent	L	semi shade
Crassula expansa *	Crassula	succulent	L	semi shade to full shade
Crassula fascicularis	Crassula	succulent	L	semi shade
Crassula flanaganii	Crassula	succulent		semi shade
Crassula garibina	Crassula	succulent	L	semi shade
Crassula inandensis	Crassula	succulent	M	full shade
Crassula intermedia	Crassula	succulent		semi shade
Crassula lactea *	Crassula	succulent		semi shade to full shade
Crassula latibracteata	Crassula	succulent		semi shade
Crassula multicava **	Crassula	succulent	L	semi shade to full shade
Crassula muscosa	Crassula	succulent	L	semi shade
Crassula obtusa	Crassula	succulent	L	semi shade
Crassula orbicularis	Crassula	succulent	L	semi shade
Crassula ovata *	Crassula	succulent	L	semi shade to full shade
Crassula peculiaris	Crassula	succulent		semi shade to full shade
Crassula pellucida *	Crassula	succulent	M	semi shade to full shade
Crassula perfoliata	Crassula	succulent	L	semi shade to full sun
Crassula perforata	Crassula	succulent	L	semi shade
Crassula pseudohemispherica	Crassula	succulent	L	semi shade
Crassula pubescens *	Crassula	succulent	L	semi shade to full shade
Crassula rubricaulis	Crassula	succulent	L	semi shade
Crassula sarcocaulis	Crassula	succulent	L	semi shade to full shade
Crassula sarmentosa *	Crassula	succulent	L	semi shade to full shade
Crassula scabra *	Crassula	succulent		semi shade
Crassula socialis *	Crassula	succulent		semi shade to full shade
Crassula spathulata *	Crassula	succulent		semi shade to full shade
Crassula streyi	Crassula	succulent	M	semi shade to full shade
Crassula swaziensis	Crassula	succulent	L	semi shade
Crassula tetragona	Crassula	succulent	L	semi shade
Crinum buphanoides	Amaryllida	bulbous		semi shade
Crinum moorei *	Amaryllida	bulbous	M	semi shade to full shade
Crinum variabile	Amaryllida	bulbous	M	semi shade
Crocosmia aurea *	Irida	bulbous		semi shade
Crossandra greenstockii *	Acantha	herbaceous perennial		semi shade to full shade
Cryptocarya angustifolia	Laura	woody plants	M	semi shade
Cryptocarya latifolia *	Laura	woody plants	M	semi shade
Cryptocarya liebertiana	Laura	woody plants	M	semi shade
Cryptocarya myrtifolia	Laura	woody plants	M	semi shade
Cryptocarya woodii	Laura	woody plants	M	semi shade to full shade
Cryptocarya wyliei	Laura	woody plants	M	full shade
Curtisia dentata **	Corna	woody plants	M-H	semi shade to full sun
Cussonia arenicola **	Aralia	woody plants		semi shade
Cussonia gamtoosensis *	Aralia	woody plants		semi shade
Cussonia nicholsonii **	Aralia	woody plants		semi shade
Cussonia sphaerocephala *	Aralia	woody plants	M	full shade
Cussonia spicata **	Aralia	woody plants	M	semi shade to full shade
Cussonia thyrsiflora *	Aralia	woody plants		semi shade
Cussonia transvaalensis *	Aralia	woody plants		semi shade
Cussonia zuluensis *	Aralia	woody plants	M	semi shade
Cyanella hyacintoides	Tecophilaea	bulbous	L	semi shade
Cynanchum gerrardii	Asclepiada	succulent	M	semi shade
Cyperus albostriatus *	Cypera	herbaceous perennial	M	semi shade
Cyphostemma cirrhosum	Vita	succulent	L	semi shade
Cyphostemma simulans *	Vita	succulent	L	semi shade
Cyrtanthus brachyscyphus	Amaryllida	bulbous	M	semi shade to full sun
Cyrtanthus brachysiphon	Amaryllida	bulbous	M	semi shade
Cyrtanthus elatus *	Amaryllida	bulbous	M	semi shade
Cyrtanthus eucallus	Amaryllida	bulbous	H	full shade

Name	Family	Habit	Water	Exposure
Cyrtanthus falcatus *	Amaryllida	bulbous		semi shade
Cyrtanthus galpinii	Amaryllida	bulbous		semi shade
Cyrtanthus herrei	Amaryllida	bulbous	L	semi shade
Cyrtanthus labiatus	Amaryllida	bulbous	M	semi shade
Cyrtanthus mackenii *	Amaryllida	bulbous	M	semi shade to full shade
Cyrtanthus montanus	Amaryllida	bulbous	L	semi shade
Cyrtanthus obliquus	Amaryllida	bulbous		semi shade
Cyrtanthus sanguineus	Amaryllida	bulbous	M	semi shade
Cyrtorchis arcuata	Orchida	orchid		semi shade
Cyrtorchis praetermissa	Orchida	orchid		semi shade
Dactyloctenium australe	Poa	perennial grass		full shade to full sun
Deinbollia oblongifolia	Sapinda	woody plants		full shade
Delosperma ecklonis	Mesembryanthema	succulent	L	semi shade
Delosperma laxipetalum	Mesembryanthema	succulent	L	semi shade
Delosperma pottsii	Mesembryanthema	succulent	L	semi shade
Delosperma truteri	Mesembryanthema	succulent	L	semi shade
Delosperma zoutpansbergense	Mesembryanthema	succulent	L	semi shade
Desmodium repandum	Faba	herbaceous perennial	M	full shade
Dianthus caespitosus	Caryophylla	herbaceous perennial	M	semi shade
Diaphananthe caffra	Orchida	orchid	M	full shade
Diascia fetcaniensis *	Scrophularia	herbaceous perennial		semi shade
Diascia integerrima **	Scrophularia	herbaceous perennial	M	semi shade to full sun
Diascia mollis *	Scrophularia	herbaceous perennial	H	semi shade to full shade
Dicliptera capensis	Acantha	herbaceous perennial		semi shade
Dicliptera clinopodia	Acantha	herbaceous perennial		semi shade
Dicliptera eenii	Acantha	herbaceous perennial		semi shade
Dicliptera heterostegia	Acantha	herbaceous perennial		full shade
Dicliptera zeylanica	Acantha	herbaceous perennial		full shade
Dietes bicolor	Irida	bulbous		full shade to full sun
Dietes butcheriana *	Irida	bulbous	M	semi shade to full shade
Dietes grandiflora *	Irida	bulbous	H	full shade to full sun
Dietes iridioides	Irida	bulbous	M	semi shade to full shade
Dilatris ixioides *	Haemodora	bulbous	L-M	semi shade to full sun
Dinebra retroflexa	Poa	annual grass		semi shade to full sun
Dioscorea dregeana	Dioscorea	climber	M	semi shade
Dioscorea elephantipes *	Dioscorea	climber	L	semi shade
Dioscorea sylvatica *	Dioscorea	climber	M	full shade
Diosma aristata	Ruta	woody plants	M	semi shade
Diosma fallax	Ruta	woody plants	M	semi shade
Diospyros glabra	Ebena	woody plants	L	semi shade
Diospyros natalensis **	Ebena	woody plants		semi shade to full shade
Diospyros scabrida	Ebena	woody plants	L	semi shade
Diospyros villosa	Ebena	woody plants	L	semi shade
Diospyros whyteana ***	Ebena	woody plants	M-H	semi shade to full shade
Disa aurata	Orchida	orchid	H	semi shade
Disa cardinalis	Orchida	orchid	M	semi shade
Disa draconis	Orchida	orchid	L	semi shade
Disa glandulosa	Orchida	orchid	M	semi shade
Disa longicornu	Orchida	orchid	H	semi shade
Disa rosea	Orchida	orchid	M	semi shade
Disa saxicola	Orchida	orchid	M	semi shade
Disa tripetaloides	Orchida	orchid	H	semi shade
Disa unicata	Orchida	orchid		semi shade
Disa uniflora *	Orchida	orchid	H	semi shade to full shade
Disa vaginata	Orchida	orchid	M	semi shade
Disa venosa	Orchida	orchid		full shade
