

THE BIOLOGY OF *Vines*

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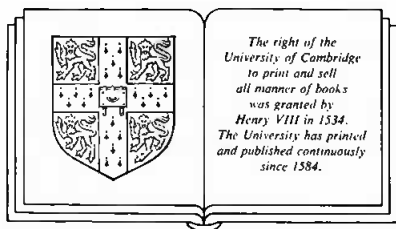
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Heteroblastic development in vines

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Introduction

All plants pass through a series of developmental changes from seedling to reproductive age. In many plants the shifts in development are subtle, involving internode distance or small changes in leaf size and shape. In others the changes are profound, so much so that early and late stages have been identified as separate species. Goebel (1900) recognized these differences in the degree of developmental change, designating the former as **homoblastic** and the latter as **heteroblastic**. Since Goebel's treatment, the concept of heteroblastic development has been extended to species in which the juvenile to adult transition is more gradual, which includes the majority of plants (Allsopp, 1965), and the term has been applied to developmental changes in floral form in the reproductive phase (Lord, 1979).

The following traits can change during heteroblastic development: (i) leaf size and shape; (ii) leaf anatomy; (iii) phyllotaxis; (iv) internode length; (v) stem thickness; (vi) shoot apex structure and zonation; (vii) tropic response; (viii) regenerative capacity; (ix) physiology; (x) reproductive status (Goebel, 1900; Troll, 1937, 1939; Allsopp, 1965, 1967; Doorenbos, 1965; Richards, 1983). The change from juvenile to adult character states can occur at different times for each of these characters, e.g. changes in leaf shape can occur before changes in reproductive status. This temporal variability indicates that the concept of heteroblasty probably includes a number of indirectly related developmental changes (Allsopp, 1965; Borchert, 1976).

The complexity of the interrelationships of heteroblastic characters can be seen when considering the relationship of heteroblastic development to apical meristem size. Apical meristem size commonly increases during plant ontogeny. Heteroblastic changes, such as an increase in leaf size, have thus been shown to be accompanied by an increase in apical meristem size (Crotty,

1955; Franck, 1976; Kaplan, 1980; Mueller, 1982a). This increase in apical meristem size is also found in lateral branch reiterations, which often resemble heteroblastic sequences (Kaplan, 1973). Changes in leaf *shape* during heteroblastic development, however, are not necessarily a direct result of increased leaf size (Hammond, 1941; Kaplan, 1980). Thus, the changes in leaf morphology associated with heteroblastic development cannot be attributed solely to increases in meristem size, although this increase may contribute to or allow such changes.

Although heteroblastic development is considered to be under intrinsic control, environmental factors can affect the course of the developmental changes. To Goebel (1900) the differences between the juvenile (non-reproductive) and adult (reproductive) stages showed that **'the adaptation of the juvenile form to external relationships is different from that of the adult form . . .'** Emergent aquatics, some xerophytes, and vines have some of the most extreme heteroblastic changes in the plant kingdom. Emergent aquatics and vines also show extensive environmentally induced variation in form (plasticity) that can be superimposed on heteroblastic development. The term heterophylly is commonly used to describe the marked variation in leaf form seen in aquatics and vines. Although controls on environmental plasticity have been investigated experimentally in aquatics (e.g. Bodkin, Spence & Weeks, 1980; Deschamps & Cooke, 1983; Richards & Lee, 1986; Goliber & Feldman, 1990), such data are non-existent for vines. In addition, the relationship of heterophylly to heteroblastic development has not been well defined for either of these types of plants.

The problems of understanding the role of intrinsic vs. extrinsic (i.e. environmental) controls on heteroblastic transitions are especially apparent in the literature on vine development. Juvenile vines appear adapted to the extreme shade conditions to which the plants are exposed in nature, but research defining the microenvironment in which vines develop is lacking, as are experimental data on effects of different environmental parameters on heteroblastic development and heterophylly in vines. The purpose of this chapter is to describe heteroblastic development in a variety of vines, to present a model for vine development, and to suggest approaches to research on the adaptive significance and environmental control of vine heteroblasty.

Heteroblasty in vines: examples

Most vines exhibit marked changes in development from juvenile to adult stages – they are heteroblastic in Goebel's original sense of the term. The vine growth habit allows plants to begin life in the profound shade under vegetation, then ascend to more direct exposure to sunlight.

The challenge that a vine faces during development is to survive in a



Figure 8.1. Juvenile and adult stages of *Hedera helix*. Drawing from Sinott (1960).

particular microenvironment and to accumulate enough resources in that environment to allow directed growth into a new microenvironment. In order to understand the types of variations seen in heteroblastic development, we describe below the developmental ecology of some of the best studied or most remarkable vine taxa.

Temperate dicotyledons

The English ivy (*Hedera helix* L., Araliaceae) is a woody vine native to European forests and widely introduced into temperate areas of the world. In its juvenile stage the vine develops palmately lobed leaves, an alternate phyllotaxis, pubescent stems, and a plageotropic, climbing growth habit (Figure 8.1). The climbing stems are anchored by adventitious roots. The adult form, in addition to the development of flowers, produces ovate leaves spirally arranged on orthotropically growing branches (Figure 8.1; Wareing & Frydman, 1976). These branches extend away from the juvenile form's support and do not produce roots. The juvenile stage is associated with high endogenous gibberellin levels, and the transition to the adult stage may result from reduced gibberellic acid (GA) production in the absence of roots. Rogler & Hackett (1975) showed that applications of GA₃ caused a reversion of the mature phase to a juvenile-like plant.

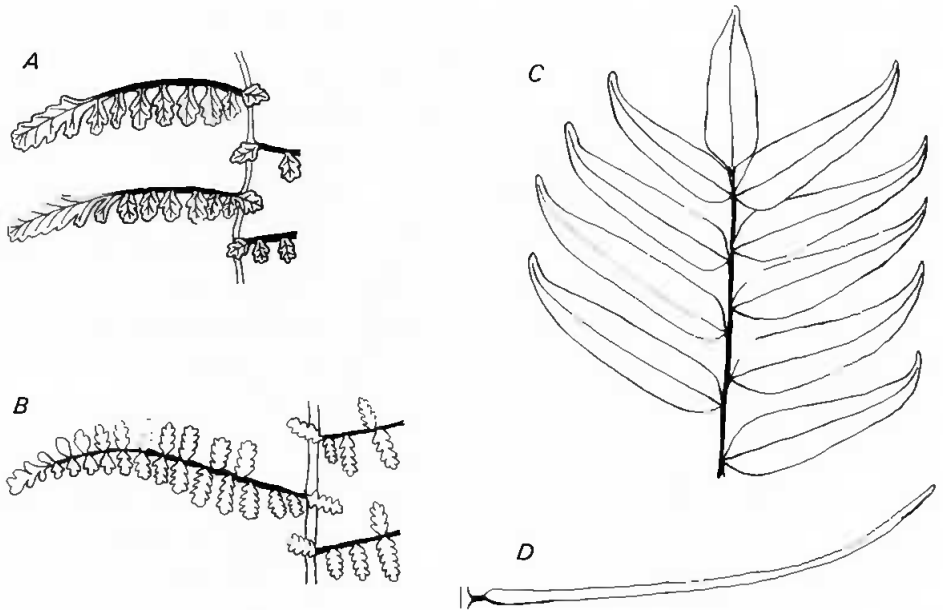


Figure 8.2. A diagram of leaf morphology in *Teratophyllum aculeatum* (Aspleniaceae). Four markedly different leaf types are produced at different stages in the life cycle. *A*, Leaves on young plants; *B*, intermediate leaf in heteroblastic series; *C*, tip of adult leaf; *D*, pinna of fertile frond. Redrawn from Holttum (1968).

Ferns

Many vining ferns exhibit marked differences in leaf morphology during their life, particularly between sterile and fertile leaves. The most extreme examples are found in the genus *Teratophyllum* (Aspleniaceae), which has 12 species in Southeast Asia. These ferns are root climbers that grow high in rainforest trees. In *T. aculeatum*, native to lowland rainforest in the region, four markedly different leaf types are produced at different stages in the life cycle (Holttum, 1968; Figure 8.2). Young plants produce very small pinnate leaves that bear pinnae only on the lower side of the midrib. Successively produced leaves are larger and develop pinnae on both sides. Transitional leaves with larger, lobed pinnae jointed to the rachis may occur. Adult plants produce fronds up to 40 cm long with 16 or more pairs of simple pinnae. Fertile fronds are similar, but the pinnae are less than 2 mm wide. A second climbing genus in the region, *Lomagramma*, also has a striking heteroblastic leaf sequence (Holttum, 1968).

The best-studied vining fern is undoubtedly the genus *Lygodium* (Schizaeaceae), which is widely distributed in disturbed vegetation throughout the tropics. Mueller (1982a, b; Figure 8.3) has studied the shoot morphology and

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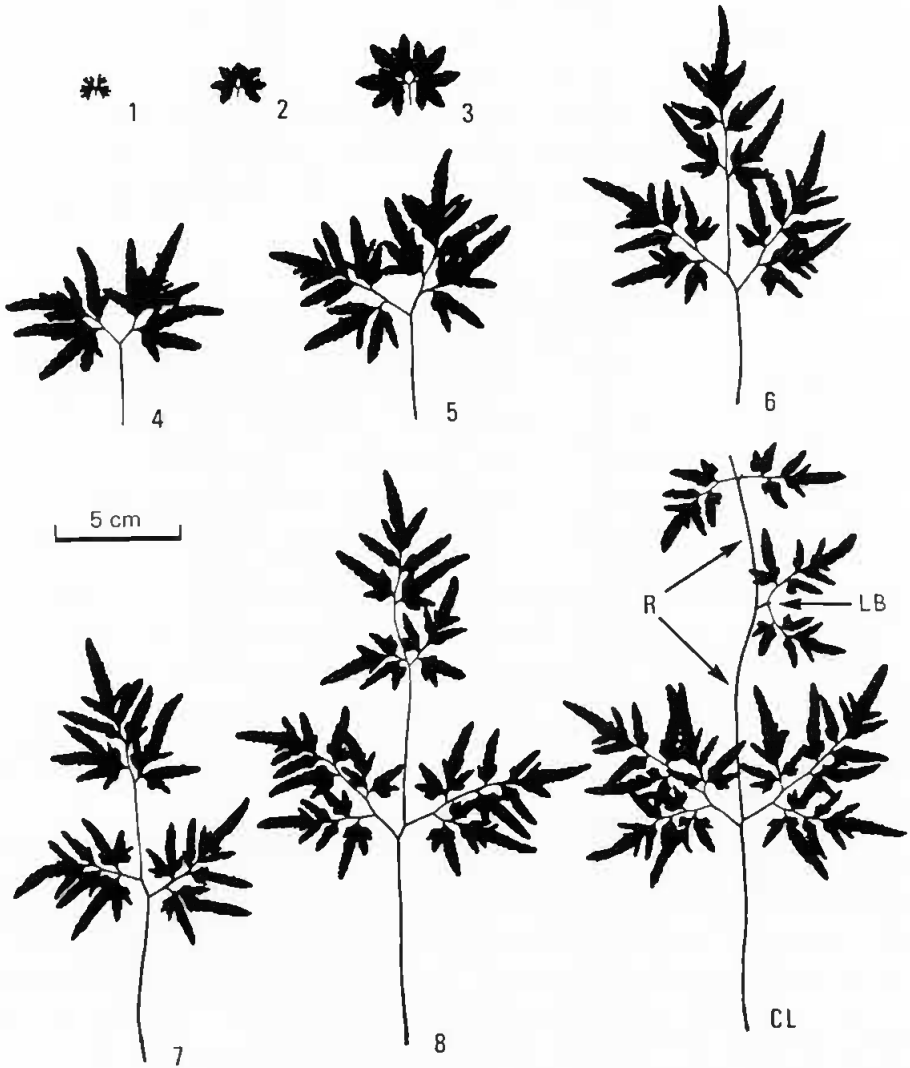


