SHADE-TOLERANT FLOWERING PLANTS: ADAPTATIONS AND HORTI-CULTURAL IMPLICATIONS

Lorraine Middleton
Manie van der Schijff Botanical Garden
Department of Botany
University of Pretoria
Pretoria 0002
South Africa
rswart@postino.up.ac.za

Abstract

It is quite difficult to select suitable ornamental plants for shady and low-light environments, but understanding the adaptations of plants that grow naturally in such conditions can lead to greater chances of success in horticulture.

Shade-plants essentially follow strategies of optimum use of available energy and of conservation of energy. Adaptations to achieve these strategic goals include thinner leaves with a relatively higher chlorophyll content per unit leaf volume; lens-shaped epidermal cells that focus incoming light into and within the mesophyll; a red abaxial cell layer that reflects outgoing light back into the mesophyll; the greater allocation of available energy to defence-mechanisms against herbivory (as opposed to replacement of damaged tissue)—including camouflaging strategies such as mottled leaves; a distichous phyllotaxis; and flowers and fruit that are inconspicuous in size and colour.

Many of the adaptations of shade-plants have a pronounced effect on their ornamental value, and can therefore also determine their differing possible horticultural uses.

Knowledge of physiological adaptations and growth requirements is important in the successful cultivation and sustained utilization of ornamental shade-plants.

1. Introduction

With their ability to physically, aesthetically, economically and psychologically enhance and enliven our surroundings, ornamental plants form an important part of our everyday lives. They add generously to our enjoyment of life and environment, and also to our general well being. There is, however, a price attached to these plants. Not only do they have an initial procurement and planting cost; they also must be cared for and maintained for the duration of their lives. While some plants grow easily and seem to need little or no care, others require a small fortune and much time and effort to plant and maintain.

As public and private gardens become more common and expensive to maintain, the people responsible for such plantings are becoming more concerned about the proper selection and care of landscape and plants (Harris, 1992). There is, as a consequence, a growing need for better information on the ecology and physiology—i.e. the environmental requirements and adaptations to various environmental conditions—of ornamental plants.

In nature, plants make use of a variety of specialized adaptations to survive and even flourish under stressful conditions such as aridity, extremely high or low temperatures, nutrient limitations and shade (low light-intensity). If these adaptations are understood, it may be possible to eliminate—or at least minimize—some of the problems associated with the care and maintenance of ornamental plants.

2. Heliophytes, sciophytes and plasticity

Plants that grow best in full sunlight are called heliophytes; while sciophytes are those that grow best at lower light intensities. Obligate and facultative plants occur in both groups, with the facultative plants showing much variation in their degree of plasticity. True shade plants are obligate sciophytes and cannot tolerate full sunlight at all (Daubenmire, 1974).

In terrestrial habitats, other factors, especially relative humidity and temperature vary concomitantly with light intensity; and it is very often difficult to evaluate light effects in isolation. The unexpected large percentage (22 %) of succulents—plants that are usually seen as sun-loving—in the southern African shade-tolerant flora can, for example, be explained by the opportunistic utilization of the slightly higher available moisture and slightly lower temperature in niche habitats, rather than by the shade *per se* (Middleton, 1998).

Stress-tolerance and stress-avoidance are the major strategies employed by living organisms to cope with environmental variation and extremities. Species that are stress-tolerant occupy habitats of low productivity and limited resources. This holds true for shade plants. Survival in a shaded understorey demands maximization of light capture for photosynthesis with concurrent minimization of losses of energy and carbon.

Plasticity in shade tolerance is expressed primarily during vegetative growth. The leaves and other organs of shade-growing species are long-lived and exhibit less plasticity in size and shape than do sun-growing species. The degree of plasticity shown by any plant species is regarded as being under genetic control and is an important characteristic determining the potential for survival of a plant under shaded conditions (Dengler, 1994). Plastic responses, which essentially depend on changes in gene expression and protein function, are continuously implemented in the plant, and serve a number of functions—including the maintenance of metabolic homeostasis and foraging for resources and defence. In most cases, plastic responses involve metabolic as well as morphological and developmental components (Aphalo *et al.,* 1999).