Dissotis princeps	Melastomata	woody plants	M	semi shade
Dombeya pulchra *	Sterculia	woody plants		semi shade
Dombeya rotundifolia	Sterculia	woody plants		full shade
Dombeya tiliacea	Sterculia	woody plants	L	semi shade
Dracaena hookeriana ***	Dracaena	woody plants	M	full shade
Dracaena mannii ***	Dracaena	woody plants		full shade
Drimiopsis maculata *	Hyacintha	bulbous	M	semi shade to full shade
Drosanthemum candens	Mesembryanthema	succulent	L	semi shade
Drosera alba	Drosera	carnivorous	H	semi shade
Drosera aliciae	Drosera	carnivorous	H	semi shade
Drosera capensis *	Drosera	carnivorous	H	semi shade to full sun
Drosera cistiflora	Drosera	carnivorous	H	semi shade
Drosera hilaris	Drosera	carnivorous	M	full shade

Name	Family	Habit	Water	Exposure
Drosera pauciflora	Drosera	carnivorous	M	semi shade
Drosera trinerva	Drosera	carnivorous	M	semi shade
Drypetes argutta	Euphorbia	woody plants		semi shade
Drypetes gerrardii	Euphorbia	woody plants	M	semi shade
Drypetes natalensis	Euphorbia	woody plants		semi shade
Duvalia corderoyi	Asclepiada	succulent	L	semi shade
Duvalia radiata	Asclepiada	succulent	L	semi shade
Duvernoia aconitiflora *	Acantha	woody plants		semi shade
Duvernoia adhatodoides *	Acantha	woody plants		semi shade
Elegia capensis *	Restiona	restio	M-H	semi shade to full sun
Empodium veratrifolium	Hypoxida	bulbous	M	semi shade
Encephalartos altensteinii **	Zamia	cycad	M-H	semi shade to full sun
Encephalartos ferox *	Zamia	cycad		semi shade
Encephalartos friderici-guilielmi *	Zamia	cycad		semi shade
Encephalartos ghellinckii **	Zamia	cycad	M-H	semi shade to full sun
Encephalartos horridus *	Zamia	cycad		semi shade
Encephalartos humilis *	Zamia	cycad		semi shade
Encephalartos lebomboensis *	Zamia	cycad		semi shade
Encephalartos lehmannii *	Zamia	cycad		semi shade
Encephalartos longifolius **	Zamia	cycad	M-H	semi shade to full sun
Encephalartos natalensis *	Zamia	cycad		semi shade
Encephalartos paucidentatus *	Zamia	cycad	M	semi shade to full shade
Encephalartos princeps	Zamia	cycad	L	semi shade
Encephalartos transvenosus *	Zamia	cycad		semi shade
Encephalartos trispinosus	Zamia	cycad	L	semi shade
Encephalartos umbeluziensis	Zamia	cycad	M	semi shade
Encephalartos villosus	Zamia	cycad	M	semi shade to full shade
Englerodaphne pilosa **	Thymela	woody plants	M	semi shade
Englerodaphne subcordata	Thymela	woody plants		semi shade
Englerophytum magalismontanum	Sapota	woody plants	M	semi shade
Englerophytum natalense *	Sapota	woody plants	M	full shade
Ensete ventricosum *	Musa	woody plants		semi shade
Enteropogon monostachyus	Poa	perennial grass		semi shade to full sun
Ephippiocarpa orientalis	Apocyna	woody plants		semi shade
Eragrostis biflora	Poa	annual grass		semi shade to full sun
Eragrostis micrantha	Poa	perennial grass		semi shade to full sun
Erica adunca	Erica	woody plants	M	semi shade
Erica aneimena	Erica	woody plants	M	semi shade
Erica annectens	Erica	woody plants	H	full shade
Erica atrovinosa	Erica	woody plants	L	semi shade
Erica bergiana	Erica	woody plants	M	semi shade
Erica blancheana	Erica	woody plants	M	semi shade
Erica bodkinii	Erica	woody plants	M	semi shade
Erica bruniades	Erica	woody plants	H	semi shade
Erica caffra	Erica	woody plants	H	semi shade
Erica calycina	Erica	woody plants	M	semi shade
Erica canaliculata	Erica	woody plants	M	semi shade
Erica caterviflora	Erica	woody plants	M	semi shade
Erica cerinthoides	Erica	woody plants	M	semi shade
Erica chamissonis	Erica	woody plants	M	semi shade
Erica chionophila	Erica	woody plants	M	semi shade
Erica chrysocodon	Erica	woody plants	H	semi shade
Erica clavisepala	Erica	woody plants	M	semi shade
Erica coccinea	Erica	woody plants	M	semi shade
Erica colorans	Erica	woody plants	M	semi shade
Erica cordata	Erica	woody plants	M	semi shade
Erica corydalis	Erica	woody plants	M	semi shade
Erica cubica	Erica	woody plants	M	semi shade
Erica curviflora	Erica	woody plants	M	semi shade
Erica demissa	Erica	woody plants	M	semi shade
Erica depressa	Erica	woody plants	M	semi shade
Erica diaphana	Erica	woody plants	H	semi shade
Erica fourcadei	Erica	woody plants	M	semi shade
Erica glauca	Erica	woody plants	L	semi shade
Erica glomiflora	Erica	woody plants	M	semi shade
Erica gracilis	Erica	woody plants	M	semi shade
Erica heleogena	Erica	woody plants	M	semi shade
Erica heliophila	Erica	woody plants	M	semi shade
Erica hispidula	Erica	woody plants	M	semi shade

Name	Family	Habit	Water	Exposure
Erica lehmannii	Erica	woody plants	M	semi shade
Erica lerouxiae	Erica	woody plants	M	semi shade
Erica leucantha	Erica	woody plants	H	semi shade
Erica limosa	Erica	woody plants	H	semi shade
Erica longifolia	Erica	woody plants	L	semi shade
Erica longipedunculata	Erica	woody plants	M	semi shade
Erica macowanii	Erica	woody plants	M	semi shade
Erica marifolia	Erica	woody plants	M	semi shade
Erica melanthera	Erica	woody plants	M	semi shade
Erica modesta	Erica	woody plants	L	semi shade
Erica mollis	Erica	woody plants	M	semi shade
Erica nudiflora	Erica	woody plants	M	semi shade
Erica plukenetii	Erica	woody plants	L	full shade
Erica retorta	Erica	woody plants	M	semi shade
Erica scabriuscula	Erica	woody plants	M	semi shade
Erica sitiens	Erica	woody plants	M	semi shade
Erica sphaeroidea	Erica	woody plants	M	semi shade
Erica tenuis	Erica	woody plants	M	semi shade
Erica thomae	Erica	woody plants	M	semi shade
Erica transparens	Erica	woody plants	L	semi shade
Erica triflora	Erica	woody plants	M	semi shade
Erica verecunda	Erica	woody plants	M	semi shade
Erica verticillata	Erica	woody plants	M	semi shade
Erica winteri	Erica	woody plants	M	semi shade
Erica woodii	Erica	woody plants	L	semi shade
Erythrococca berberidea	Euphorbia	woody plants		semi shade
Erythroxylum emarginatum	Erythroxyla	woody plants		semi shade
Euclea natalensis	Ebena	woody plants	L	semi shade
Eucomis autumnalis	Hyacintha	bulbous		semi shade to full sun
Eucomis bicolor *	Hyacintha	bulbous	M	semi shade
Eugenia capensis	Myrta	woody plants	M	semi shade
Eugenia verdoorniae	Myrta	woody plants	M	semi shade
Eulophia fridericii	Orchida	orchid	L	semi shade
Eulophia leachii	Orchida	orchid	L	semi shade
Eulophia petersii	Orchida	orchid	L	semi shade
Eulophia speciosa	Orchida	orchid		semi shade
Eulophia streptopetala	Orchida	orchid		semi shade
Eulophia welwitschii	Orchida	orchid	L	semi shade
Euphorbia confinalis	Euphorbia	succulent		semi shade
Euphorbia grandicornis	Euphorbia	succulent	L	semi shade