Figure 8.3. Diagram of the foliar heteroblastic sequence in *Lygodium japonicum* showing the first 8 leaves on the shoot (1–8), and part of the adult climbing leaf (CL). The juvenile (1–3) and adult (CL) leaves are connected by a series of transitional forms (4–8) that gradually increase in size and asymmetry of pinnae outgrowth. Diagram from Mueller (1982a).

ontogeny of *L. japonicum*. The first leaves on the sporophyte are small, determinate, and dichotomously lobed. The pinnate adult leaves are remarkable for their essentially indeterminate growth and can grow to a length in excess of 5 m. These leaves also have leaf 'buds' which are arrested pinnae that can grow out as replacements for the original leaf apex. The circumnating leaf apex is the basis for the twining habit of the plant. Juvenile and adult leaves are connected by a series of transitional forms. Changes in leaf form are correlated with increase in size and complexity of the shoot meristem during development (Mueller, 1982a).

Aroids

Members of the monocotyledonous family Araceae are among the most abundant vines in tropical humid forests and have some of the most remarkable examples of heteroblastic development. We will discuss development in the best studied vine genera in the family, *Monstera* and *Syngonium*.

The genus *Monstera*, common in neotropical rainforests, has many species with extreme differences between simple, saucer-shaped juvenile leaves that are appressed to a support and erect, elaborate adult leaves. In his monograph on the systematics of the genus Madison (1977) described the general features of development in *Monstera*. Species within the genus vary in the degree of heteroblasty (Figure 8.4). Taxa in the sections *Marcgraviopsis* and *Echinospadix* exhibit marked differences between juvenile and adult plants. Madison (1977) hypothesized that taxa that produce only saucer-shaped leaves throughout their life cycles, e.g. *M. tuberculata* (Figure 8.4), are neotenous forms.

In most species of *Monstera* seeds germinate to form a stolon that produces minute scale leaves (cataphylls) at long intervals. Through an orientation phenomenon termed skototropism ('growth towards dark': Strong & Ray, 1975), the stolons grow towards the darkest sectors on the horizon, which are usually tree trunks. When a plant begins to ascend a tree trunk, it produces asymmetric foliage leaves that are flattened against the tree, overlap each other, and completely cover the stem. These juvenile plants have been called shingle plants (Madison, 1977). The leaves of shingle plants frequently appear velvety and/or variegated. The plant ascends the trunk, each successive leaf larger than the previous one. Some distance up the trunk there is a transition to the adult form, which produces large erect lobed leaves with holes in the laminae (Figure 8.5) as well as inflorescences. Should the vine outgrow its support, the stem hangs free and grows down to the forest floor. These descending axes, described as 'flagelliform' shoots (Madison, 1977; Blanc, 1980), produce long internodes and reduced leaves.

This description indicates that shoot growth in *Monstera* species displays

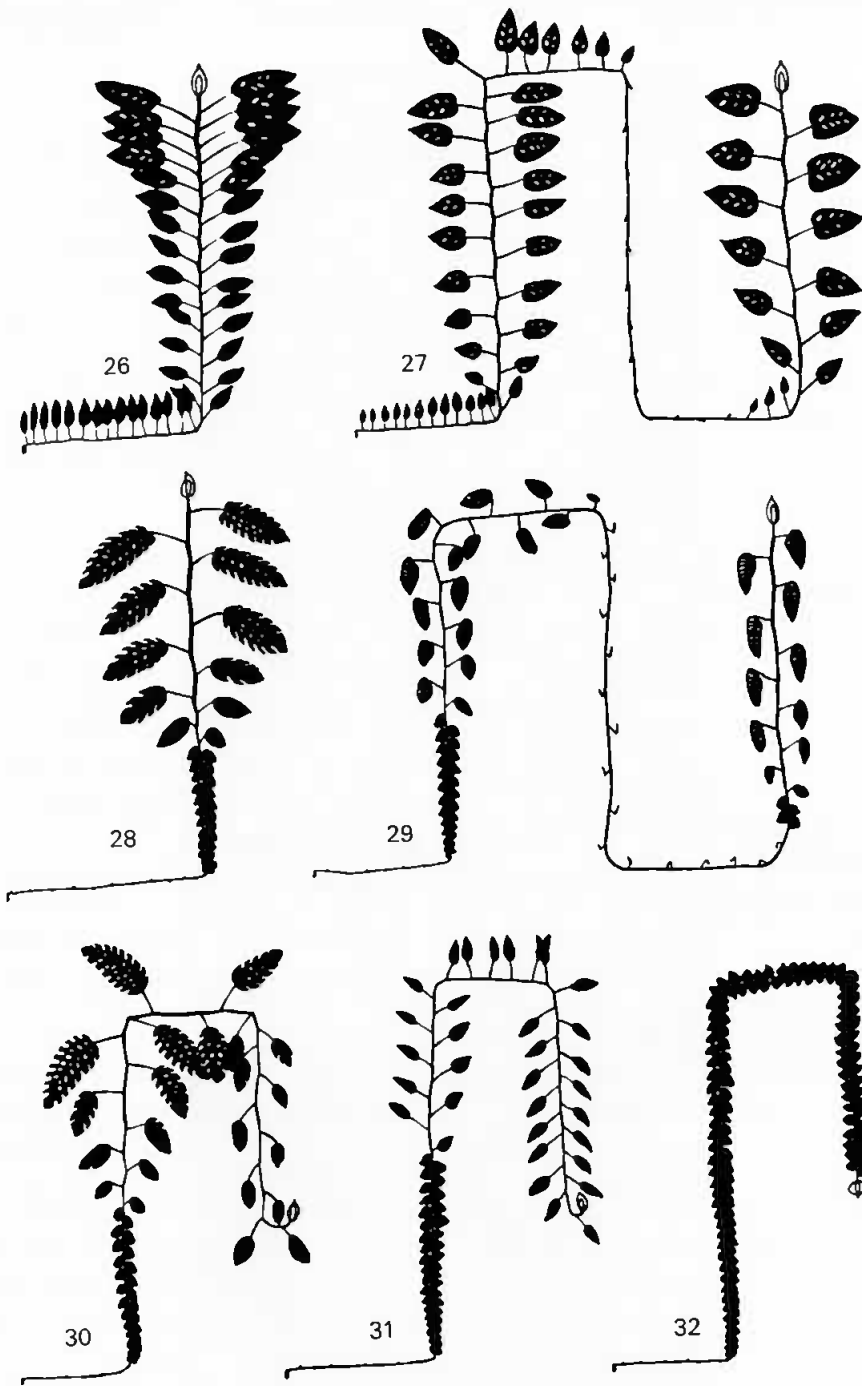


Figure 8.4. Diagram showing the general features of shoot development in the genus *Monstera*. Species differ from those having no leaf heteromorphy (e.g. *M. tuberculata*) to those with very marked heteromorphy (e.g. *M. siltepecana*). In each diagram the shoot begins at the seed on the left. 26. *M. lechleriana*; 27. *M. siltepecana*; 28. *M. punctata*; 29. *M. acuminata*; 30. *M. dubia*; 31. *M. pittieri*; 32. *M. tuberculata*. Diagram from Madison (1977).



Figure 8.5. Climbing vine of *Monstera tenuis* in lowland tropical forest at La Selva, Costa Rica. S, shingle leaf stage; T, transitional leaves; A, adult leaves.

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both marked heteroblasty and great plasticity. The exact nature and interrelationship of these two phenomena need to be defined experimentally and in relation to the environments in which these plants grow (see section on developmental ecology, below).

The shifts between heteroblastic forms in *Monstera* are correlated with changes in the vine's light environment. Other observations, however, indicate the importance of endogenous growth patterns or other environmental controls on heteroblastic transitions (Ray, 1983a). For example, individuals of *M. tenuis* growing on exposed tree trunks still showed the progression of gradually increasing saucer leaf sizes, and the switch from juvenile to adult form occurred once these leaves reached a maximum diameter (Oberbauer *et al.*, 1980). Light also appears to have little influence on the transition from adult to flagelliform stages.

The genus *Syngonium* is abundant in the same neotropical forests as *Monstera*. It exhibits a different and much more uniform developmental strategy than *Monstera*. Ray (1983b, 1987) has described the life history patterns of taxa native to Costa Rica, particularly *S. triphyllum*. Seeds germinate on the forest floor and initially develop into small plants with a rosette of about 10 small leaves (Figure 8.6). The rosette stem tip then produces a slender prostrate stem with very small leaves at 8 cm intervals. These stems are skototropic (Ray, 1983b). If a tree is not encountered after 30 internodes, the plant reverts to its rosette form, produces 10–15 leaves, then switches back to the prostrate form. This alternation continues until a tree trunk is encountered. The stem then begins to climb the trunk and produces successively thicker stems and larger leaves. Each leaf has deeper lobes than the previous leaves. When the stem attains a diameter of approximately 14 mm, terminal inflorescences can be produced, in which case axillary branches continue the vegetative growth. The axillary branches repeat the trunk-based portion of the growth cycle.

Climbing stems that reach the top of a tree become detached and hang down. Successive internodes then decrease in diameter and increase in length, while the leaves decrease in size. When this hanging stem reaches the ground, it elongates rapidly and produces extremely small leaves, until it contacts another tree trunk and repeats the trunk-based cycle.

Tropical dicotyledons

Considerable diversity in growth strategies occurs among the dicotyledonous tropical vines. This variability probably results in part from diversity among species in the method of climbing (adventitious roots, hooks or tendrils, twining, etc.). The taxa described here are representative of this diversity.