In assessing the value of the light factor, it must not be overlooked that photosynthesis is not the only function with a light-requirement. Phototropism, photoperiodism, photomorphogenesis (stem extension and apical dominance), seed germination, stomatal aperture, chloroplast orientation, and nastic (sleep) movements are all physiological manifestations of environmental light perception mechanisms (Morgan and Smith, 1981).

3. The changing light environment

A remarkable feature of the photosynthetic apparatus is its adaptability to a wide range of light inputs. The time scale over which the complicated photosynthetic reaction results is of paramount importance.

3.1. Sunflecks

An important character of understorey light environments is the degree of spatial and temporal variability caused by sunflecks. Although present for only a small fraction of the day, these sunflecks can contribute more than two-thirds of the daily photosynthetically active radiation (Pearcy, 1988). Canopies of different species can differ markedly in cover density and architecture—affecting the sunfleck density and distribution.

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 variations at a much higher frequency. Cloud movement can cause additional variation. The usual diurnal pattern of light in the understorey subsequently comprises of periods with relative frequent sunflecks separated by periods with few or no sunflecks.

Records show that 70% of the sunflecks occur within one minute of the preceding sunfleck while only 5% are preceded by low light periods of an hour or more (Pearcy, 1990).

Several factors are important in determining the capacity of a leaf to utilise sunflecks. Following long low-light periods, the induction state of the photosynthetic apparatus is limiting. During induction, 20–60 min may be required before maximum assimilation rates are reached. 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 carbon dioxide fixation resulting from utilization of metabolite pools built up during the sunfleck can significantly enhance carbon gain during short (5–20 s) sunflecks.

The decline in assimilation occurring after a sunfleck will be very slow, and most of the carbon dioxide 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 measurement of oxygen and carbon dioxide exchange (Pearcy, 1990). 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 in the low light between sunflecks. The occurrence of a sunfleck thus effectively acts to prime the leaf so that it is better able to utilize subsequent sunflecks (Pearcy 1990).

3.2. Acclimatization

Changes in the light environment experienced by forest understorey plants during their lifetime may range from the fleeting changes caused by sunflecks to the more sustained changes that occur when gaps are formed or when canopies develop.

Because acclimatization to a changed light environment involves changes in enzymes, pigment counts, as well as in leaf anatomy and resource allocation (since new leaves must be produced in the new environment); the time scale over which these processes take place is important.

Acclimatization changes in the concentration of enzymes or in leaf anatomy are a redeployment of internal resources (primarily nitrogen and carbon) in a way that enhances the resistance to stress in the new environment. This redeployment appears to require at the minimum a few days to take place, and may, in some cases, need up to several weeks. To be beneficial, redeployment should not occur in response to regular, short term changes such as the day/night light fluctuations; but only in response to more sustained changes lasting for longer periods of time (Pearcy and Sims, 1994).

High photosynthetic plasticity in certain lianas of tropical forest canopies is reflected in their almost immediate ability to respond to significant changes in the light environment. Rapid responses to light changes include functional adjustment of already expanded foliage and increases in leaf production in places with a large potential for carbon gain (Avalos and Mulkey, 1999).

The sun and shade sides of plants can be considered as acclimatized for the specific conditions experienced at either side. Differences in morphology, anatomy and physiology of "sun" and "shade" leaves from exposed and shaded portions of the canopy of the same individual have been observed and documented over many years (Salisbury and Ross, 1992).

4. Anatomical adaptations

Generally, "sun leaves" are relatively thick and have a well-developed palisade layer with a high proportion of columnar cells. "Shade leaves" on the other hand, are thinner, have a more poorly defined palisade layer, better developed sponge mesophyll, larger intercellular spaces, and a higher chlorophyll content per unit leaf volume than

"sun leaves".

A common feature of plants that live in deep shade is the dark green colour of the foliage. This is because of the increase of chlorophyll *b,* which results in a lower chlorophyll *a* to chlorophyll *b* ratio. As chlorophyll 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).

4.1. Lens-shaped epidermal cells

Optical phenomena occur at a fine microscopic scale within the leaf. Individual epidermal cells can act as lenses that focus light into and within the mesophyll. This is a relatively widespread occurrence, but is especially prevalent among understorey plants. Leaves with this characteristic often have a glossy appearance.