Euphorbia ingens *	Euphorbia	succulent	L	semi shade to full shade
Euphorbia ledienii	Euphorbia	succulent	L	semi shade
Euphorbia lydenburgensis	Euphorbia	succulent	L	semi shade
Euphorbia nesemannii	Euphorbia	succulent	L	semi shade
Euphorbia tetragona *	Euphorbia	succulent	L	semi shade to full shade
Euphorbia triangularis	Euphorbia	succulent	L	semi shade
Euryops decipiens	Astera	woody plants	M	semi shade
Euryops othonnoides	Astera	woody plants	L	semi shade
Faucaria britteniae	Mesembryanthema	succulent	L	semi shade
Faucaria felina	Mesembryanthema	succulent	L	semi shade
Faucaria hooleae	Mesembryanthema	succulent	L	semi shade
Faurea macnaughtonii	Protea	woody plants		full shade
Festuca scabra	Poa	perennial grass		semi shade to full sun
Ficus bizanae	Mora	woody plants	L	semi shade
Ficus craterostoma	Mora	woody plants	L	semi shade to full shade
Ficus glumosa	Mora	woody plants		semi shade
Ficus lutea **	Mora	woody plants		semi shade to full shade
Ficus natalensis **	Mora	woody plants	M	semi shade to full shade
Ficus polita	Mora	woody plants	L	semi shade
Ficus sur *	Mora	woody plants		semi shade to full shade
Ficus trichopoda **	Mora	woody plants		semi shade to full shade
Flagellaria guineensis	Flagellaria	herbaceous perennial	M	full shade
Fockea edulis	Asclepiada	succulent	L	semi shade
Garcinia gerrardii ***	Clusia	woody plants	M	semi shade to full shade
Garcinia livingstonei *	Clusia	woody plants		semi shade to full shade
Gasteria acinacifolia *	Asphodela	succulent	L	semi shade
Gasteria angustiarum *	Asphodela	succulent		semi shade
Gasteria batesiana *	Asphodela	succulent	L	semi shade
Gasteria baylissiana *	Asphodela	succulent	L	semi shade to full shade

Name	Family	Habit	Water	Exposure
Gasteria bicolor **	Asphodela	succulent	L	semi shade to full shade
Gasteria brachyphylla	Asphodela	succulent	L	semi shade
Gasteria carinata *	Asphodela	succulent	L	semi shade
Gasteria croucheri **	Asphodela	succulent	L	semi shade to full shade
Gasteria disticha *	Asphodela	succulent	L	semi shade
Gasteria ellaphieae *	Asphodela	succulent	L	semi shade
Gasteria ernestii-ruschii *	Asphodela	succulent		semi shade
Gasteria excelsa *	Asphodela	succulent	L	semi shade
Gasteria glomerata *	Asphodela	succulent	L	semi shade
Gasteria liliputana	Asphodela	succulent	L	semi shade
Gasteria rawlinsonii	Asphodela	succulent	L	semi shade
Gasteria vlokii	Asphodela	succulent	L	semi shade
Geissorhiza mathewsii	Irida	bulbous	M	semi shade
Geranium incanum *	Gerania	herbaceous perennial		semi shade
Geranium ornithopodon	Gerania	herbaceous perennial	M	semi shade
Gerbera cordata *	Astera	herbaceous perennial		full shade
Gerbera jamesonii	Astera	herbaceous perennial		semi shade
Gerbera tomentosa	Astera	herbaceous perennial	M	semi shade
Gerrardanthus macrorhizus	Cucurbita	succulent	L	semi shade
Gerrardina foliosa	Flacourtia	woody plants	M	semi shade
Gethyllis gregoriana	Amaryllida	bulbous	L	semi shade
Gibbaria ilicifolia	Astera	woody plants	M	semi shade
Gladiolus alatus	Irida	bulbous	M	semi shade
Gladiolus buckerveldii	Irida	bulbous	H	semi shade
Gladiolus cardinalis	Irida	bulbous	M	semi shade
Gladiolus carinatus	Irida	bulbous	M	semi shade
Gladiolus carmineus	Irida	bulbous	M	semi shade
Gladiolus caryophyllaceus	Irida	bulbous	M	semi shade
Gladiolus floribundus	Irida	bulbous	M	semi shade
Gladiolus permeabilis	Irida	bulbous	M	semi shade
Gladiolus rogersii	Irida	bulbous	M	semi shade
Gladiolus stefaniae	Irida	bulbous		semi shade to full sun
Gladiolus virescens	Irida	bulbous	M	semi shade
Gladiolus watermeyeri	Irida	bulbous	M	semi shade
Gloriosa superba **	Colchica	bulbous		semi shade to full sun
Gonatopus angustus	Ara	bulbous		semi shade to full sun
Gonatopus boivinii	Ara	bulbous		semi shade to full sun
Gonatopus marattioides	Ara	herbaceous perennial	L	semi shade
Grewia caffra	Tilia	woody plants		semi shade
Grewia occidentalis	Tilia	woody plants		semi shade
Habenaria arenaria	Orchida	orchid	L	semi shade
Haemanthus albiflos **	Amaryllida	bulbous	M	semi shade to full shade
Haemanthus amarylloides	Amaryllida	bulbous	M	semi shade
Haemanthus carneus	Amaryllida	bulbous	M	semi shade
Haemanthus coccineus	Amaryllida	bulbous	L	semi shade
Haemanthus deformis **	Amaryllida	bulbous	M	semi shade to full shade
Haemanthus graniticus	Amaryllida	bulbous	L	semi shade
Haemanthus humilis *	Amaryllida	bulbous	M	semi shade
Haemanthus namaquensis	Amaryllida	bulbous	L	semi shade
Haemanthus sanguineus	Amaryllida	bulbous	L	semi shade
Haemanthus unifoliatus	Amaryllida	bulbous	M	semi shade
Halleria elliptica *	Scrophularia	woody plants		semi shade
Halleria lucida *	Scrophularia	woody plants		semi shade
Halleria ovata	Scrophularia	woody plants	M	semi shade
Haplocarpha lanata	Astera	herbaceous perennial	L	semi shade
Harpephyllum caffrum	Anacardia	woody plants	M	semi shade
Haworthia angustifolia	Asphodela	succulent	L	semi shade
Haworthia attenuata	Asphodela	succulent	L	semi shade
Haworthia bruynsii	Asphodela	succulent	L	semi shade
Haworthia chloracantha	Asphodela	succulent	L	semi shade
Haworthia coarctata	Asphodela	succulent	L	semi shade
Haworthia cooperi *	Asphodela	succulent	L	semi shade to full shade
Haworthia cymbiformis *	Asphodela	succulent		semi shade to full shade
Haworthia divergens	Asphodela	succulent	L	semi shade
Haworthia glauca	Asphodela	succulent	L	semi shade
Haworthia herbacea	Asphodela	succulent	L	semi shade
Haworthia isabellae	Asphodela	succulent		semi shade
Haworthia koelmaniorum	Asphodela	succulent	L	semi shade
Haworthia limifolia	Asphodela	succulent		semi shade

Name	Family	Habit	Water	Exposure
Haworthia lockwoodii	Asphodela	succulent		semi shade
Haworthia longiana	Asphodela	succulent	L	semi shade
Haworthia magnifica	Asphodela	succulent	L	semi shade
Haworthia marumiana	Asphodela	succulent	L	semi shade
Haworthia maughanii	Asphodela	succulent	L	semi shade
Haworthia minima	Asphodela	succulent	L	semi shade
Haworthia mirabilis	Asphodela	succulent	L	semi shade
Haworthia nigra	Asphodela	succulent	L	semi shade
Haworthia pumila	Asphodela	succulent	L	semi shade
Haworthia pygmaea	Asphodela	succulent	L	semi shade
Haworthia reinwardtii	Asphodela	succulent	L	semi shade
Haworthia reticulata *	Asphodela	succulent	L	semi shade to full shade
Haworthia retusa	Asphodela	succulent	L	semi shade
Haworthia scabra	Asphodela	succulent	M	semi shade
Haworthia semiviva	Asphodela	succulent	L	semi shade
Haworthia translucens	Asphodela	succulent	L	semi shade
Haworthia truncata	Asphodela	succulent	L	semi shade