Morning glory vines (*Ipomoea* spp., Convolvulaceae) climb by twining.

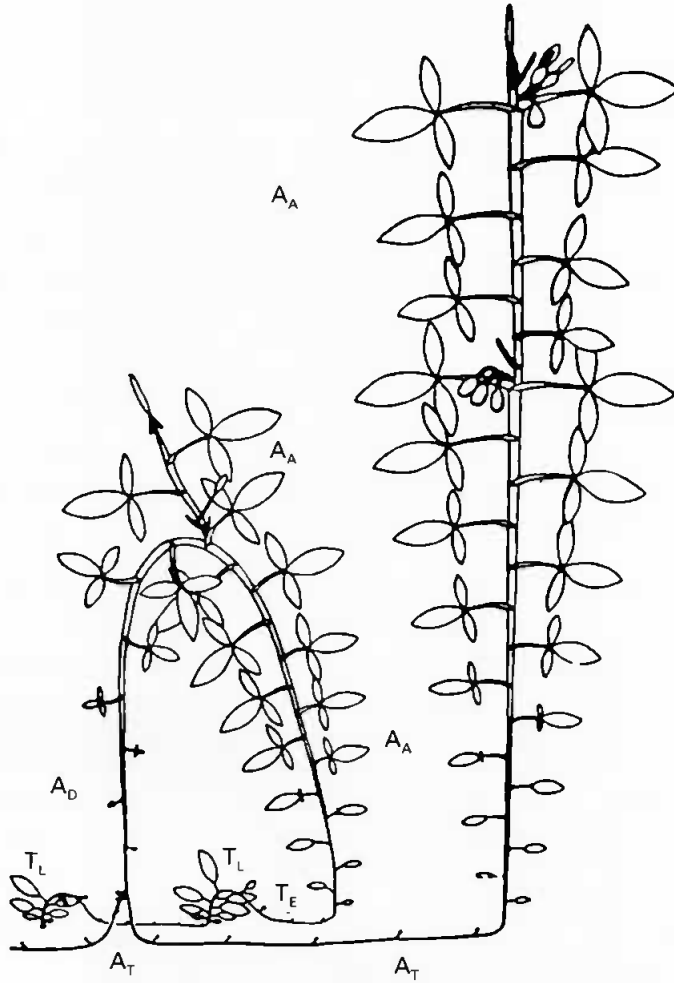


Figure 8.6. Diagram of shoot growth in *Syngonium* as exemplified by *S. triphyllum*. Growth begins with a terrestrial leafy stage (T_L) on left. T_E, terrestrial elongate; A_A, aerial ascending; A_D, aerial descending; A_T, aerial terrestrial. Diagram from Ray (1987).

Many morning glory vines exhibit a transition with age from simple cordate to deeply lobed leaves. The influence of environmental factors on this transition was first investigated by Ashby (1948a, b), Ashby & Wangerman (1950), and later by Njoku (1956, 1957, 1958). Temperature and mineral nutrition affected the shift in leaf development but were not as important as light intensity. Njoku (1956) showed that reduced light intensity retarded the rate of change in leaf morphology from juvenile to adult, and that plants grown in 72% and 78% shade did not produce adult leaves during the course

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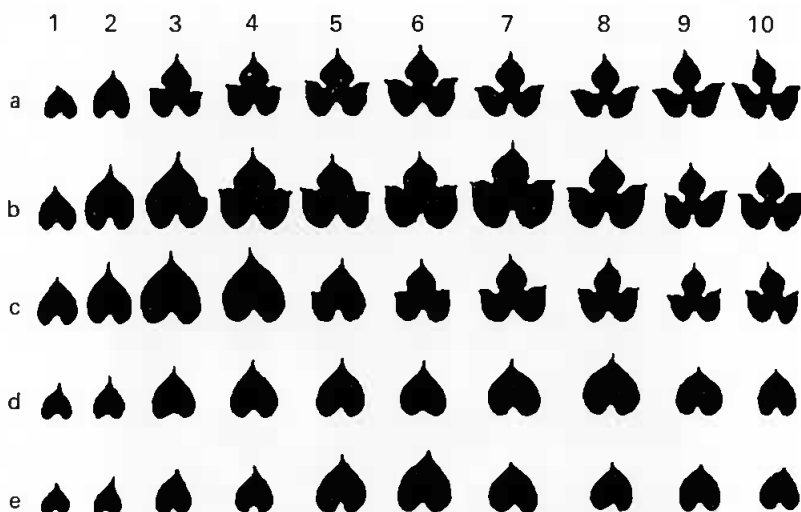


Figure 8.7. Diagram of the first ten leaves produced by seedlings of *Ipomoea caerulea* under different light intensities. a, full daylight; b, 26% shade; c, 44% shade; d, 72% shade; e, 78% shade. Diagram from Njoku (1956).

of the experiment (Figure 8.7). Njoku (1958) also showed that application of gibberellin to mature plants induced a shift to juvenile leaf shape.

Peñalosa (1983) investigated the demography of shoot types produced by *Ipomoea phillomega*, which grows in primary and secondary forest in Central America. This species produces two primary shoot types: (i) rapidly extending stolons with early deciduous leaves; (ii) erect twiners with longer-lived leaves and slower elongation rates. In studying the demography of these shoot types Peñalosa showed that high light intensity favors the development of twining shoots. Primary twining shoots originate from buds on stolons, and secondary twining shoots originate from buds on primary twining shoots.

The passion fruits (*Passiflora* spp., Passifloraceae) are important vines in neotropical forests (Killip, 1938). *Passiflora vitifolia*, which is native to tropical forests in Central America, initially develops as a compact plant with short internodes (Smiley, 1983). Juvenile plants are found in shady understory conditions and can persist for an undetermined amount of time. In bright light the internode distance lengthens, the plant develops a vining growth form, and the leaves progressively become more lobed. Larger vines grow into the canopy, but the scarlet flowers and mottled fruits generally occur on lower, leafless branches in the understory.

Cat-claw (*Macfadyena unguis-cati* (L.) A. Gentry, Bignoniaceae) is a common forest liana that occurs from Mexico to Argentina and has been

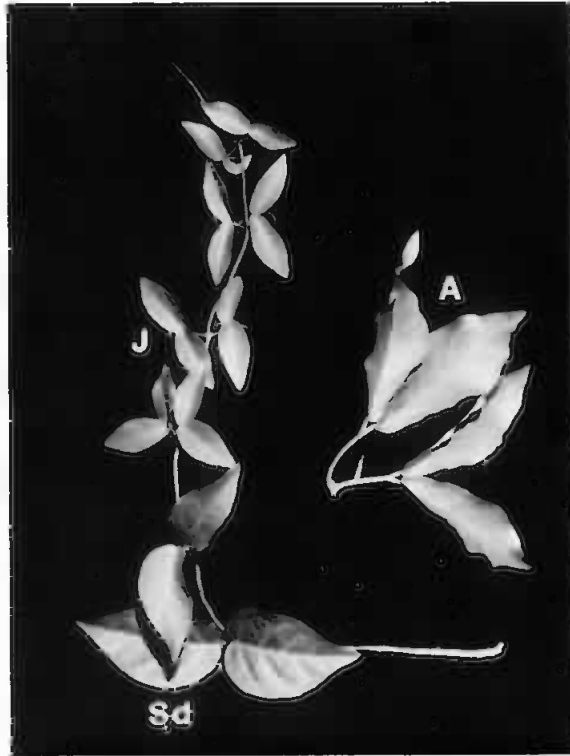


Figure 8.8. Juvenile and adult foliage of *Macfadyena unguis-cati* in Miami, FL. Sd, seedling stage; J, juvenile vining stage; A, a single node from the adult vine.

introduced into the USA around the Gulf of Mexico. It has two juvenile forms (Figure 8.8; Gentry, 1983). The seedlings are erect with opposite and simple leaves. Seedlings develop into juvenile vines with bifoliate leaves. Each leaf develops a tendril with hooked 'cat-claw' tips. This stage is apparently skototropic and grows toward tree trunks or other dark silhouettes. After ascending the trunk, the vine produces free-hanging shoots with large bifoliate leaves that lack cat-claws (Figure 8.8). These adult shoots flower and fruit profusely.

Some insectivorous plants, which are often strongly heteroblastic (Franck, 1976), are also vines (e.g. *Nepenthes*). A spectacular example of extreme leaf dimorphism in an insectivorous plant is the tropical African liana *Triphyophyllum peltatum* (Dioncophyllaceae: Cremers, 1973; Green, Green & Heslop-Harrison, 1979). The seedling of *T. peltatum* produces lanceolate leaves up to 35 cm long and arranged spirally on a stout stem (Figure 8.9). Groups of these leaves alternate in an annual cycle with groups of filiform glandular

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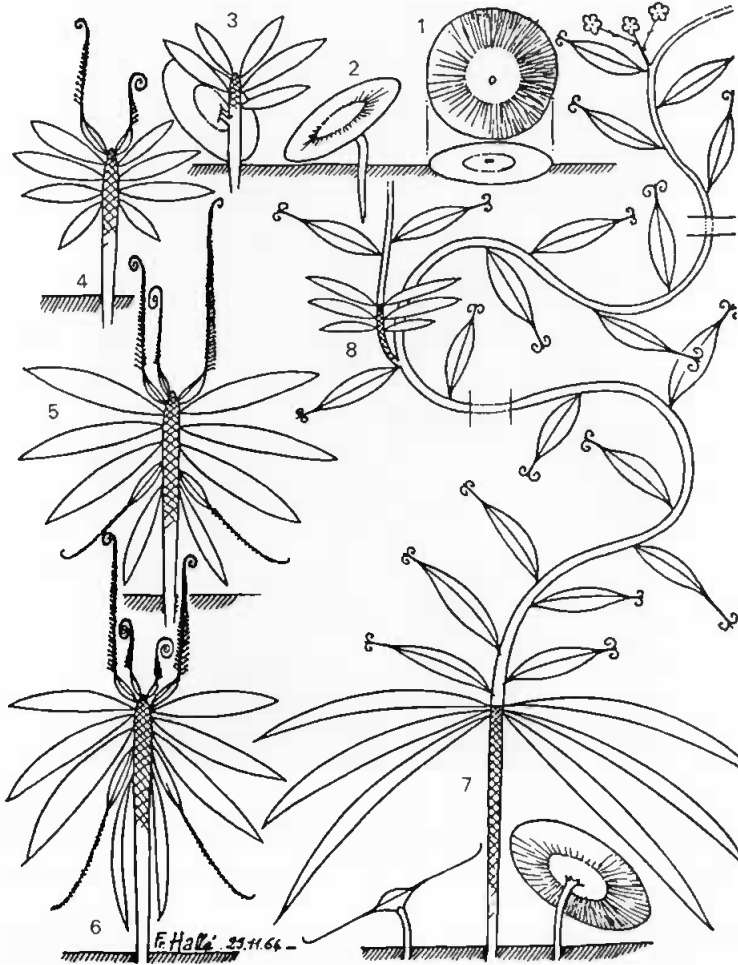


Figure 8.9. Diagram of developmental stages in the tropical African liana *Triphyophyllum peltatum* (Dioncophyllaceae), which combines the vining habit with insectivory. Seedling stage with lanceolate leaves (1–3); juvenile stage with lanceolate and insectivorous leaves (4–6); adult vine produced by juvenile plant (7) and showing reiteration from axillary buds (8). Drawing by Francis Hallé.

leaves up to 30 cm long. The glandular leaves trap and digest insects. Adult vines, which can be up to 50 m long, are produced from the terminal or axillary buds of juvenile plants. Adult leaves are about half the length of juvenile ones, leathery, and oblong-elliptic, with two short hooks produced at the tip of each leaf (Figure 8.9). Thus, insectivory is limited to the juvenile, non-vining form. This species might lend itself readily to a study of the effect



Figure 8.10. Juvenile and adult shoots of *Ficus pumila* in Miami, FL. J, juvenile stage; A, adult stage.

of mineral nutrition and biomass accumulation on the transition to the vining habit.

