# Leaf venation patterns and principles of evolution

Ulrich Kull and Astrid Herbig

## Summary

Leaf venation patterns (of dicots and for comparison of ferns) are analyzed according to form and function. From topological investigations of the gross vein system and the patterns of small veins forming areolae (vertices and adjacents, geometry of gross veins, scaling exponents) and from results of physiological anatomy and ecophysiology we deduce a major contribution of selforganization processes in the development of the angiosperm leaf vein system. The resulting plasiticity of the construction of small veins, allowing function under a variety of circumstances, is a prerequisite for the adaptation of angiosperms to very different environmental conditions. In the ontogenetic selforganization process of the small veins the phloem initiation probably acts as a pace-maker. Methods of morphodynamics and functional morphology are used to discuss, when, why and how this key invention for the angiosperm leaf arose during the evolutionary process.

Key words:
leaf vein system, evolution, selforganization, topology, ecophysiology

## Introduction

Leaf vein systems have two major functions: they constitute the transport system and the mechanical reinforcement system of the leaf. Through a comparison of leaves of a fern, a dicotyledoneous plant and a typical monocot the great variability of the venation pattern becomes obvious. Ferns usually have open vein systems with dichotomous branching, where angiosperms in most cases have closed vein systems. From a midrib arise lateral veins (of second order), which branch again; in this way a hierarchical system of vascular bundles forming several orders of veins and veinlets results. They ultimately divide the lamina into areolae (intercostal areas), small compartments in which no mesophyll cell is far from vascular supply (distance < 7 cells). In some cases the closed system exclusively results from anastomoses of small veinlets, but more frequently a network is also established by thicker veins. Often veinlets intruding into the areolae - and sometimes branching further - are developed. They form dead ends, which usually are composed from only one phloem and one xylem element or one tracheid alone and do not contain any reinforcement-tissue. This tissue further is lacking in the veinlets of the areolae, local reinforcement then is met by the tracheids.

The different pattern of the vein system results from leaf growth processes. In fern leaves growth is realized by the meristematic tissues of the leaf margin. In angiosperm leaves growth starts by activity of a submarginal meristem, but later on is taken over by a plate meristem, which causes the development of the lamina by a diffuse expansion process. The vein development usually is completed as the lamina attains about 80% of its final area. Some ferns have a closed vein pattern, however, for most cases it was shown that the network results from a dichotomous branching. Fern leaves usually have no plate meristem, but for some exceptional cases a corresponding mode of growth was postulated (Troll 1939). Gymnosperms in most cases possess open vein systems (*Ginkgo*, conifers, cycads), however, in *Gnetum* a dicotyledoneous pattern is developed. The vein systems of monocots are uniform, rather simple and always closed. In dicots a great variety of types may be seen, occasionally even open systems are present.

The experimental methods used in our investigations were described earlier (Herbig and Kull 1991). The following description of vein patterns according to form and function is concerned mainly with dicots, which are compared with ferns.

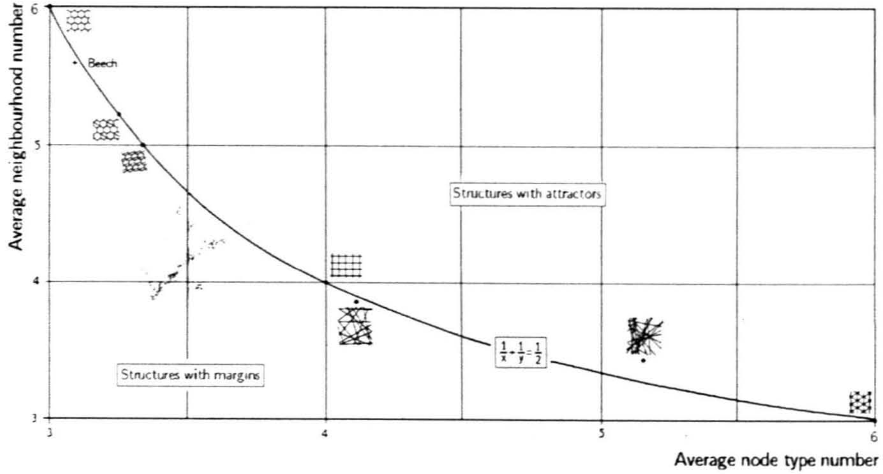

**Fig. 1:** Diagram of grid topology: types of nodes (math.: valence of vertices) versus neighbourhood numbers (math.: number of adjacents). The equation follows as a special case from Euler's theorem for tilings.