Haworthia turgida	Asphodela	succulent	L	semi shade
Haworthia venosa	Asphodela	succulent	L	semi shade
Haworthia viscosa	Asphodela	succulent	L	semi shade
Haworthia woolleyi	Asphodela	succulent	L	semi shade
Haworthia xiphiophylla	Asphodela	succulent	L	semi shade
Haworthia zantnerana	Asphodela	succulent	L	semi shade
Helichrysum fruticans	Astera	herbaceous perennial	M	semi shade
Helichrysum grandiflorum	Astera	herbaceous perennial	M	semi shade
Helichrysum petiolare *	Astera	herbaceous perennial		semi shade
Helichrysum populifolium	Astera	herbaceous perennial	M	semi shade
Hemizygia obermeyerae *	Lamia	woody plants	H	semi shade to full sun
Hermannia coccocarpa	Sterculia	woody plants	L	semi shade
Hermannia filifolia	Sterculia	herbaceous perennial	L	semi shade
Hermannia scabra	Sterculia	woody plants	L	semi shade
Hesperantha bachmannii	Irida	bulbous	M	semi shade
Hesperantha huttonii	Irida	bulbous	M	semi shade
Hesperantha pauciflora	Irida	bulbous		semi shade
Heywoodia lucens	Euphorbia	woody plants	M	full shade
Hibiscus calyphyllus	Malva	woody plants		semi shade
Hibiscus pedunculatus	Malva	herbaceous perennial		semi shade
Hibiscus platycalyx	Malva	woody plants		semi shade
Hippia frutescens	Astera	woody plants	M	semi shade
Hippia pilosa	Astera	woody plants	M	semi shade
Huernia punctata	Asclepiada	succulent	L	semi shade
Hyperacanthus amoenus	Rubia	woody plants		semi shade
Hypoestes aristata *	Acantha	herbaceous perennial		semi shade
Hypoestis triflora	Acantha	herbaceous perennial		full shade
Hypoxis hemerocallidea	Hypoxida	bulbous		semi shade
Ilex mitis	Aquifolia	woody plants		semi shade
Impatiens flanaganiae *	Balsamina	herbaceous perennial	M	semi shade to full shade
Impatiens hochstetteri *	Balsamina	herbaceous perennial	M-H	semi shade to full shade
Impatiens sylvicola	Balsamina	herbaceous perennial	M	full shade
Impatiens zombensis *	Balsamina	herbaceous perennial	M	full shade
Indigofera frutescens *	Faba	woody plants	L	semi shade
Indigofera natalensis *	Faba	woody plants	M	semi shade to full shade
Ipomoea albivenia	Convolvula	succulent	L	semi shade to full shade
Ischyrolepis sieberi	Restiona	restio	M	semi shade
Ischyrolepis subverticillata *	Restiona	restio	H	semi shade
Isoglossa bolusii	Acantha	herbaceous perennial		full shade
Isoglossa ciliata	Acantha	herbaceous perennial		full shade
Isoglossa cooperi	Acantha	herbaceous perennial		full shade
Isoglossa delicatula	Acantha	herbaceous perennial		full shade
Isoglossa densa	Acantha	herbaceous perennial		full shade
Isoglossa eckloniana	Acantha	herbaceous perennial		full shade
Isoglossa grantii	Acantha	herbaceous perennial		semi shade to full shade
Isoglossa hypoestiflora	Acantha	herbaceous perennial		full shade
Isoglossa macowanii	Acantha	herbaceous perennial		full shade
Isoglossa origanoides	Acantha	herbaceous perennial		full shade
Isoglossa prolixa	Acantha	herbaceous perennial		full shade
Isoglossa stipitata	Acantha	herbaceous perennial		full shade
Isoglossa sylvatica	Acantha	herbaceous perennial		full shade
Isoglossa woodii	Acantha	herbaceous perennial	L	semi shade

Name	Family	Habit	Water	Exposure
Jasminum angulare *	Olea	climber		semi shade
Jasminum breviflorum *	Olea	woody plants		semi shade
Jasminum multipartitum ***	Olea	climber	M	semi shade to full sun
Jasminum streptopus	Olea	climber		semi shade
Jubaeopsis caffra *	Areca	palm		semi shade
Jumellea filicornoides	Orchida	orchid	M	semi shade
Justicia betonica	Acantha	herbaceous perennial		semi shade
Justicia bolusii	Acantha	herbaceous perennial		full shade
Justicia campylostemon	Acantha	herbaceous perennial	L	semi shade to full shade
Justicia capensis	Acantha	herbaceous perennial	L	semi shade to full shade
Justicia flava	Acantha	herbaceous perennial	L	semi shade
Justicia odora	Acantha	herbaceous perennial		semi shade
Justicia petiolaris *	Acantha	herbaceous perennial	M	semi shade
Justicia protracta	Acantha	herbaceous perennial	L	semi shade
Kalanchoe crenata	Crassula	succulent	L	full shade
Kalanchoe longiflora	Crassula	succulent	L	semi shade
Kalanchoe rotundifolia	Crassula	succulent	L	semi shade
Kalanchoe sexangularis	Crassula	succulent	L	semi shade
Kedrostis africana	Cucurbita	succulent	L	semi shade
Kedrostis nana	Cucurbita	succulent	L	semi shade
Kleinia stapeliiformis	Astera	succulent	L	semi shade
Kniphofia laxiflora *	Asphodela	bulbous		semi shade
Kniphofia linearifolia	Asphodela	bulbous	M	semi shade
Kniphofia uvaria *	Asphodela	bulbous		semi shade
Knowltonia capensis	Ranuncula	herbaceous perennial		semi shade
Knowltonia vesicatoria **	Ranuncula	herbaceous perennial	M	semi shade to full shade
Kraussia floribunda *	Rubia	woody plants		semi shade
Lachenalia aloides	Hyacintha	bulbous	M	semi shade
Lachenalia bolusii	Hyacintha	bulbous	M	semi shade to full shade
Lachenalia bulbifera	Hyacintha	bulbous	L	semi shade
Lachenalia capensis	Hyacintha	bulbous	L	semi shade
Lachenalia elegans	Hyacintha	bulbous	M	semi shade
Lachenalia fistulosa	Hyacintha	bulbous	M	semi shade
Lachenalia longibracteata	Hyacintha	bulbous	M	semi shade
Lachenalia marginata	Hyacintha	bulbous	M	semi shade
Lachenalia mediana	Hyacintha	bulbous	L	semi shade
Lachenalia mutabilis	Hyacintha	bulbous	M	semi shade
Lachenalia nordenstamii	Hyacintha	bulbous	L	semi shade
Lachenalia orchioides	Hyacintha	bulbous	M	semi shade
Lachenalia orthopetala	Hyacintha	bulbous	M	semi shade
Lachenalia pustulata	Hyacintha	bulbous	M	semi shade
Lachenalia rosea	Hyacintha	bulbous	M	semi shade
Lachenalia splendida	Hyacintha	bulbous	M	semi shade
Lachenalia thomasiae	Hyacintha	bulbous	L	semi shade
Lachenalia trichophylla	Hyacintha	bulbous	M	semi shade
Lachenalia unicolor	Hyacintha	bulbous	M	full shade
Lachenalia variegata	Hyacintha	bulbous	M	semi shade
Lachenalia ventricosa	Hyacintha	bulbous	M	semi shade
Lachenalia violacea	Hyacintha	bulbous	M	semi shade
Lampranthus deltoides	Mesembryanthema	succulent	M	semi shade
Lampranthus falciformis	Mesembryanthema	succulent	L	semi shade
Landolphia kirkii	Apocyna	climber	L	semi shade
Lantana rugosa	Verbena	herbaceous perennial		semi shade
Laportea grossa *	Urtica	herbaceous perennial		full shade
Ledebouria floribunda	Hyacintha	bulbous	L	semi shade
Ledebouria socialis *	Hyacintha	bulbous	M	semi shade
Leucadendron strobilinum	Protea	woody plants	M	semi shade
Littonia modesta	Colchica	bulbous		semi shade to full sun
Lobelia anceps	Lobelia	herbaceous perennial	H	semi shade
Lobelia erinus	Lobelia	herbaceous perennial	M	semi shade