Many dicotyledonous root climbers also produce the distinct 'shingle plant' juvenile morphology that was described for *Monstera*. This heteroblastic stage has been observed in the genera *Piper* (Blanc & Andraos, 1983), *Marcgravia*, *Metrosideros*, *Hoya*, *Conchophyllum*, and *Ficus* (Madison, 1977). Taxa in *Ficus* section *Rhizocladus* (76 species in Asia and Australasia: Corner, 1965) grow in this manner. *F. pumila* L., which belongs to this section, is an important ornamental vine in tropical and subtropical regions (Figure 8.10). Seedlings of this species establish on walls or tree trunks, grow vertically, and produce velvet-surfaced leaves that are appressed to the support. Older shoots produce lateral branches that grow away from the surface and develop leathery, oval leaves. These branches can bear flowers and fruits.

This survey shows that vines employ a variety of developmental patterns. Upon germination, seedlings can grow erect or can immediately begin horizontal growth in search of a support. Juvenile stages can be erect and self-supporting, stoloniferous and searching, or climbing. Adult stages can be climbing or free-hanging. What controls the sequence of growth forms that characterizes a particular species?

Development ecology of vine heteroblasty

Vine heteroblasty and environmental plasticity: models

Plant developmental patterns cover a range from those that are internally controlled, pre-programmed, and not sensitive to environmental factors to those that are very responsive to environmental changes. Heteroblastic development is generally considered to be an internally controlled, relatively predictable progression. Heteroblastic development in vines is interesting because control of this progression from juvenile to adult has been subjected to substantial environmental regulation. Figure 8.11 presents models for heteroblastic development in herbs or trees and in vines. In the former, the progression through developmental stages proceeds predictably from the seedling stage (1) to the adult (5). Change from one stage to the next is controlled primarily by some internal regulatory mechanism that, presumably, assesses the developmental status of the plant and causes the appropriate phase shifts. The mechanism for this control is unknown.

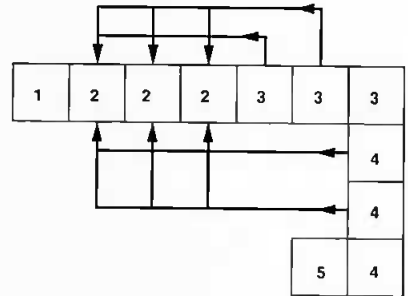
In vines (Figure 8.11*B*), in contrast, particular stages in the developmental progression can be prolonged (e.g. the increased number of stages 2, 3 and 4, compared with Figure 8.11*A*) or even re-entered (e.g. Figure 8.11*B*, arrows from stages 3 and 4 to stage 2), depending on the plant's environment. Figure 8.11*B* shows diagrammatically the prolonged stages as similar throughout with sudden shifts between stages. Alternatively, gradual changes may occur within each stage, as in Figure 8.11*C*. Progression from one stage to the next probably still depends on an internal control, but sensitivity to external conditions has been superimposed on this internal control. These models emphasize that what is striking about heteroblastic development in vines is not the phenomenon *per se* but the environmental regulation of the phenomenon, which allows for the prolongation or repetition of certain stages.

The models presented here for vine heteroblastic development make testable predictions. For example, in Figure 8.11*B, C* a step-wise progression is shown in going from stage 1 to 5, but reversions can skip steps. Is this realistic? Madison's (1977) and Ray's (1987) studies of aroids imply that unique stages are involved in reversions (e.g. descending shoots, Figure 8.4;

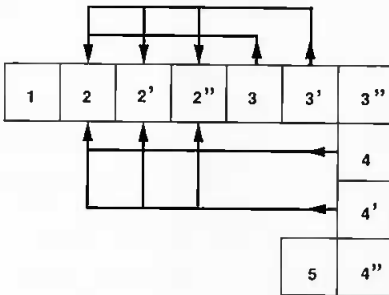
A Heteroblastic development in herbs or trees



B Heteroblastic development in vines



C Gradual heteroblastic development in vines



D Unique reversion stages in vine heteroblasty

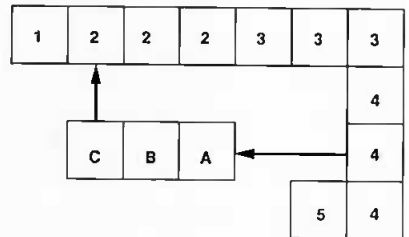


Figure 8.11. Models of heteroblastic development in herbs or trees (*A*) and vines (*B*, *C*, *D*). Numbers 1–5 represent particular stages in a heteroblastic sequence. The arrows show reversions. *B* and *C* differ in whether a particular stage is stable until it switches to the next stage (*B*) or whether a gradual change occurs within each stage (*C*). *D* illustrates the possibility that reversions involve unique developmental stages (*A*, *B*, *C*).

A_D and A_T , Figure 8.6). Such stages could be modeled as in Figure 8.11*D*. Experiments that attempt to induce reversions and that carefully analyze the nature of reversions in a number of vines are needed to evaluate this aspect of these models. Such experiments would also show whether reversions can occur at any stage or are limited to only some stages (e.g. stages 3 and 4 can revert, but not 5).

Consideration of these models raises questions about the architecture of vine heteroblastic development and how it differs among species. For example, when reversions occur, are they transformations of the original shoot apex, or are they reiterations of the heteroblastic sequence by lateral branches? Answers to this latter question have basic implications for how heteroblastic development is controlled in a given species, i.e. can a single apex be returned to a prior developmental stage? More detailed descriptions of the architecture and development of a number of vine species are needed before we will be able to generalize about vine architecture.

Heteroblastic development in vines

These models of heteroblasty in vines emphasize that vines are subjected to drastic changes in environmental factors as they grow. This observation raises two questions. The first is, why do canopy trees, which pass through the same environmental gradient, not show the same marked heteroblastic development; while the second is, what are the significant environmental factors that regulate vine heteroblasty?

Heteroblasty in vines vs. canopy trees

Although both canopy trees and vines germinate and grow in the forest understory but expand into the very different environment of the canopy, canopy trees do not have as marked heteroblasty as vines. Several reasons for this difference seem possible.

The first reason focuses on the basic difference between trees and vines: trees support themselves, whereas vines rely on external support. The two habits represent different resource allocation responses to the problem of growing from shade into sunlight. Trees invest in support, pushing their apical meristems to higher light levels. Vines invest in mobility. They have to find a support that will enable them to grow into the canopy. To do this they must have a low-cost developmental stage that allows them to seek a support in an energy-limited environment. Juvenile stages are generally smaller and simpler than adult stages. Thus, juvenile stages of vines may have been prolonged and further modified through selection for horizontal, searching growth.

A second possible reason for differences between trees and vines in their heteroblastic development relates to environmental differences that are an outcome of their different growth habits. Trees occupy a more predictable environment than vines. They are fixed in place and must either survive in place until a gap occurs in their vicinity or push themselves up through the canopy. Although the changes that they perceive in their environment can be gradual or sudden, those changes are unidirectional (e.g. increased light, decreased humidity, increased temperature).

Vines, in contrast, are more likely to encounter alternating changes in environmental parameters. If they overgrow their support or if it breaks, they will re-enter an environment that they have previously outgrown. Thus, whereas the tree's environment is either radically or gradually changing in one direction along a gradient, the vine's environment has cyclical changes that involve recurring increases and decreases in environmental factors. Vines must be able to respond to these changes and, therefore, plasticity must have greater selective advantage in heteroblastic development of vines than of trees.

A third possible reason for differences in vine and tree heteroblasty again

derives from their differences in habit. Because trees have internal mechanical support, displaying flowers and bearing fruit do not represent new structural demands on plant resources. For vines, however, the need to expose flowers to pollinators and then to support the weight of developing fruit may present a new mechanical demand, which requires a new architecture. Thus, many root climbers, such as *Hedera* spp. and *Ficus pumila*, produce a rootless adult phase that grows away from the external support.

These hypotheses generate testable predictions for studies of the development and architecture of particular vine species. If support for reproductive parts is a significant factor in the evolution of adult vine morphology, then relative investment in support structures should be greater in the adult than in the juvenile phases. How do support costs change between juvenile and adult phases of species like *Triphyophyllum peltatum*, that are erect as juveniles and vining as adults? How does resource allocation in this type of vine compare with that of a species such as *Ficus pumila*, which is vining in the juvenile phase, but free-hanging in the adult?

If juvenile vines are both energy-limited and environmentally plastic, then their developmental stage could be controlled experimentally. For example, many vines begin growth with an upright stage similar to tree seedlings, then transform to a horizontal searching stage (cf. *Syngonium*, *Passiflora*, *Macfadyena*, above). If biomass accumulation regulates transformation to the searching stage, then experimental removal of leaf area from the upright stage should delay the change.

If developmental plasticity and environmental responsiveness have been selected for in vines, then vines should show a greater ability to respond to experimental manipulations of the environment than related tree or herb species. Studies of environmental plasticity in vine and tree species of *Bauhinia* could be used to test this hypothesis.