Maximum epidermal focal intensification of up to 25 times incident light has been calculated in leaves irradiated with collimated light and intensification of up to 10 times has also been measured in replicas of epidermal cells. Focusing is either greatly reduced or eliminated when leaves are irradiated with diffuse light. There is some evidence that elimination of epidermal focusing decreases light harvesting (Vogelmann and Martin, 1993).

4.2. Red abaxial layer of sciophyte leaves

Not only is the light intensity low on a forest floor, it is also poor in photosynthetically active wavelengths. Those available are mainly of longer wavelength, and lie in the red region of the optical spectrum. It is therefore to be expected that plants growing in this habitat will show adaptations enhancing the utilization of red light.

Long wavelength pigments (Photosystem I chlorophyll red forms) are extremely important in light harvesting by leaves, and may be responsible for up to 40 % of the total photon capture in "shadelight" as opposed to the only 4–5 % of light absorption in a normal "daylight" environment (Rivadossi *et al.*, 1999).

Some species grow in habitats so deeply shaded that sunflecks are of relatively less importance than what would have been the case if they were growing in slightly more open habitats. It should also be remembered that sunflecks are not entirely random phenomena, but are repetitive to a degree. There will consequently be a discreet zone of greater net light intensity in some zones relative to others that do not receive these repetitive "fleck-tracks". In habitats where light intensity is very close to the energetic limit for plant growth there will be effects caused by these repetitive "fleck-tracks".

Species that are mainly restricted to deeply shaded habitats often show permanent abaxial anthocyanin colouration (Lee *et al.,* 1979). The location of the pigment and the known optical properties of cyanins indicate that the only possible influence of the cyanic layer would be to enhance reflectance. Light that would otherwise pass straight through the lower surface of the leaf could instead be reflected back up through the photosynthetic tissue—giving the plant a second chance to utilize the light. The one cell layer thick cyanin layer is located immediately beneath the chlorenchyma; and above the lower epidermis that contains no anthocyanin. This cyanic layer functions like a mirror and reflects substantially more light between 600 nm and 750 nm than do green lower surfaces.

Colour polymorphism is seen in many species where individuals with green leaves as well as individuals with red leaves are common. Colour polymorphism could therefore be of adaptive value in itself.

In some species the juvenile leaves may have a red lower surface, while adult leaves do not. It is fairly common in species that emerge out of the understorey into higher strata—especially in plants that become tall shrubs, trees and high-climbing lianas. The red colour can be considered as an adaptation that is functional only during the period in which the plant occupies a deep-shade habitat—i.e. during the juvenile phase (Lee *et*

al., 1979).

5. Morphological, architectural and reproductive adaptations

5.1. Leaf morphology

The dominant factor controlling leaf size of plants in different habitats is not considered to be the capture of light, but rather the optimizing of efficiency of water-usage. There is a great deal of variability in the leaf size of the herbaceous vegetation of the forest floor (Givnish, 1987).

Asymmetric leaf bases and anisophylly (unequal leaves at each node in species with opposite leaves) are more common in forest understorey and other shady habitats than in sunny environments. Leaves with long acuminate drip-tips are common in wet rain forests and cloud forests, again particularly among understorey species. Leaves with cordate bases are common among vines, forest herbs and aquatic herbs. Sagittate, hastate and auriculate bases are also more common in shade than sun plants (Givnish, 1987).

5.2. Colour patterns and indumentum

Angiosperms display an extraordinary range in the kind of chemical, physical and biological defences they deploy against herbivores. As the effective cost of leaf tissue lost to herbivory is larger in slow growing shade plants than in sun plants, shade-adapted species must allocate more to defence than sun-adapted species. The opposing strategy in sun plants results from the greater opportunity-cost associated with a given amount of defence in fast growing sun plants.

Assessing the cost associated with visual defences such as mimicry, aposematic- or cryptic colouration can be difficult. Mottled leaves are less heavily attacked than unmottled leaves where they occur at similar frequencies. Mottled leaves are much more common in herbs of shady forest understorey than in any other growth form, and are essentially absent in trees, shrubs, herbs or vines of sunny sites (Givnish, 1988).

It is suggested that sunny conditions should favour carbon-based defence compounds (e.g. tannins and phenols), whereas shady conditions should instead favour nitrogen-based defences (e.g. alkaloids). This is because fixed carbon is likely to be in less abundant supply under shaded conditions (Givnish, 1988).