Lobelia neglecta	Lobelia	herbaceous perennial	M	semi shade
Lobelia pteropoda	Lobelia	herbaceous perennial	L	full shade
Macaranga capensis	Euphorbia	woody plants	H	semi shade
Mackaya bella **	Acantha	woody plants		semi shade to full shade
Maurocenia frangularia *	Celastra	woody plants		semi shade
Maytenus abbottii	Celastra	woody plants	M	semi shade
Maytenus acuminata *	Celastra	woody plants		semi shade
Maytenus cordata	Celastra	woody plants	L	semi shade
Maytenus filiformis	Celastra	woody plants	M	full shade

Name	Family	Habit	Water	Exposure
Maytenus mossambicensis	Celastra	woody plants	M	full shade
Maytenus tenuispina	Celastra	woody plants	L	semi shade
Maytenus undata	Celastra	woody plants		semi shade
Megastachya mucronata	Poa	perennial grass		semi shade to full sun
Melasphaerula ramosa	Irida	bulbous	M	semi shade to full shade
Melhania prostrata	Sterculia	herbaceous perennial		semi shade
Memecylon bachmannii *	Melastomata	woody plants	L	semi shade
Memecylon natalense	Melastomata	woody plants		semi shade
Metarungia galpinii	Acantha	herbaceous perennial		semi shade
Metarungia longistrobus	Acantha	woody plants		semi shade
Micrococca capensis	Euphorbia	woody plants	M	semi shade to full shade
Microcoelia exilis	Orchida	orchid		semi shade
Mimusops obovata	Sapota	woody plants		semi shade
Mitriostigma axillare **	Rubia	woody plants		semi shade to full shade
Monanthotaxis caffra *	Annona	climber	L	semi shade
Monilaria moniliformis	Mesembryanthema	woody plants		semi shade
Monopsis lutea *	Lobelia	herbaceous perennial		semi shade
Monopsis unidentata	Lobelia	herbaceous perennial	M	semi shade
Moraea garipensis	Irida	bulbous	L	semi shade
Moraea spathulata	Irida	bulbous	M	semi shade
Myrsine africana **	Myrsina	woody plants		semi shade
Myrsiphyllum asparagoides *	Asparaga	climber	M	semi shade to full shade
Myrsiphyllum declinatum *	Asparaga	herbaceous perennial		semi shade
Myrsiphyllum kraussianum *	Asparaga	climber		full shade
Myrsiphyllum ramosissimum *	Asparaga	herbaceous perennial	M-H	semi shade to full shade
Myrsiphyllum scandens *	Asparaga	herbaceous perennial	M-H	semi shade to full shade
Mystacidium braybonae	Orchida	orchid		semi shade
Mystacidium gracile	Orchida	orchid	M	semi shade to full shade
Mystacidium venosum	Orchida	orchid		semi shade
Nebelia paleacea	Brunia	woody plants		semi shade
Nebelia sphaerocephala	Brunia	woody plants	H	semi shade
Nemesia strumosa	Scrophularia	annual	M	semi shade
Nerine filifolia	Amaryllida	bulbous	M	semi shade
Nerine humilis	Amaryllida	bulbous	M	semi shade
Nerine krigei	Amaryllida	bulbous	M	semi shade
Nerine masonorum	Amaryllida	bulbous	M	semi shade
Nerine sarniensis	Amaryllida	bulbous	M	semi shade
Nerine undulata	Amaryllida	bulbous	M	semi shade
Ochna arborea	Ochna	woody plants	L-M	semi shade to full sun
Ochna barbosae	Ochna	woody plants		semi shade to full sun
Ochna holstii	Ochna	woody plants	M	semi shade to full sun
Ochna natalitia **	Ochna	woody plants	M-H	semi shade to full sun
Ochna serrulata **	Ochna	woody plants	M-H	semi shade to full sun
Ocotea bullata	Laura	woody plants	M	semi shade
Oldenlandia tenella	Rubia	annual		semi shade to full shade
Olinia ventosa	Olinia	woody plants	M	semi shade
Oplismenus hirtellus **	Poa	perennial grass		semi shade to full shade
Orbea variegata	Asclepiada	succulent	L	semi shade
Orbeanthus hardyi	Asclepiada	succulent		semi shade
Orbeopsis lutea	Asclepiada	succulent		full shade to full sun
Ornithogalum longibracteatum	Hyacintha	bulbous	L	semi shade
Orphium frutescens	Gentiana	herbaceous perennial	H	semi shade
Orthosiphon labiatus	Lamia	woody plants	M-H	semi shade to full shade
Osteospermum caulescens	Astera	herbaceous perennial	L	semi shade
Osteospermum ecklonis	Astera	woody plants	L	full shade
Osteospermum oppositifolium	Astera	woody plants	L	semi shade
Osteospermum spinosum	Astera	woody plants	L	semi shade
Otholobium decumbens *	Faba	herbaceous perennial		semi shade
Othonna armiana	Astera	succulent	L	semi shade
Othonna natalensis	Astera	succulent	M	semi shade
Othonna triplinervia	Astera	woody plants	L	semi shade
Oxyanthus latifolius **	Rubia	woody plants	M	semi shade to full shade
Oxyanthus pyriformis **	Rubia	woody plants	M	semi shade to full shade
Oxyanthus speciosus **	Rubia	woody plants	M-H	semi shade to full shade
Pancovia golungensis *	Sapinda	woody plants		semi shade
Panicum deustum	Poa	perennial grass		semi shade to full sun
Pavetta cooperi	Rubia	woody plants		semi shade
Pavetta eylesii	Rubia	woody plants	L	semi shade
Pavetta galpinii	Rubia	woody plants	M	full shade

Name	Family	Habit	Water	Exposure
Pavetta gardeniifolia *	Rubia	woody plants		semi shade
Pavetta inandensis	Rubia	woody plants		semi shade to full shade
Pavetta lanceolata **	Rubia	woody plants	H	semi shade to full sun
Pavetta natalensis	Rubia	woody plants	M	semi shade
Pavetta revoluta	Rubia	woody plants	M-H	semi shade to full shade
Pavonia burchellii	Malva	woody plants		semi shade
Peddiea africana **	Thymela	woody plants		semi shade to full shade
Pelargonium reniforme	Gerania	herbaceous perennial	L	semi shade
Pelargonium acetosum *	Gerania	herbaceous perennial		semi shade
Pelargonium alchemilloides	Gerania	herbaceous perennial	L	semi shade
Pelargonium alpinum	Gerania	herbaceous perennial	M	semi shade
Pelargonium antidysentericum	Gerania	woody plants	L	semi shade
Pelargonium auritum	Gerania	bulbous	M	semi shade
Pelargonium barklyi	Gerania	bulbous	L	semi shade
Pelargonium betulinum	Gerania	woody plants	M	semi shade
Pelargonium capillare	Gerania	herbaceous perennial	L	semi shade
Pelargonium capitatum	Gerania	herbaceous perennial	M	semi shade
Pelargonium chelidonium	Gerania	bulbous	L	semi shade
Pelargonium citronellum **	Gerania	herbaceous perennial	L-H	semi shade to full sun
Pelargonium coronopifolium	Gerania	herbaceous perennial	L	semi shade
Pelargonium crispum *	Gerania	herbaceous perennial	L-M	semi shade to full sun
Pelargonium cucullatum	Gerania	woody plants	M	semi shade
Pelargonium denticulatum *	Gerania	woody plants	M	semi shade
Pelargonium divisifolium	Gerania	herbaceous perennial	M	semi shade
Pelargonium elongatum	Gerania	herbaceous perennial	M	semi shade
Pelargonium fruticosum *	Gerania	herbaceous perennial	L	semi shade
Pelargonium furgisoniae	Gerania	bulbous	L	semi shade
Pelargonium gibbosum	Gerania	bulbous	M	semi shade
Pelargonium glutinosum *	Gerania	herbaceous perennial		semi shade
Pelargonium grandiflorum	Gerania	herbaceous perennial	M	semi shade