Environmental influences on heteroblasty in vines

Possible environmental influences on vine heteroblasty include gravity, tactile stimulation, temperature, water availability and light. Vines that overtop the trees on which they grow hang free and frequently revert to a more juvenile condition. As they hang down, they are re-oriented in the gravitational field, so gravity could stimulate the reversion. Movement of the free-swinging vine (similar to touch) could also be a stimulus. Tactile stimulation is important in the transformation of young shoots or tendrils when they come into contact with a vertical trunk, but because climbing a support involves a re-orientation, gravity could also play a role. Changes in relative humidity are likely to be correlated with other variables, such as temperature and light. The higher temperatures of more exposed environ-

ments could stimulate heteroblastic transitions in vines, and temperature affected the heteroblastic series in leaf form reported by Njoku (1957).

Although all of these environmental parameters may affect vine heteroblasty, light is likely to be the major environmental factor influencing phase shifts in vines. Mechanisms are known that regulate plant responses to changes in both light quantity and quality (Smith, 1981; Kendrick & Kronenberg, 1986), and both aspects of light change as vines climb. In order to study light effects on vine heteroblastic development, we must first know how the light climate differs between the forest floor and canopy.

Light climates. Light available for plant photosynthesis (quanta at 400–700 nm or photosynthetic photon flux [PPF]) decreases as it passes through a canopy. In tropical humid forests light levels are often less than 0.5% of light above the canopy, with average values between 1 and 2% (Chazdon & Fetcher, 1984a, b; Pearcy, 1983; Lee & Paliwal, 1988; Oberbauer *et al.*, 1988). In a tropical deciduous forest understory after the rainy season the light level was about 10% of that above the canopy, although PPF during the rainy seasons may be similar to levels in the understory of humid tropical forests (Lee, 1989).

The understory spectrum results from radiation transmitted through and reflected by leaves, penumbral radiation, skylight and direct sunlight. Radiation passing through the canopy is strongly altered in spectral quality. The most significant change is in the ratio of red to far-red quanta (quanta in a 10 nm band width centering on 660 and 730 nm, or R:FR), which affects the equilibrium between phytochrome P_r and P_{fr} (Smith, 1982). The change in R:FR beneath the canopy results from the optical properties of leaves, which absorb in the visible and reflect or transmit in the far-red (Gates *et al.*, 1965). Typical R:FR values for rainforest understory are 0.30–0.40, compared with 1.25 for sunlight. Extreme-shade R:FR values may be less than 0.25 (Lee, 1987). Differences in spectral quality at a rainforest site on Barro Colorado Island in Panama are illustrated in Figure 8.12, which shows that the greatest shift in spectral quality occurs at the lowest PPF, as in going from shade to a light fleck.

Even under the shady conditions in a forest, light quality is heterogenous. Spectral alteration is greater toward the horizon because solar radiation passes through more foliage layers, and there are fewer gaps in the canopy. Horizontal measurements in humid tropical forest at La Selva, Costa Rica, were substantially lower in PPF (less than 0.2%) and in R:FR (approximately 0.10) than vertical ones (see Lee, 1987, for methods).

Tree trunks also contribute to the understory light climate. Tree barks measured at Barro Colorado Island (five species; see Lee & Graham, 1986, for methods) reflected approximately 10% of incident light, with a range of

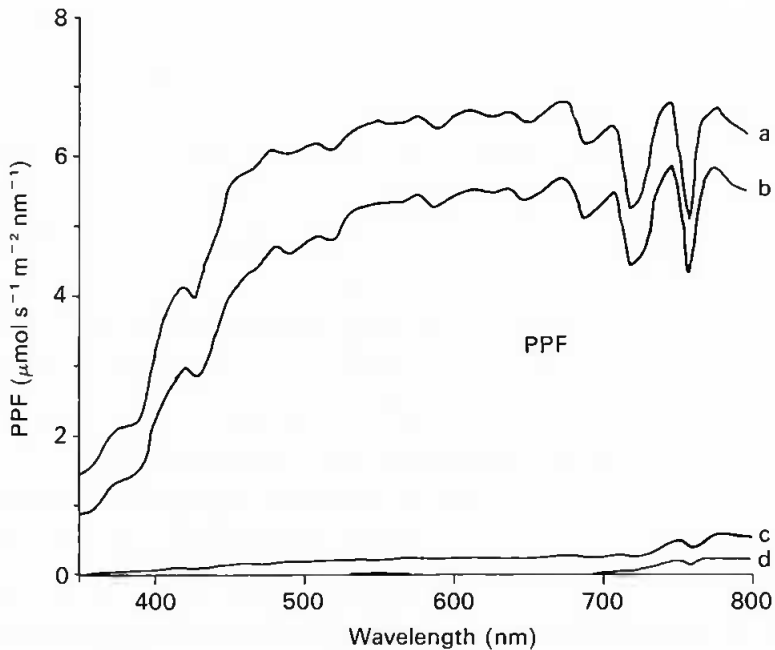


Figure 8.12. Graph of spectral radiation from 300 to 800 nm in a tropical rainforest on Barro Colorado Island, Panama. Measurements were taken in full sun (a), a large gap (b), a sunfleck in the understory (c), and deep shade in the understory (d). A comparison of radiation at 660 nm and 730 nm shows that a large shift in R:FR occurs at low PPF in going from shade (d) to a light fleck (c). Data from Lee (1987).

4–25%. More interestingly, the trunks reflected light that was even more strongly altered in R:FR than the diffuse background radiation, since bark reflects much more strongly in the far-red region (Figure 8.13). The mean R:FR of radiation reflected by the bark of five species was reduced to 0.047, compared with R:FR = 0.103 for understory radiation.

This discussion of light climates shows that since vines begin their growth on the rainforest floor, then ascend to the canopy, they experience extreme differences in radiation quantity (PPF) and spectral quality (R:FR). Vines undergo developmental changes, however, at intermediate elevations in the forest, such as on trunks or upper branches. To know if light climates are important in regulating developmental states in a heteroblastic series, we must know what the light conditions are at these intermediate elevations. Yoda (1974) has measured gradients in intensity with elevation in the forest. By extrapolating from a correlation between percentage of solar PPF and

Heteroblastic development in vines

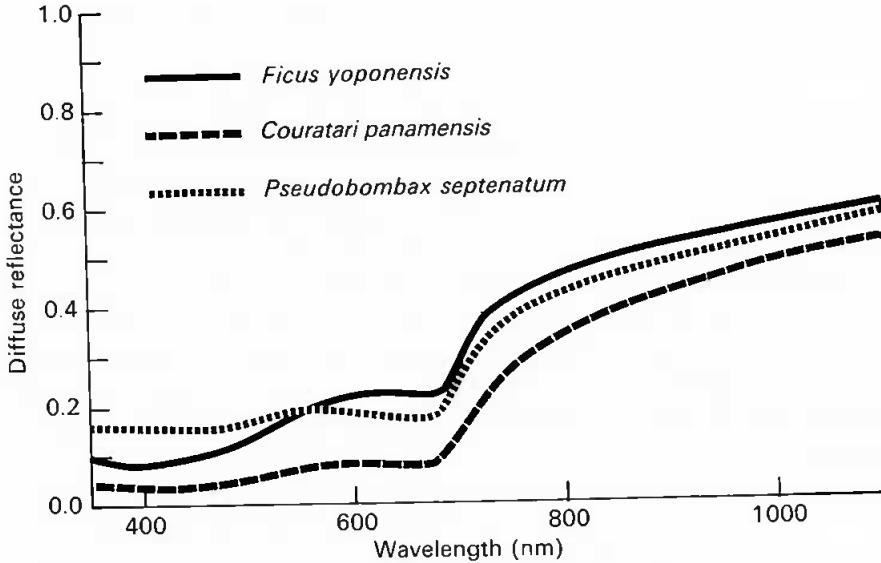


Figure 8.13. A graph of the radiation from 300–1100 nm reflected from the bark of three trees in the lowland tropical rainforest at Barro Colorado Island, Panama.

R:FR for measurements on the rainforest floor (Lee, 1987), we can predict R:FR for light at different elevations from Yoda's (1974) study. Such predictions suggest that light levels at 10 m above the forest floor could have R:FR as high as 0.70, which represents a rapid change in light quality between the forest floor and intermediate levels in the forest. If we are to learn more about the effects of light climates on vine development, however, we need actual measurements of the light microenvironments in which developmental changes occur, as well as evidence that environmentally significant levels of PPF and R:FR can influence vine development.

Skototropism. Light climates *can* exert a profound effect on early vine development, as illustrated by skototropism. Responses similar to skototropism have also been observed in the tendrils of vines in the Bignoniaceae, as in *Macfadyena unguis-cati* and *Bignonia capreolata*, studied by Darwin (1876).

The mechanism for the skototropic response is not known and merits further study. Strong & Ray (1975) suggested that skototropism may be the classic negative phototropic response, where seedlings are positively phototropic at very low quantum flux densities, then negatively phototropic at intermediate levels, then positively phototropic at still higher levels (Briggs, 1963). Although this phototropic response is mediated by a blue-light

sensitive pigment, the sensitivities of the three response ranges are modified by red and far-red wavelengths. Skototropism may therefore involve the perception of spectral quality as well as light quantity.

Future research on the early development of vines will need to distinguish between the directed growth of seedlings over long periods and tropism *sensu stricto*, which is a very rapid change in axis orientation. It will also be interesting to analyze the varying light responses of different shoot organs within a single plant and how the light responses of one organ change during heteroblastic development. An instance of within-plant variation in light response is seen in *M. unguis-cati*, where the claws are skototropic, while the shoot tips are positively phototropic. An example of a heteroblastic change in tropism is the light response of *Monstera* seedlings, which are initially skototropic but become positively phototropic after contact is established with a trunk.

The adaptive significance of vine heteroblastic stages in relation to light

If light is the environmental factor to which vine heteroblastic development is responding, then vine morphology at different stages in development must represent adaptations to the light environments encountered at those stages. The vine characteristics most obviously correlated with light climate involve plant architecture, leaf morphology, and leaf anatomy. Here we will discuss research on (i) the relationship of vine architecture and leaf form to light environment and (ii) the significance of changes in leaf anatomy on the efficiency of light capture.

Architecture

An important strategy in plant survival is the optimization of energy capture through leaf surface display (Givnish, 1987). For xeric and very sunny environments, plants may minimize radiation absorption through pubescence or surface waxes and diurnal leaf movements. Extreme-shade adapted plants, however, expose foliar surfaces so as to maximize absorption of radiation. Strategies of leaf display are in part dependent on intrinsic patterns of branching and phyllotaxy, which have been called a plant's architecture (Hallé, Oldeman & Tomlinson, 1978).

Plants in extreme shade must minimize self-shading or the lower leaves may not have sufficient radiation to support photosynthesis. Branching patterns in shade-adapted plants typically produce monolayers of foliage

(Horn, 1971). Monolayers are formed by (i) branching horizontally; (ii) altering phyllotaxy or bending petioles to display leaves plagiotropically; (iii) combining leaf size, shape and display to minimize overlapping.