## Form: Topological investigations

Nodes (vertices) and neighbours (adjacents): Networks of very different origin (railway or street systems, insect wings, leaf veins) may be described and compared by topological methods. A simple description uses the valence of the nodes (math.: vertices) and the number of neighbours (math.: adjacents) (Schaur 1991). A simple square grid has 4-valent nodes, each square has 4 neighbours. If the network is condensed (more connections) it develops to a 6-node/3-neighbour system. If we want to have less-valent nodes, we get a 3-valent node/6-neighbour system, which may be a hexagonal grid (honey comb) or - by lateral compression - a brick-wall system. If considering an unlimited network and allowing only convex meshes, we get a diagram showing a curve as in fig. 1. Real networks have margins, causing border effects: in our diagram such systems are situated below the ideal curve. Network structures with centers (attractors) with many-armed nodes are found above the curve. Data of Schaur show that self-generating structures

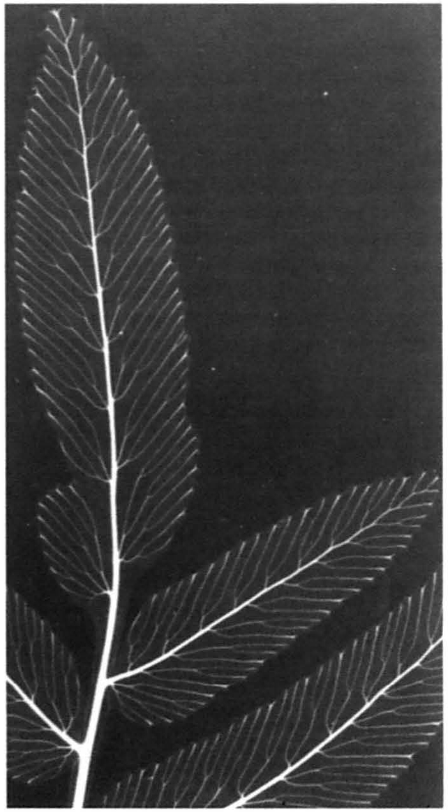

**Fig. 2:** *Osmunda regalis*, vein system of a part of the leaf. Thickening of the midrib causes a development of 3-valent to 4-valent nodes and by further thickening again to 3-valent nodes.

**Fig. 3:** *Aneimia phyllitis*, detail of the leaf vein system. The meeting veins consist of separate tracheids; no connecting tracheids between the two traces exist.

as bubble floats or crack patterns are found near the point of a 3-valent/6-neighbour grid. Deviations seem to be caused only by the margins. Leaf vein systems preferably have 3-valent nodes; the observed 4-valent nodes are in most cases caused by growth processes (fig. 2). Fig. 3 shows that in the leaf-vein system of the fern *Aneimia* veins meet and in this way form a network. For leaf vein systems from a functional point of view, the number of neighbours is not very interesting, because in reality the neighbours are not the areolae, but the much smaller cells. However, in leaves with extended bundle-sheaths forming a reinforcement system by mechanical compartmentation the areolae have an independent integrative function. Vein extensions form borders in the mesophyll tissue and may e.g. stop the spreading of a parasite (e.g. mold, virus).

Vein pattern and supply: The vein system in dicots shows a species specific compactness. The maximum distance of cells to vascular bundles are limited. The arrangement of the veinlets influences the distances, therefore the supply system may be more or less homogenous (fig. 4). Ferns have less efficient supply systems (great distances between veinlets) than angiosperms. Generally in trees the systems are more homogenous than in herbs. In herbs even within one species and on the same plant the differences may be conspicuous (for herbs water transport is not a limiting factor if high water content in the soil is assumed, because transport through guttation is possible).