Pelargonium graveolens	Gerania	herbaceous perennial	M	semi shade
Pelargonium greytonense	Gerania	woody plants	M	semi shade
Pelargonium heterolobum	Gerania	bulbous	L	semi shade
Pelargonium hispidum	Gerania	woody plants	M	semi shade
Pelargonium incarnatum	Gerania	herbaceous perennial	L	semi shade
Pelargonium inquinans	Gerania	herbaceous perennial	L	semi shade
Pelargonium laevigatum	Gerania	woody plants	L	semi shade
Pelargonium longicaule	Gerania	herbaceous perennial	L	semi shade
Pelargonium longifolium	Gerania	bulbous	L	semi shade
Pelargonium mutans	Gerania	succulent	L	semi shade
Pelargonium myrrhifolium	Gerania	herbaceous perennial	M	semi shade
Pelargonium oblongatum	Gerania	herbaceous perennial	L	full shade
Pelargonium odoratissimum	Gerania	woody plants		semi shade
Pelargonium ovale	Gerania	herbaceous perennial	M	semi shade
Pelargonium panduriforme *	Gerania	herbaceous perennial		semi shade
Pelargonium papilionaceum	Gerania	woody plants	H	semi shade
Pelargonium peltatum	Gerania	climber	M	semi shade
Pelargonium pinnatum	Gerania	bulbous	L	semi shade
Pelargonium praemorsum	Gerania	woody plants	L	semi shade
Pelargonium radens *	Gerania	herbaceous perennial		semi shade
Pelargonium rapaceum	Gerania	bulbous	L	semi shade
Pelargonium scabroide	Gerania	herbaceous perennial	L	semi shade
Pelargonium scabrum	Gerania	herbaceous perennial	M	semi shade
Pelargonium setulosum	Gerania	herbaceous perennial	M	semi shade
Pelargonium sidoides	Gerania	herbaceous perennial	L	semi shade
Pelargonium stipulaceum	Gerania	succulent	L	semi shade
Pelargonium sublignosum	Gerania	woody plants	L	semi shade
Pelargonium tenuicaule	Gerania	herbaceous perennial	L	semi shade
Pelargonium tetragonum	Gerania	succulent	L	semi shade
Pelargonium tomentosum **	Gerania	herbaceous perennial	M	semi shade to full sun
Pelargonium tongaense	Gerania	woody plants	L	semi shade
Pelargonium tricolor	Gerania	herbaceous perennial	L	semi shade
Pelargonium trifidum	Gerania	herbaceous perennial	L	semi shade
Pelargonium triste *	Gerania	bulbous	L-M	semi shade to full sun
Pelargonium vitifolium	Gerania	woody plants	M	semi shade
Pelargonium zonale	Gerania	woody plants	M	semi shade
Penaea cneorum	Penaea	woody plants	H	semi shade
Peperomia blanda *	Pipera	herbaceous perennial	M	full shade
Peperomia retusa *	Pipera	herbaceous perennial	M	semi shade to full shade

Name	Family	Habit	Water	Exposure
Peperomia rotundifolia	Pipera	herbaceous perennial		semi shade
Peperomia tetraphylla *	Pipera	herbaceous perennial	M	semi shade
Peristrophe natalensis	Acantha	herbaceous perennial		semi shade
Petopentia natalensis	Periploca	succulent	L	semi shade
Peucedanum ferulaceum	Apia	herbaceous perennial	M	semi shade
Phaulopsis imbricata	Acantha	herbaceous perennial		full shade
Phaulopsis longifolia	Acantha	herbaceous perennial		full shade
Phoenix reclinata	Areca	palm	L	semi shade
Phygelius capensis	Scrophularia	herbaceous perennial	M	semi shade
Phygelius aequalis	Scrophularia	herbaceous perennial	H	semi shade
Phylica paniculata *	Rhamna	woody plants	M	semi shade
Piper capense	Pipera	herbaceous perennial	M	full shade
Platythyra haeckeliana	Mesembryanthema	succulent		full shade
Plectranthus ambiguus *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus ambionicus	Lamia	herbaceous perennial		semi shade
Plectranthus ciliatus *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus dolichopodus *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus ecklonii *	Lamia	herbaceous perennial		full shade
Plectranthus elegantulus *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus ernstii *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus fruticosus *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus grallatus *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus hadiensis *	Lamia	herbaceous perennial	L	semi shade
Plectranthus hereroensis *	Lamia	herbaceous perennial	M	semi shade
Plectranthus hilliardiae *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus laxiflorus	Lamia	herbaceous perennial		semi shade
Plectranthus madagascariensis *	Lamia	herbaceous perennial	L	semi shade to full shade
Plectranthus mutabilis	Lamia	herbaceous perennial	M	semi shade
Plectranthus neochilus *	Lamia	herbaceous perennial		semi shade
Plectranthus oertendahlii *	Lamia	herbaceous perennial		semi shade
Plectranthus oribiensis	Lamia	herbaceous perennial		semi shade
Plectranthus petiolaris	Lamia	herbaceous perennial	M	semi shade
Plectranthus praetermissus *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus purpuratus	Lamia	herbaceous perennial	M	semi shade
Plectranthus reflexus *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus rehmannii *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus saccatus *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus spicatus	Lamia	herbaceous perennial		semi shade
Plectranthus strigosus *	Lamia	succulent		semi shade to full shade
Plectranthus swynnertonii *	Lamia	herbaceous perennial	M	semi shade to full shade
Plectranthus tetensis	Lamia	succulent	L	semi shade
Plectranthus verticillatus *	Lamia	herbaceous perennial	L	semi shade to full shade
Plectranthus zuluensis *	Lamia	herbaceous perennial	M	semi shade to full shade
Plumbago zeylanica	Plumbagina	woody plants	L	semi shade
Podocarpus henkelii *	Podocarpa	woody plants		semi shade
Podocarpus latifolius *	Podocarpa	woody plants	M	semi shade to full shade
Podranea ricasoliana	Bignonia	climber	L	semi shade
Polyarrhena imbricata	Astera	herbaceous perennial	M	full shade
Polygala myrtifolia	Polygala	woody plants	L-M	semi shade to full sun
Polyspaeria lanceolata	Rubia	woody plants		semi shade
Polystachya modesta	Orchida	orchid		semi shade
Polystachya ottoniana	Orchida	orchid	M	semi shade
Polystachya pubescens	Orchida	orchid	M	semi shade
Polystachya sandersonii	Orchida	orchid		semi shade
Polystachya tessellata	Orchida	orchid		semi shade
Polystachya transvaalensis	Orchida	orchid		semi shade
Portulacaria afra	Portulaca	succulent	L	semi shade
Prosphytochloa prehensilis	Poa	perennial grass		semi shade to full shade
Protasparagus aethiopicus	Asparaga	herbaceous perennial	L	semi shade
Protasparagus densiflorus **	Asparaga	herbaceous perennial	M	semi shade to full shade
Protasparagus falcatus *	Asparaga	herbaceous perennial	M	semi shade
Protasparagus laricinus	Asparaga	herbaceous perennial	L	semi shade
Protasparagus macowanii	Asparaga	herbaceous perennial	M	semi shade
Protasparagus multiflorus	Asparaga	herbaceous perennial	M	semi shade