The architecture of vines has been neglected compared to that of tropical trees (Hallé *et al.*, 1978). Cremers (1973, 1974) described the architecture of 20 African vines. Many of these conformed to the architectural models characteristic of trees, but some vines developed by models that differed from the 24 tree models described by Hallé *et al.*, (1978).

In most of the vines that Cremers (1973, 1974) described the initial axis growth was orthotropic with leaves produced in a spiral. In the juvenile vining stage leaves were typically smaller than seedling leaves and were displayed plagiotropically, while axis extension varied from monopodial to sympodial. Some vines produced lateral branches that formed remarkably flat foliar surfaces at long intervals, as in *Raphiostylis beninensis* (Icacinaceae). For vines that were tendril-climbers, the production of tendrils was often one of the modifications in growth patterns that distinguished seedling and climbing stages.

Additional careful studies of vine architecture in relation to specific habitats would enable us to classify the diversity in developmental patterns responsible for the vining habit and to relate these patterns to the light environments of different species.

Leaf morphology

Building on the work of Parkhurst & Loucks (1972) and Taylor (1975), Givnish & Vermeij (1976) postulated that leaf form represents a compromise that maximizes the difference between photosynthetic profits and transpirational costs. A significant variable affecting gas exchange, water loss and leaf temperature is boundary layer resistance, which varies as a function of the effective leaf diameter. Givnish & Vermeij (1976) predicted that leaves along a vertical forest profile should be small in the shady and mesic understory, increase in size with elevation, then decrease in size in the more xeric and sunny conditions of the canopy. Superficial field observations in Venezuela and Costa Rica seemed consistent with their predictions (Givnish & Vermeij, 1976).

Many vines develop extensive lobing or holes in the lamina as they climb. These changes in form may decrease the effective leaf size and reduce boundary layer resistance, resulting in a functionally smaller leaf. Fetcher (1981) measured leaf temperatures and water vapor conductance of vine leaves of different sizes and solar exposures. He observed no significant correlations in leaf temperature with leaf diameter for the five taxa studied,

although measurement was limited to a brief period during the rainy season (Fetcher, 1981). Both experimental studies and field analyses are needed to understand the interaction of boundary-layer effects and light climate effects on leaf form in vine heteroblastic development.

'Shingle plants' are found in the juvenile stages of phylogenetically diverse taxa, such as *Teratophyllum*, *Monstera*, and *Syngonium* (cf. Figures 8.4 and 8.5). This convergence in form suggests that shingle plant form provides a solution to some environmental problem(s) (Givnish, 1987). A number of hypotheses have been advanced to explain the adaptive significance of shingle leaves in juvenile vines. Goebel (1900) suggested that shingle leaves protect adventitious roots. Givnish & Vermeij (1976) speculated that these appressed leaves have lower support costs and are better oriented for light capture, since they face away from the trunk silhouette. Madison (1977) suggested that transpiration is reduced in such appressed leaves. Shingle leaves may also trap CO₂ from trunk respiration and so increase photosynthesis.

Measurements of microenvironmental parameters such as temperature, CO₂ concentration, humidity, and light climates, could eliminate some of these hypotheses. For example, is CO₂ concentration higher beneath shingle leaves? Oriented measurements of light microenvironments immediately adjacent to trunks are needed to substantiate Givnish & Vermeij's (1976) speculations, especially since light from the horizon in a forest is generally reduced in both quantity and quality, compared with vertical illumination (see section on environmental influences, above). An analysis of differences in allocation to support between appressed and non-appressed leaves in a heteroblastic series could begin to test the importance of support costs. Experimental manipulations could also contribute to understanding the adaptive significance of shingle plant morphology. For example, what is the effect on plant survival if shingle leaves are lifted away from the trunk to expose adventitious roots?

In twiners and tendril- or hook-climbers leaf form does not so closely correspond with Givnish & Vermeij's (1976) predictions. The climbing stage of *Passiflora vitifolia* produces progressively larger and more lobed leaves, and leaves at maturity are not smaller in size. In *Macfadyena unguis-cati* the seedling leaves are large and simple, the vine stage produces very small leaves with hooks, and the adult stage develops large bifoliate leaves. In *Ipomoea* spp. leaf size and lobing increase with age, and presumably, exposure to sunlight. Reduction in light quantity retards this transition (Njoku, 1956). Although lobing would tend to decrease the effective leaf diameter, it is difficult to discuss the functional significance of these changes without a detailed examination of the separate effects of size and lobing and studies of the ecological requirements of individual taxa.

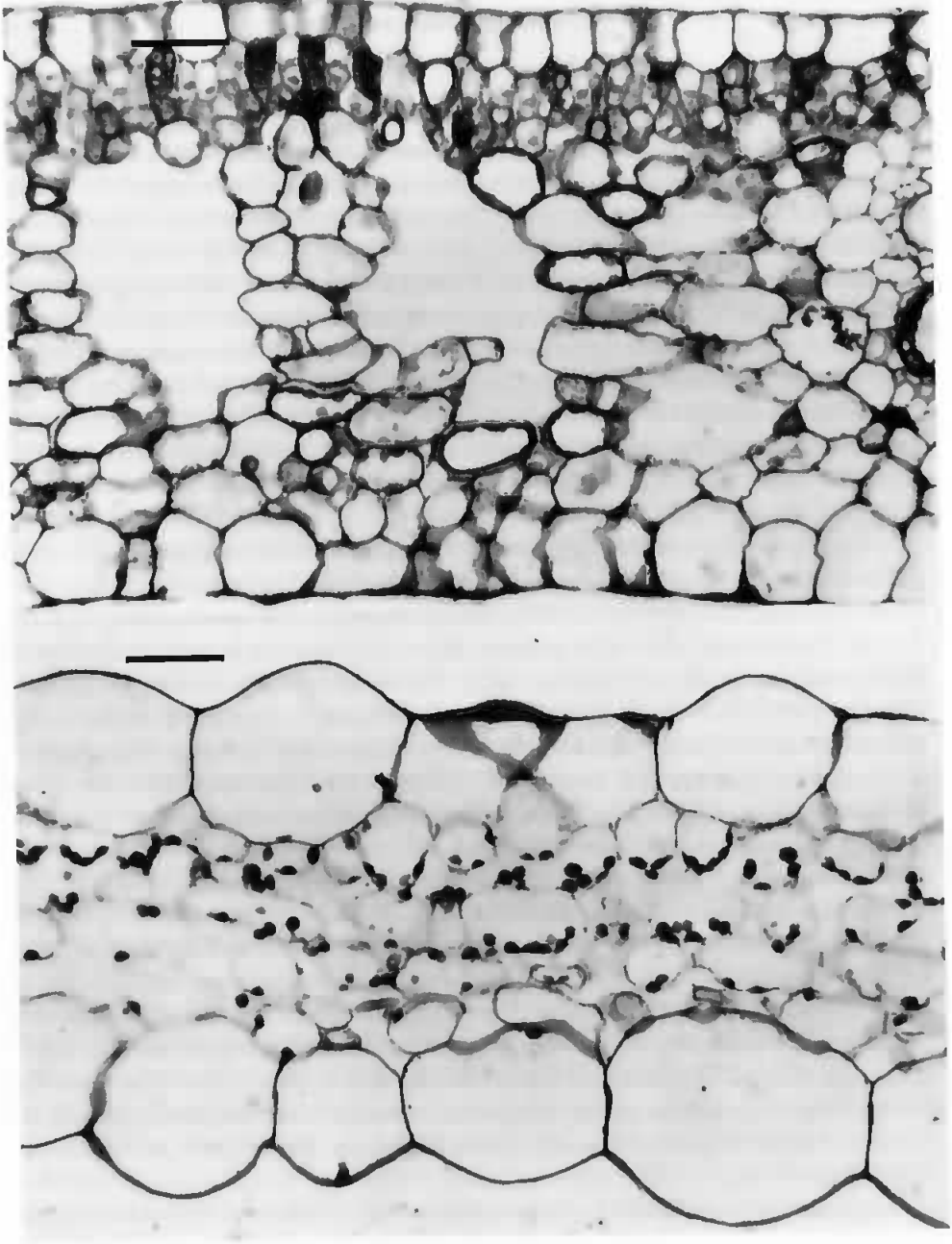
Leaf anatomy and optical properties

Leaves of vine heteroblastic stages frequently differ in anatomy, particularly among the root climbers. Juvenile leaves appear to be adapted to shade conditions (D. W. Lee, personal observation). Shade-adapted leaves are generally thinner and have lower specific weights than sun-adapted leaves. The thinner leaves have fewer cell layers and fewer columnar palisade parenchyma cells. In order to determine whether these are features characteristic of a particular heteroblastic stage or whether these are anatomical adaptations to light conditions, plants from different stages must be grown under experimental light conditions. Here we will discuss some implications for physiological function of leaf anatomical characteristics and then present preliminary data on differences between juvenile and adult leaves of two root-climbing vines.

Variations in leaf anatomy can be understood as adaptations to the photosynthesis/transpiration compromise discussed previously. Adult vine leaves typically possess the anatomical features seen in Figures 8.14 and 8.16. The columnar palisade cells contain most of the chloroplasts but allow a portion of absorbed radiation to reach chloroplasts in the spongy mesophyll (Sharkey, 1985; Lee *et al.*, 1990). Intercellular spaces allow gas exchange, and the amount of cell surface exposed to air is a major determinant in photosynthesis (Nobel, Zaragoza & Smith, 1975). Intercellular spaces also contribute to light scatter within leaves, and their extent and distribution partially determine the degree of absorption of light by leaves (Willstatter & Stoll, 1918; Gausman *et al.*, 1969; Allen, Gausman & Richardson, 1973).

Juvenile leaves of vines often differ from the above description. Juvenile vine leaves can have (i) a satiny sheen due to convexly curved epidermal cells; (ii) anthocyanic coloration on the abaxial surface; (iii) variegation; (iv) lack of differentiation into a palisade and spongy mesophyll. In the root climbers *Monstera*, *Marcgravia* and *Ficus*, for example, most juvenile saucer leaves have the first and fourth characteristics, and a few *Monstera* taxa are variegated. Similar characteristics are found in extreme-shade plants of tropical rainforests (Haberlandt, 1914; Richards, 1952; Burtt, 1978; Roth, 1984; Lee, 1986).

The adaptive significance of these features in juvenile vines and extreme-shade plants are probably similar. Convexly curved epidermal cells can refract light onto specially oriented chloroplasts and increase photosynthetic efficiency (Bone, Lee & Norman, 1985). Such cells can also increase light capture efficiency at oblique angles under diffuse light conditions. Anthocyanic undersurface coloration is associated with greater absorption above 650 nm (Lee, Lowry & Stone, 1979; Lee & Graham, 1986; Lee, 1986).