Geometry of the vein pattern: The question of a geometric optimization of the vein-arrangement is discussed controversely since Schuster (1908) who expressed the construction of the areolae to be economical and Goebel (1932) who illustrated his contrary opinion by monocot leaves. Each "point" within an areole must be supplied by the surrounding veins. Therefore, not the intercostal area as a whole is important but the radius of the maximum possible inscribed circle. Presuming a constant inscribed circle radius, it may be shown by geometric comparison that the periphery/area-proportions for equilateral polygons are the same as for the circle (limiting case), however, the enclosed areas are different. If we presume that two contact-points with the inscribed circle are sufficient, we can still get more favourable proportions using rectangles (table 1).

Table 1: Radii r of maximum inscribed circle and proportion of periphery (P) : area (A) as a function of r for different geometric figures

| Geometric figure (side length a) | r | P/A (r) |
|---|---|---|
| square | $a/2$ | $2/r$ |
| equilateral triangle | $a/2\sqrt{3}$ | $2/r$ |
| equilateral hexagon | $a\sqrt{3}/2$ | $2/r$ |
| rectangle with $b=2a$ | $a/2$ | $3/2r$ |

Within a leaf the problem is to minimize the distances of the "points" (cells) to be supplied by an economic vein-system (this means: with the least investment of energy or mass). When we exclude margin-problems and compare grids of squares, triangles, hexagons, and rectangles, we find that the investment is the same for all polygon-grids, but rectangular systems are more favourable regarding supply (table 2). The limiting case would be a system of only parallel veins. This is important especially for the pattern of "expensive" veins - that means the thick veins of