The reflective properties of the leaf are extremely important to the absorption of light. Pubescence (hairiness) can increase the reflectance of light from the leaf surface, thereby decreasing the absorption of the light. A glabrous (smooth) leaf with a chlorophyll content equal to that of a pubescent leaf may absorb as much as up to 54 % more light than a hairy leaf (Ehleringer and Björkman, 1978). Shade plants seldom show pubescence.

5.3. Architecture

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 fruit in the biomass borne by the stem.

Herbs predominate in forest understorey. The lower light requirements of shorter plants (e.g. 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 shorter less expensive stems in herbs predominating in forest understorey. This has important implications not only for trends in the relation of forest strata to each other, but also for overall forest diversity (Givnish, 1995).

Leaves tend to be borne in a spiral phyllotaxis in erect twigs in sunny

environments and in a distichous (two vertical rows on opposite sides of an axis) phyllotaxis on horizontal twigs in the shade. This last arrangement minimizes self-shading and structural costs (Givnish, 1986).

5.4. 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).

Energetically efficient means of reproduction have evolved. Flowers and fruits are, for example, very expensive in terms of energy, and are therefore often inconspicuous in colour and size in shade-adapted species. In the southern African flora, however, there are shade-plants in the geophyte-group that have quite spectacular flowers—14 % of the S.African shade-flora fall in this group.

Woody plants—with their energy-expensive lignified stems—will (in shaded habitats) often have white, cream or greenish flowers (that are less expensive in terms of energy than large, brightly coloured flowers). Herbaceous plants, on the other hand, will more often have flowers in the pink, violet, mauve, and purple colour groups. These colours are the result of the pigment anthocyanin, which is dissolved in the cell sap. This pigment needs acidic plant cell sap; a need which can be provided for by an acidic soil rich in leaf compost such as that of the forest floor. Interestingly, this corresponds with the many herbs showing the adaptation of an abaxial anthocyanin layer in leaves; and these flower colours are often combined with red abaxial leaves (Middleton, 1998).

Plants that grow on the forest floor are divided into three groups as far as their life cycles are concerned. The competitors are usually perennial plants with a well-developed capacity for resource capturing that have high levels of input of resources into new organs. The stress-tolerators are perennials that use captured resources conservatively and have the ability to survive for long periods. Lastly, the ruderals are plants with high growth rates and short life spans that are often capable of prolonged seed dormancy and of exploiting irregular occurrences in suitably disturbed habitats (Crawford, 1989).

6. Concluding remarks

The explanation of differences between successful heliophytes and successful sciophytes is complex. Factors such as humidity, temperature, and minerals can vary greatly along with light intensity, and it is therefore difficult to evaluate light effects in isolation. Adaptation to the irradiance level at leaf-level alone does not explain shade-plant behaviour satisfactorily. A holistic perspective is therefore important.

Acclimatization is a well-known phenomenon. Taking cuttings from the shaded side of a plant could be beneficial for propagation success for shade adapted plants. Sunfleck utilization is a specialized capacity, and simulations for horticultural purposes might yield interesting results.

A slow metabolism means that shade plants are slow growers. Considerable more time, space and effort than for sun plants are needed to cultivate them. Shade plants spend a great share of their energy budget on perennation and vegetative parts. An annual growth habit has not been observed in true shade plants.

The tendency for shade plants is to have a herbaceous perennial growth habit, with the second largest group being woody plants. It must be remembered that young forest trees are obligate sciophytes for the first part of their lives. This substantiates the idea to use these seedlings as indoor container plants.

Small and few flowers and fruit are a negative as far as ornamental value is concerned, but are generously made up for by the attractive foliage. Many of the anatomical and morphological adaptations of shade plants are visually attractive to the human eye, and greatly increase the ornamental value of these plants. Glossy leaves, dark green leaves, red undersurfaces, a variation of camouflage colouration patterns, and leaf

shape all add to the ornamental value.

The perennial evergreen habit means that no seasonal variation can be created in a shade garden by using annuals or making use of autumn leaf colour. However once established, maintenance is low, and pleasure, enduring.

Purchasing a well-adapted shade plant of reasonable size should best be seen as a long-term investment. Marketing strategies for these plants must prepare a consumer for a more expensive plant.

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