Figures 8.14 (above), 8.15 (below). Cross-sections of adult (Fig. 8.14) and juvenile (Fig. 8.15) leaves of *Monstera adansonii*. Bars = 50 μm . The juvenile leaves are thinner, lack a distinct palisade mesophyll layer, and have much larger, convexly curved, epidermal cells. Palisade cells in the thicker adult leaves are columnar, epidermal cells are flat, and chloroplasts are distributed throughout the mesophyll. In the juvenile leaves the chloroplasts are concentrated on the lower sides of the top two mesophyll layers.

Variation has been interpreted as aposematic coloration and as a means of reducing leaf temperature (Smith, 1986). The presence of equi-diameter palisade cells in shade leaves is associated with the distribution of chloroplasts either in a dense monolayer on the adaxial surface or in smaller cells packed with large chloroplasts. Such a monolayer increases the efficiency of leaf absorption by minimizing the 'sieve' effect (Duysens, 1956). In leaves of sun-adapted plants, the columnar palisade cells allow light to pass through, making the leaf less efficient in energy capture but exposing more chloroplasts to light. Leaves of extreme-shade plants also have fewer cell layers, less lignification, lower specific weights, lower chlorophyll content, and lower protein content (Björkman, 1981; Lee *et al.*, 1990). Such leaves represent a less metabolically costly production of surface for energy capture.

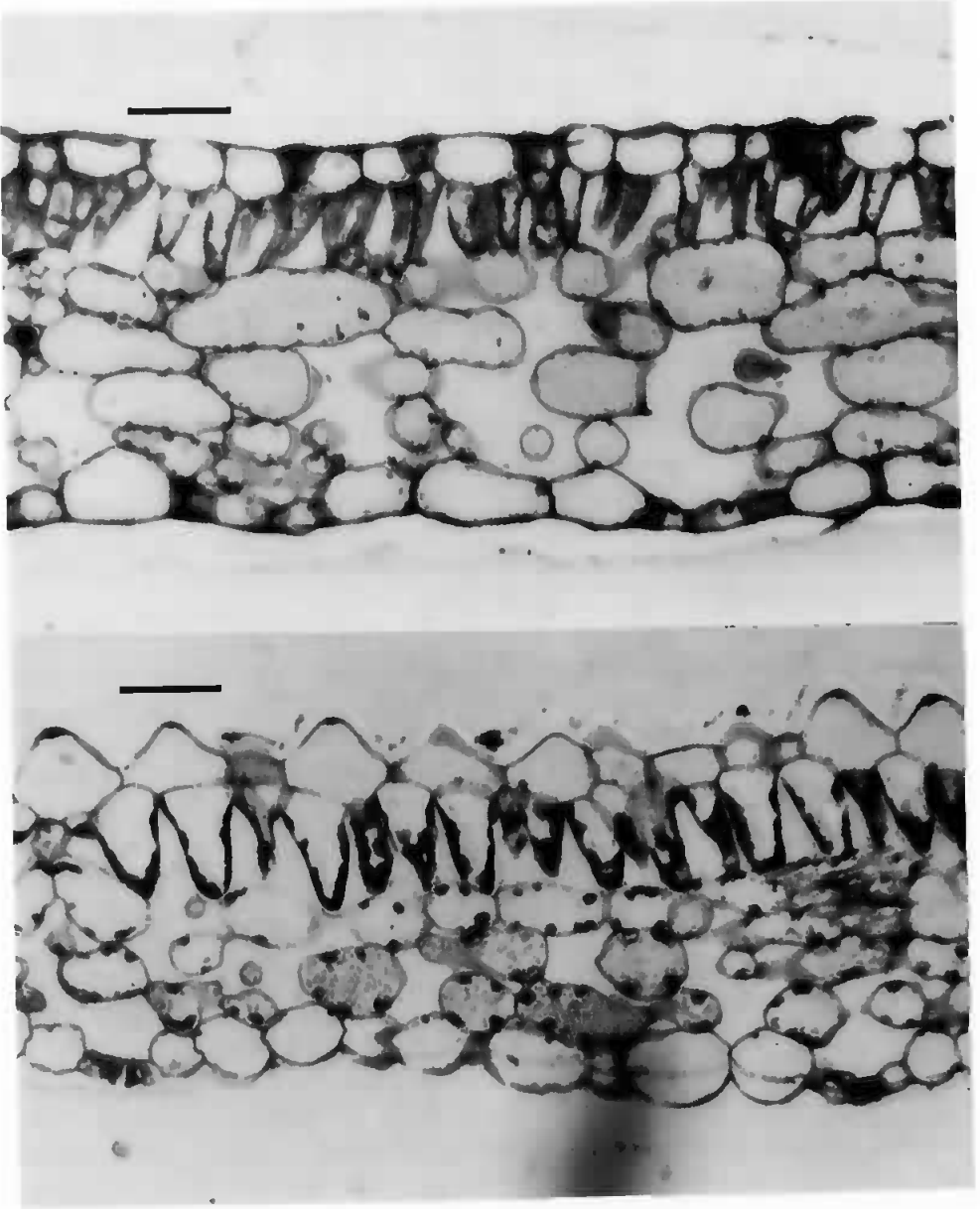
As an example of the differences between juvenile and adult vine leaf anatomy and of the similarities between juvenile vine leaves and the leaves of extreme-shade plants, we present below the results of an anatomical analysis of leaves of two root climbers. The species are *Monstera adansonii* Schott. and *Syngonium rayii* Croat & Grayum ined., both aroids common at La Selva, Costa Rica (Figures 8.14–8.17; Table 8.1).

Monstera adansonii grows in secondary forest and disturbed sites. Its shingle leaves are typical of those in the genus, and its adult leaves are not lobed but have numerous perforations (cf. Figure 8.4). The most pronounced anatomical difference between juvenile shingle leaves and adult leaves is the difference in size of epidermal cells, for the juvenile form has much larger cells. Palisade cells in the adult leaves are more columnar than those of the shingle leaves, but they are reduced in size. The chloroplasts in adult leaves are distributed throughout the mesophyll. In the juvenile leaves the chloroplasts are concentrated on the abaxial surfaces of the top two mesophyll cell layers (Figure 8.15).

The juvenile leaves have (i) a lower percentage dry weight; (ii) a lower specific weight; (iii) thinner cross-sections; (iv) equi-diametric palisade cells; (v) more air spaces; (vi) less chlorophyll per unit area (Table 8.1).

The juvenile leaves absorb less radiation than the adult leaves (Figure 8.18), but their efficiency of light absorption by chlorophyll is greater. The ratio of attenuation (*in vivo* absorbance by chlorophyll) to absorbance (absorbance by chlorophyll extract at an equivalent concentration) is higher than in the adult leaf. This implies reduced sieve effects in the juvenile leaves and a more efficient distribution of chloroplasts for absorption (Lee *et al.*, 1990).

The convexly curved cells of the juvenile leaves focus light (Bone *et al.*, 1985). Focusing increases light intensity at the upper level of the chloroplasts (57 μm) by 11.7 times. The adult leaves have flat epidermal cell walls with no focusing effects. Thus, the epidermal cells of juvenile leaves increase the



Figures 8.16 (above), 8.17 (below). Cross-sections of the adult (Fig. 8.16) and juvenile (Fig. 8.17) leaves of *Syngonium rayii*. Bars = 50 μm . The juvenile and adult leaves do not show the marked differences seen in *Monstera adansonii*, although the juvenile leaves have convexly curved epidermal cells.

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Table 8.1. Comparisons of anatomical and optical characteristics of juvenile and adult leaves of two vines

Character	<i>Monstera adansonii</i>		<i>Syngonium rayii</i>	
	Juvenile	Adult	Juvenile	Adult
Percentage dry weight	10.0 ± 0.8	14.7 ± 0.7	14.4 ± 1.0	17.7 ± 2.7
Specific weight (mg cm ⁻²)	2.78 ± 0.58	4.98 ± 0.21	2.45 ± 0.19	3.50 ± 0.68
Thickness (μm)	206 ± 44	360 ± 46	169 ± 18	188 ± 19
Palisade height/width	0.91 ± 0.22	2.17 ± 0.35	1.98 ± 0.35	2.66 ± 0.32
Number of cells thick	5.9 ± 0.3	13.2 ± 1.0	5.8 ± 0.4	6.8 ± 0.4
Portion of air space	0.25 ± 0.06	0.12 ± 0.02	0.22 ± 0.05	0.27 ± 0.04
Chlorophyll area (μg cm ⁻²)	27 ± 3	43 ± 6	63 ± 11	45 ± 7
Percentage of PFD absorbance	84.9 ± 1.5	88.4 ± 1.9	94.9 ± 0.6	89.4 ± 1.6
Attenuance/absorbance at 652 nm	1.06 ± 0.05	0.80 ± 0.09	0.57 ± 0.02	0.76 ± 0.04
Concentration factors for direct sunlight/depth				
chloroplast	11.7 × 57 μm	—	6.00 × 22 μm	—
optimal	13.9 × 70 μm	—	7.55 × 33 μm	—

efficiency of light capture by refracting light onto the chloroplasts, although the rounded cells are not likely to increase the absorption of more oblique light rays (Bone *et al.*, 1985). This comparison of the structure of adult and juvenile leaves of *M. adansonii* shows that the shade-adapted juvenile leaves are less costly in construction and more efficient in energy capture than the adult leaves.

Syngonium rayii is a root climber that ascends to 2–3 m in the forest at La Selva, especially in disturbed areas. The juvenile form is a small rosette of almost black leaves found on the forest floor in deep shade. Juvenile leaves are velvety and about 3 cm long. Adult leaves are a glossy green, cordate, and up to 10 cm long.