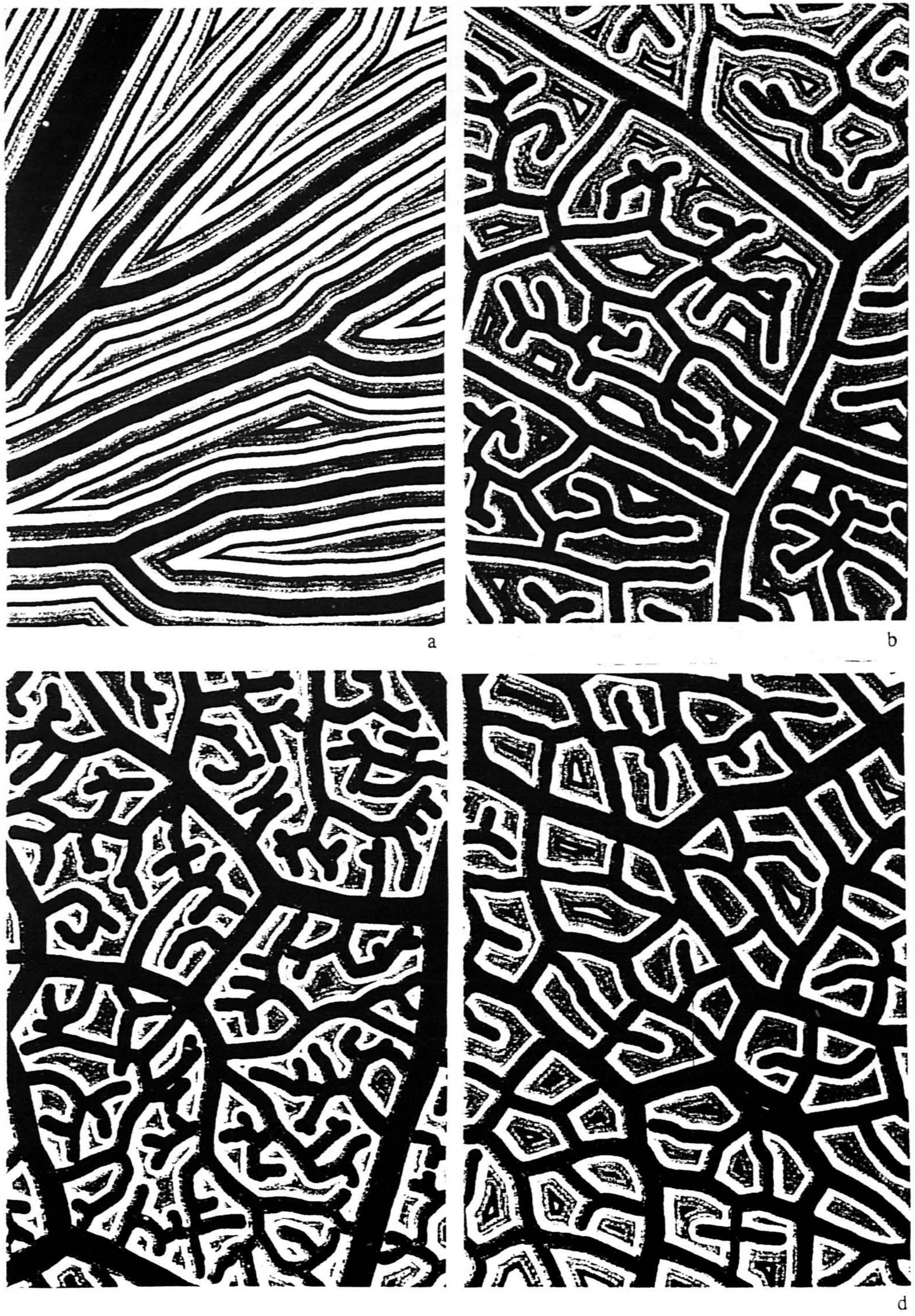

**Fig. 4:** Equidistances of cells from veins characterize the supply system. More different signs means a more heterogenous supply system.
a *Osmunda regalis* (a fern), b *Tropaeolum maius* (a dicot herb), c *Liquidambar styraciflua* (a tree), d *Acer rubrum* (a tree)

Table 2: Geometric characteristics of grid patterns of unlimited area (n grid units)

| grid pattern (side length a) | total path length L | total area A | L/A | L/A (r) |
|---|---|---|---|---|
| square grid | $n \cdot 2a$ | $n \cdot a^2$ | $2/a$ | $1/r$ |
| triangular | $n \cdot 3a$ | $n\sqrt{3} \cdot a^2/2$ | $2\sqrt{3}/a$ | $1/r$ |
| hexagonal | $n \cdot 3a$ | $n \cdot 3\sqrt{3} \cdot a^2/2$ | $2/a\sqrt{3}$ | $1/r$ |
| rectangular ($b=2a$) | $n \cdot 3a$ | $n \cdot 2a^2$ | $3/2a$ | $3/4r$ |
| parallels, length l | $n \cdot l$ | $n \cdot l \cdot a$ | $1/a$ | $1/2r$ |

secondary order. In fact, in very different leaf types parallel veins are realized (comp. fig. 2, 5, 6). The advantages of a network with parallel major elements have long been understood by man: drainage systems and streets in a town (fig.7) show such patterns where in nature self-forming river-systems in an invariable stratum constitute another example.

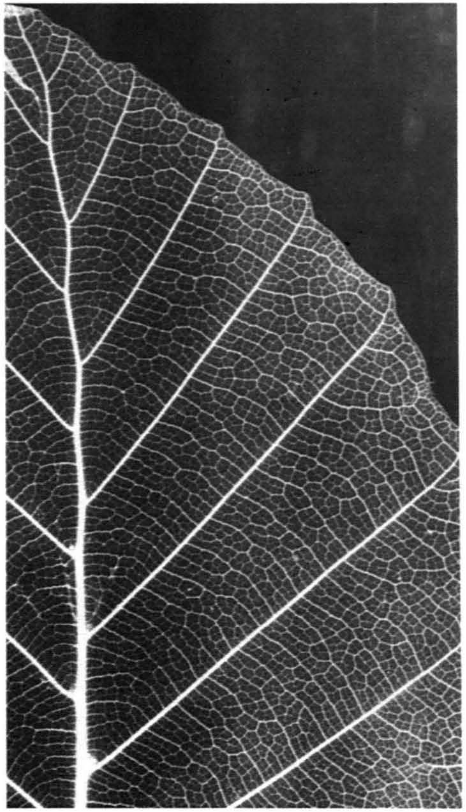

**Fig. 5:** *Fagus sylvatica* (beech), parallel system of secondar veins and partially parallel system of tertiary veins.