Protasparagus oxyacanthus	Asparaga	herbaceous perennial	L	semi shade
Protasparagus plumosus *	Asparaga	herbaceous perennial	M	semi shade
Protasparagus setaceus **	Asparaga	herbaceous perennial	M	semi shade to full shade
Protasparagus virgatus *	Asparaga	herbaceous perennial		semi shade to full shade
Protea angustata	Protea	woody plants	M	semi shade

Name	Family	Habit	Water	Exposure
Pseuderanthemum subviscosum	Acantha	herbaceous perennial		full shade
Pseudobaeckea africana	Brunia	woody plants	H	semi shade
Pseudobaeckea cordata	Brunia	woody plants	H	semi shade to full shade
Psoralea asarina	Faba	herbaceous perennial	M	semi shade
Psoralea cordata	Faba	herbaceous perennial	M	semi shade
Psuedoscolopia polyantha	Flacourtia	woody plants	M	semi shade
Psychotria capensis ***	Rubia	woody plants	M-H	full shade to full sun
Psychotria zombamontana	Rubia	woody plants		semi shade
Pterocelastrus rostratus	Celastra	woody plants	M	semi shade
Pterygodium alatum	Orchida	orchid	M	semi shade
Putterlickia retrospinosa	Celastra	climber	M	full shade
Raspalia virgata	Brunia	woody plants	M	semi shade
Rawsonia lucida *	Flacourtia	woody plants		semi shade to full shade
Restio quadratus	Restiona	restio	M	semi shade
Rhinacanthus gracilis	Acantha	herbaceous perennial		semi shade
Rhipsalis baccifera	Cacta	succulent	L	semi shade to full shade
Rhoicissus digitata *	Vita	climber		semi shade
Rhoicissus rhomboidea *	Vita	climber		semi shade to full shade
Rhoicissus tomentosa *	Vita	woody plants		semi shade to full shade
Rhoicissus tridentata	Vita	woody plants		semi shade
Rhus nebulosa	Anacardia	woody plants	L	semi shade
Rhus transvaalensis	Anacardia	woody plants		semi shade
Rhynchosia caribaea	Faba	herbaceous perennial		semi shade to full sun
Rinorea angustifolia	Viola	woody plants		semi shade
Rinorea ilicifolia	Viola	woody plants		semi shade
Riocreuxia picta	Asclepiada	climber	M	semi shade
Rothmannia capensis	Rubia	woody plants		semi shade
Rothmannia fisheri	Rubia	woody plants		semi shade
Rothmannia globosa *	Rubia	woody plants		semi shade to full sun
Ruellia otaviensis	Acantha	herbaceous perennial		semi shade
Ruellia patula	Acantha	herbaceous perennial		semi shade
Ruschia rigidicaulis	Mesembryanthema	succulent	L	semi shade
Salacia gerrardii	Celastra	woody plants	M	full shade
Salpinctium hirsutum	Acantha	herbaceous perennial		semi shade
Salvia africana-lutea	Lamia	woody plants		semi shade
Salvia chamelaeagnea	Lamia	herbaceous perennial	L	semi shade
Salvia runcinata	Lamia	herbaceous perennial	M	semi shade
Sansevieria hyacinthoides *	Dracaena	succulent		semi shade to full shade
Sansevieria pearsonii *	Dracaena	succulent		semi shade to full shade
Sansevieria trifasciata	Dracaena	succulent		semi shade
Satyrium bracteatum	Orchida	orchid	M	semi shade
Satyrium erectum	Orchida	orchid	L	semi shade
Scadoxus membranaceus *	Amaryllida	bulbous	M	semi shade to full shade
Scadoxus multiflorus **	Amaryllida	bulbous	H	semi shade to full shade
Scadoxus puniceus *	Amaryllida	bulbous		semi shade to full shade
Sceffiera umbellifera	Aralia	woody plants	M	semi shade
Schrebera alata	Olea	woody plants		semi shade
Scilla natalensis	Hyacintha	bulbous	L	semi shade
Sclerochiton harveyanus **	Acantha	herbaceous perennial	H	semi shade to full sun
Sclerochiton odoratissimus	Acantha	herbaceous perennial		full shade
Sclerochiton triacanthus	Acantha	herbaceous perennial	L	semi shade
Scoenoxiphium lanceum	Poa	perennial grass	M	semi shade
Scolopia mundii	Flacourtia	woody plants	M	semi shade
Scolopia zeyheri	Flacourtia	woody plants	M	full shade
Scutia myrtina	Rhamna	woody plants	L	semi shade
Seemannaralia gerrardii	Aralia	woody plants		full shade
Selago glutinosa	Selagina	woody plants	M	semi shade
Senecio acaulis	Astera	succulent		semi shade
Senecio angulatus	Astera	climber	M	semi shade
Senecio barbertonicus	Astera	succulent	M	semi shade
Senecio bryoniifolius	Astera	succulent	M	semi shade
Senecio bulbinifolius	Astera	succulent	L	semi shade
Senecio elegans **	Astera	annual	M	semi shade to full sun
Senecio glastifolius *	Astera	herbaceous perennial	M	semi shade to full sun
Senecio hallianus	Astera	succulent	L	semi shade
Senecio macroglossoides	Astera	herbaceous perennial	L	semi shade
Senecio macroglossus	Astera	climber	L	semi shade
Senecio medley-woodii	Astera	climber	M	full shade
Senecio muirii	Astera	succulent	L	semi shade

Name	Family	Habit	Water	Exposure
Senecio oxyodontus	Astera	succulent		semi shade
Senecio radicans *	Astera	succulent	L	semi shade to full shade
Senecio rowleyanus *	Astera	succulent		semi shade to full shade
Senecio tamoides	Astera	climber	L	semi shade
Serruria brownii	Protea	woody plants	M	semi shade
Serruria collina	Protea	woody plants	M	semi shade
Setaria lindenbergiana	Poa	perennial grass		semi shade to full sun
Setaria megaphylla ***	Poa	perennial grass		semi shade to full shade
Setaria sagittifolia	Poa	annual grass		semi shade to full sun
Setaria ustilata	Poa	annual grass		semi shade to full sun
Setaria verticillata	Poa	annual grass		semi shade to full sun
Shizostylus coccinea	Irida	bulbous		semi shade
Sida alba	Malva	herbaceous perennial		semi shade to full sun
Sida dregei	Malva	herbaceous perennial		semi shade
Sida ternata	Malva	woody plants		semi shade
Silene bellidioides	Caryophylla	herbaceous perennial	M	semi shade
Silene undulata	Caryophylla	annual	M	semi shade
Siphonochilus aethiopicus	Zingibera	bulbous	L	semi shade
Siphonoglossa leptantha	Acantha	herbaceous perennial		full shade
Siphonoglossa nkandlaensis	Acantha	herbaceous perennial		full shade
Smelophyllum capense	Sapinda	woody plants	L	semi shade
Solenostemon latifolius	Lamia	herbaceous perennial	M	semi shade
Sparrmannia africana	Tilia	woody plants		semi shade
Staavia radiata	Brunia	woody plants	M	semi shade
Stangeria eriopus *	Stangeria	herbaceous perennial	M	semi shade to full shade
Stapelia gigantea	Asclepiada	succulent	L	full shade to full sun
Stapelia glanduliflora *	Asclepiada	succulent		semi shade
Stapelia leendertziae	Asclepiada	succulent		semi shade
Stapelia pillansii *	Asclepiada	succulent		semi shade
Stapelia similis *	Asclepiada	succulent		semi shade
Steganotaenia araliacea	Apia	woody plants		semi shade
Stenoglottis fimbriata *	Orchida	orchid		semi shade to full shade
Stenoglottis longifolia **	Orchida	orchid	M	semi shade to full shade
Stenotaphrum dimidiatum	Poa	perennial grass		semi shade to full sun
Stenotaphrum secundatum	Poa	perennial grass		semi shade to full sun