Juvenile leaves of *S. rayii* have a significantly lower percentage dry weight and specific weight than adult leaves (Table 8.1). They are slightly thinner and lack approximately one cell layer present in adult leaves (Figure 8.16 vs. Figure 8.17). The proportion of air space does not differ significantly between juvenile and adult leaves, but juvenile leaves have more chlorophyll per unit area. The juvenile leaves absorb significantly more photosynthetic radiation than adult leaves (Table 8.1, Figure 8.19). Part of this increase, however, results from absorbance by anthocyanin at 525 nm and does not contribute to photosynthesis (Lee & Graham, 1986). The efficiency of energy capture (the attenuance/absorbance ratio at 652 nm) is lower in juvenile compared with adult leaves. Juvenile leaf epidermal cells have a convex

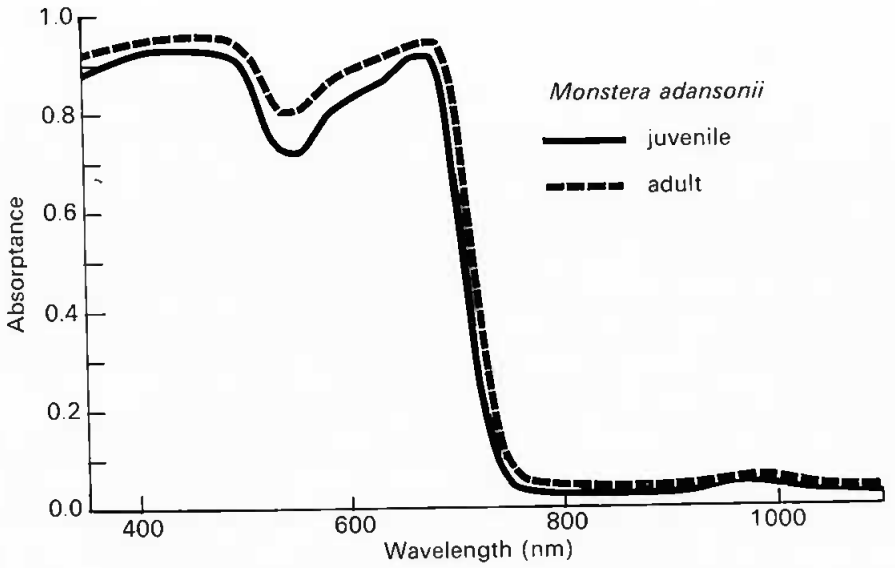


Figure 8.18. The absorbance of radiation between 300 and 1100 nm by juvenile and adult leaves of *Monstera adansonii*.

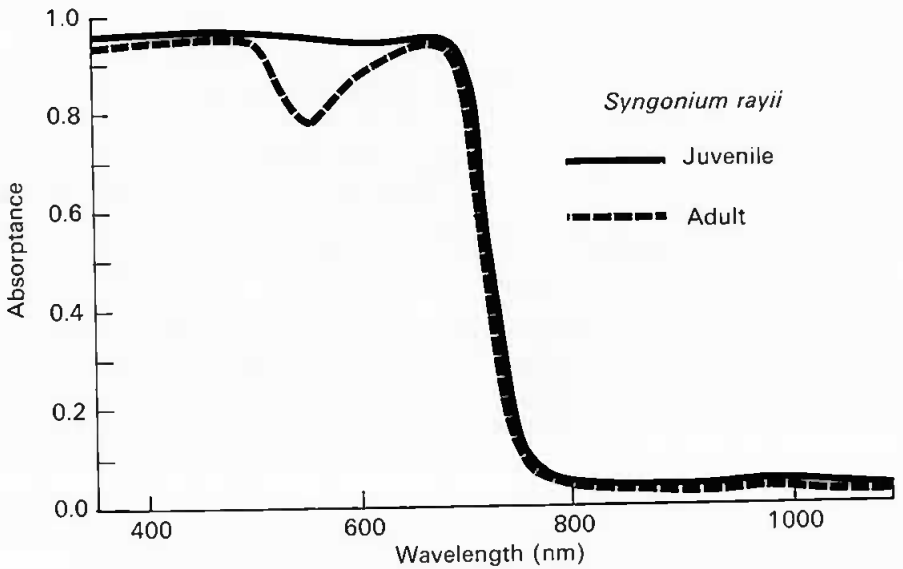


Figure 8.19. The absorbance of radiation between 300 and 1100 nm by juvenile and adult leaves of *Syngonium rayii*.

curvature that focuses light, increasing intensity 6.0 times at the level of the chloroplasts.

In *S. rayii* both juvenile and adult leaves appear shade-adapted, but the two stages have somewhat different adaptations. The adult leaves have a more efficient distribution of chlorophyll, but the juvenile leaves can concentrate light onto chloroplasts.

There are few analyses for leaves at different heteroblastic stages comparable with those presented here. Nilleson & Karetens (1955) showed similar anatomical differences between juvenile and adult leaves of *Marcgravia umbellata*. Analyses of anatomical and leaf optical properties in other vines would allow comparison of adaptive strategies among leaves of heteroblastic stages both within and between vine species.

Experimental approaches to the effects of light on vine development

As Figure 8.11*B* and *C* illustrate, a major challenge in understanding the control of heteroblastic development in vines is to distinguish between intrinsically determined and environmentally controlled components of development. A second challenge is to determine which environmental factors are significant. Here we will discuss experimental ways to study the possible effects of a major environmental factor, light, on vine heteroblastic development.

Light could affect vine development in several ways. Within a morphologically distinct phase, such as the shingle plant of root-climbers, different light regimes could alter the degree of shade adaptation by individual leaves. Light could also act as a cue to switch from one developmental stage to another, or, if some other factor controls the switch, light could change the timing of the switch.

If light affects heteroblastic development, either light quantity (PPF or blue wavelengths) or light quality (R:FR) could be the significant factor. Most research on light effects on plant, and vine, development has been limited to alterations in light quantity and has not considered the effects of light quality at all. Light quality has been shown to affect the developmental responses of some plants, particularly European woodland herbs, to shading (Smith, 1982). Because light quantity and quality tend to covary in natural environments, such as under a forest canopy, experimental approaches are needed to separate their effects.

Lee (1988) distinguished between the effects of reduced PPF and lowered R:FR on the juvenile development of three tropical leguminous vines. Shadehouses were constructed which allowed the penetration of 3% of sunlight. One house did not reduce R:FR, while the other decreased R:FR to

0.35, which was similar to the R:FR in nearby forest understory (Lee, 1989). The vines were twiners, and none were strongly heteroblastic, but the research provides an example of the approach needed to understand the effects of light quantity and quality on vine heteroblastic development.

Two of the three vines, *Mucuna pruriens* and *Caesalpinia bondicella*, were not strongly heteromorphic in their development. Reduced PPF and R:FR affected anatomy and morphology in different, often additive, ways. For example, internodes produced under reduced light quantity were longer than internodes developed in full sunlight for both species. Internodes grown in reduced light quantity and reduced R:FR were not significantly different from internodes in reduced light quantity for *C. bondicella* but were even longer for *M. pruriens* (Lee, 1988).

The third species, *Abrus precatorius*, produced a compact rosette of small compound leaves as a juvenile. After expanding 14 or 15 leaves, the internode distance suddenly increased and the plant adopted its twining habit. Reduced PPF and R:FR profoundly affected the morphology and anatomy of juvenile plants (Table 8.2). Although shade increased internodal lengths, the plants still grew erect. None of the treatments accelerated the heteroblastic change from erect to twining habit. Thus, the intrinsic pattern of heteroblastic development in *A. precatorius* was not affected by light level or quality, although the morphology and anatomy within one heteroblastic stage were altered.

Similar research has been conducted on varieties of beans (*Phaseolus vulgaris* L.) with different growth habits (Kretschmer *et al.*, 1977). Vining varieties of beans typically begin their development with a bushy growth form and later change to a climbing habit. Increased day length can moderately increase the rate of transition to a vining habit in some varieties. Plants exposed to red light in the middle of the dark period are most likely to convert to a vining habit, and this effect can be reversed by far-red irradiation (Kretschmer *et al.*, 1977). Although such a treatment is not equivalent to continuous exposure to altered spectral quality, the results strongly suggest that phytochrome is involved in developmental control of the heteroblastic transition to a vining habit in *Phaseolus*.

Future research on vine heteroblastic development should make comparisons between species and between different developmental stages within a species. These studies should include careful architectural analyses and detailed measurements of variables in the microenvironment associated with different developmental stages. Such information can be used to design experimental studies that will enable us to distinguish the internal and external factors that control heteroblastic development and to understand the adaptive nature of heteroblasty in vines. These are old but unresolved problems in plant biology.

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Table 8.2. *Effect of light treatments on the morphology and anatomy of juveniles of Abrus precatorius*

Trait	Treatment			F	shade
	100% PPF R:FR 1.10	3% PPF R:FR 0.33	3% PPF R:FR 1.10		
Percentage dry weight allocation					
Leaves	54.0 ± 2.7	57.6 ± 1.9	51.0 ± 1.9	***	***
Stems	33.6 ± 2.5	32.7 ± 3.3	39.6 ± 1.6	***	***
Roots	12.4 ± 4.6	9.7 ± 1.7	9.5 ± 2.4	*	NS
Internode distance (cm)	0.3 ± 0.1	1.0 ± 0.3	1.5 ± 0.2	***	**
Leaf					
Area (cm ²)	5.46 ± 0.80	7.97 ± 1.63	5.20 ± 0.49	***	***
Specific wt (mg cm ⁻²)	5.49 ± 1.33	1.86 ± 0.24	1.34 ± 0.21	***	***
Chlorophyll					
mg/g dry wt	4.56 ± 0.72	14.90 ± 2.72	17.59 ± 3.96	***	NS
µg/cm ² area	24 ± 4	28 ± 5	28 ± 5	NS	NS
a/b	2.35 ± 0.13	2.11 ± 0.09	2.10 ± 0.01	***	NS
Thickness					
Leaf	120 ± 15	76 ± 6	100 ± 13	***	***
Palisade	55 ± 10	19 ± 3	14 ± 3	***	**
Stomatal density (10 ³ cm ⁻²)	12.11 ± 1.47	4.88 ± 1.07	8.39 ± 0.54	***	***

Sample sizes for plants were $N=5$, and $N=10$ for leaf characteristics. Statistical comparisons show the levels of significance for ANOVA between all samples (F), and student's T test for the shade treatments (shade): $<0.01 = ***$; $<0.02 = **$; $<0.05 = *$; and $>0.05 = NS$.

From Lee (1988).

Summary

Vines display dramatic developmental changes between juvenile and adult stages and have frequently been used as striking examples of the developmental phenomenon of heteroblasty. In vines heteroblastic stages are strongly correlated with the microclimatic conditions in which each stage occurs, from the humid and shady conditions of juveniles to the sunny and drier environments of adults. We propose that the unique aspect of vine development is not heteroblasty *per se*, but the environmental control and consequent plasticity of heteroblastic development in the vining habit. Traits that vary between heteroblastic stages in vines include leaf morphology and anatomy, phyllotaxy, internode length, and physiology. Evidence suggests that these variations are adapted to the environmental conditions encountered by each stage, but experimental evidence on how the developmental changes are controlled

is lacking. Which aspects of these shifts are genetically preprogrammed and which are induced or modified by changes in environmental conditions? Light quantity and quality vary among vine microhabitats and have been shown to affect heteroblastic development in vines, as well as other plants. Research on the role of such environmental cues in regulating heteroblastic development in vines will make an important contribution to our understanding of vine biology and, more generally, of epigenetic effects on plant development.

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