Sterculia alexandri	Sterculia	woody plants	L	semi shade
Stilbe vestita	Stilba	woody plants	M	semi shade
Strelitzia caudata	Strelitzia	woody plants	H	semi shade
Strelitzia nicolai *	Strelitzia	woody plants		semi shade to full shade
Strelitzia reginae	Strelitzia	bulbous		full shade to full sun
Streptocarpus caeruleus	Gesneria	herbaceous perennial	M	semi shade
Streptocarpus candidus *	Gesneria	herbaceous perennial	M	semi shade to full shade
Streptocarpus cyaneus *	Gesneria	herbaceous perennial	M	full shade
Streptocarpus daviesii	Gesneria	herbaceous perennial	M	full shade
Streptocarpus dunnii	Gesneria	herbaceous perennial	M	full shade
Streptocarpus eylesii	Gesneria	herbaceous perennial	M	full shade
Streptocarpus fanniniae	Gesneria	herbaceous perennial	M	semi shade
Streptocarpus fasciatus	Gesneria	herbaceous perennial	M	full shade
Streptocarpus gardenii	Gesneria	herbaceous perennial	M	semi shade to full shade
Streptocarpus grandis	Gesneria	herbaceous perennial	M	full shade
Streptocarpus haygarthii	Gesneria	herbaceous perennial	M	full shade
Streptocarpus johannis *	Gesneria	herbaceous perennial	M	semi shade to full shade
Streptocarpus kentaniensis	Gesneria	herbaceous perennial	M	full shade
Streptocarpus meyeri	Gesneria	herbaceous perennial	M	semi shade to full shade
Streptocarpus modestus	Gesneria	herbaceous perennial	M	full shade
Streptocarpus parviflorus	Gesneria	herbaceous perennial	M	full shade
Streptocarpus polyanthus	Gesneria	herbaceous perennial	M	full shade
Streptocarpus porphyrostachys *	Gesneria	herbaceous perennial	M	semi shade to full shade
Streptocarpus primulifolius *	Gesneria	herbaceous perennial	M	semi shade to full shade
Streptocarpus prolixus	Gesneria	herbaceous perennial	M	full shade
Streptocarpus rexii *	Gesneria	herbaceous perennial		semi shade to full shade
Streptocarpus saxorum *	Gesneria	herbaceous perennial		full shade
Streptocarpus thompsonii *	Gesneria	herbaceous perennial		semi shade
Streptocarpus trabeculatus	Gesneria	herbaceous perennial	M	full shade
Streptocarpus vandeleurii	Gesneria	herbaceous perennial	M	full shade
Streptocarpus wendlandii *	Gesneria	herbaceous perennial	M	semi shade to full shade
Strophantus speciosus	Apocyna	climber		semi shade
Strychnos decussata	Logania	woody plants	M	semi shade
Strychnos usambarensis	Logania	woody plants		semi shade

Name	Family	Habit	Water	Exposure
Suregada africana	Euphorbia	woody plants		semi shade
Suregada zanzibariensis	Euphorbia	woody plants		semi shade
Sutera caerulea	Scrophularia	woody plants	M	semi shade
Synadenium cupulare	Euphorbia	succulent	L	semi shade
Syzygium guineense	Myrta	woody plants		semi shade
Tabernaemontana elegans	Apocyna	woody plants		semi shade
Tabernaemontana ventricosa	Apocyna	woody plants	M-H	semi shade to full sun
Tarenna barbertonensis	Rubia	woody plants		semi shade
Tarenna pavettoides	Rubia	woody plants		semi shade to full shade
Teclea gerrarardii	Ruta	woody plants		semi shade
Teclea natalensis	Ruta	woody plants		semi shade
Teedia lucida	Scrophularia	woody plants	M	semi shade
Tetragonia fruticosa	Aizoa	succulent	L	semi shade
Teucrium trifidum	Lamia	herbaceous perennial		semi shade to full shade
Thaminophyllum latifolium	Astera	herbaceous perennial	H	semi shade
Thamnea diosmoides	Brunia	woody plants	L	semi shade
Thorncroftia succulenta	Lamia	herbaceous perennial	M	semi shade
Thunbergia natalensis	Acantha	herbaceous perennial		semi shade
Thunbergia neglecta *	Acantha	herbaceous perennial		semi shade
Thunbergia purpurata	Acantha	herbaceous perennial		semi shade
Tinospora caffra	Menisperma	succulent		semi shade
Tinospora fragosa	Menisperma	succulent	L	semi shade
Toddaliopsis bremekampii	Ruta	woody plants		semi shade
Trachyandra ciliata	Asphodela	succulent	L	semi shade
Trema orientalis	Ulma	woody plants	M	semi shade
Tricalysia africana	Rubia	woody plants	M	semi shade
Tricalysia lanceolata	Rubia	woody plants		semi shade
Tricalysia sonderiana	Rubia	woody plants		semi shade
Trichilia dregeana *	Melia	woody plants		semi shade to full shade
Trichilia emetica *	Melia	woody plants		semi shade to full shade
Trichocladus crinitus *	Hamamelida	woody plants		semi shade
Trichocladus ellipticus	Hamamelida	woody plants		semi shade
Trichopteryx dregeana	Poa	perennial grass		semi shade to full sun
Tridactyle bicaudata	Orchida	orchid	M	semi shade
Tridactyle gentilii	Orchida	orchid		semi shade
Tridactyle tricuspis	Orchida	orchid	M	semi shade
Tridactyle tridentata	Orchida	orchid	M	semi shade
Tridentea choanantha	Asclepiada	succulent	L	semi shade
Trilepisium madagascariense	Mora	woody plants	M	semi shade
Tritonia disticha	Irida	bulbous	M	semi shade
Tritonia securigera	Irida	bulbous	L	semi shade
Tulbaghia simmleri *	Allia	bulbous		semi shade
Tulbaghia violacea	Allia	bulbous	L	semi shade
Turraea obtusifolia *	Meliaceae	woody plants	M	semi shade to full sun
Tylecodon decipiens	Crassula	succulent	L	semi shade
Tylecodon ellaphieae	Crassula	succulent	L	semi shade
Tylecodon hirtifolius	Crassula	succulent	L	semi shade
Tylecodon leucothrix	Crassula	succulent	L	semi shade
Tylecodon paniculatus	Crassula	succulent	M	semi shade
Tylecodon pygmaeus	Crassula	succulent	L	semi shade
Tylecodon racemosus	Crassula	succulent	L	semi shade
Tylecodon reticulatus	Crassula	succulent	L	semi shade
Tylecodon rubrovenosus	Crassula	succulent	L	semi shade
Tylecodon similis	Crassula	succulent	L	semi shade
Tylecodon singularis	Crassula	succulent	L	semi shade
Tylecodon striatus	Crassula	succulent	L	semi shade
Tylecodon torulosus	Crassula	succulent	L	semi shade
Tylecodon ventricosus	Crassula	succulent	L	semi shade
Tylecodon viridiflorus	Crassula	succulent		semi shade
Tylophora anomala	Asclepiada	climber	M	semi shade
Uvaria caffra	Anno	climber		semi shade
Uvaria lucida	Anno	climber		semi shade
Veltheimia bracteata **	Hyacyntha	bulbous	L-M	semi shade to full shade
Veltheimia capensis	Hyacyntha	bulbous	L	semi shade
Vepris lanceolata	Ruta	woody plants		semi shade
Vepris reflexa *	Ruta	woody plants		semi shade
Veronica anagallis-aquatica	Scrophularia	herbaceous perennial		semi shade
Viola decumbens	Viola	herbaceous perennial	M	semi shade
Vitellariopsis marginata	Sapota	woody plants	L	semi shade

Name	Family	Habit	Water	Exposure
Xylotheca kraussiana *	Flacourtia	woody plants		semi shade
Zamioculcas zamiifolia *	Ara	bulbous		semi shade to full shade
Zantedeschia aethiopica **	Ara	bulbous		semi shade
Zantedeschia albomaculata **	Ara	bulbous		semi shade