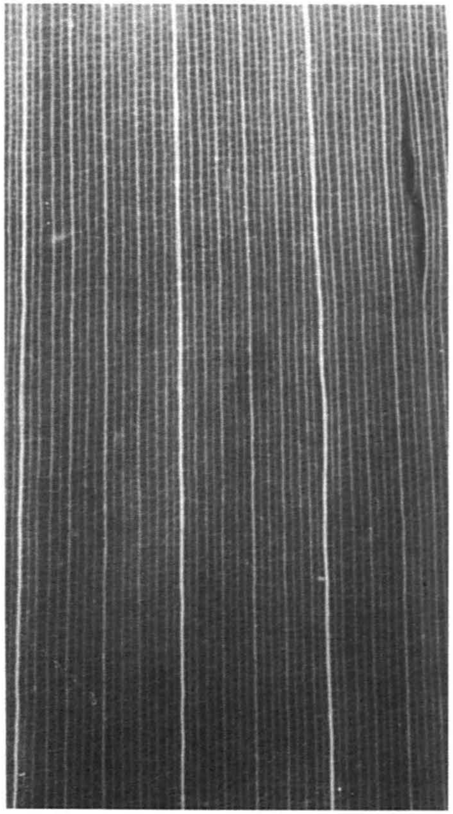

**Fig. 6:** *Musa basjoo* (a banana), typical parallel vein system of a monocot.

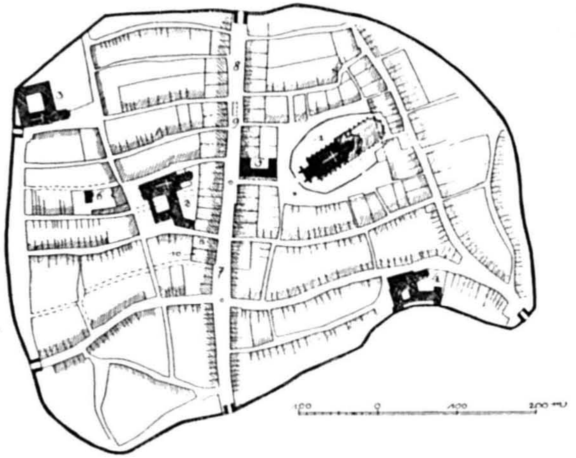

**Fig. 7:** Plan of the city of Freiburg i.Br., typical parallel street system of a planned medieval town.

Branching angles: The form and arrangement of the first order lateral veins is well known and described by a special terminology (e.g. Dilcher 1974). This results from the importance e.g. for paleobotany. However, there are only few data on the branching angles and the variability of the number of lateral veins.

Preliminary results from our investigations show a great variability of the length of leaves of a species and their length/width proportions. However, the angles of the lateral veins are rather species-specific and their small variations do not correlate with the leaf proportions. Investigations of the variations within one tree show that larger leaves have more lateral veins, but these have larger distances one vein to the next than in the smaller leaves.

During leaf development two separate processes take place: the establishment of the second order veins in a very early bud stage and the growth of the leaf lamina. The length of this growth-period and the intensity of cell divisions determines - limited by genetic constraints of pattern formation - the leaf length and area. There is plasticity in this "late" ontogenetic processes, as may be seen from the development of sun- and shade-leaves.

## Form: Scaling exponent

The fractality of a ramification pattern can be used as a scale independent value which allows a direct comparison of different branching systems. The fractal character of the leaf vein system was shown in our earlier investigations (Herbig and Kull, 1991), in which we used the grid-dimension according to Peitgen and Saupe (1988), but pointed to its limited value due to its lacking use of the vein-diminution. Therefore, now a measure is preferred in which the diameter of the veins is included. If a relation length = diameter$^d$ (for veins) is fulfilled, d is a fractality measure, called the scaling exponent. It is not a fractal dimension in a strict sense, because it may reach values > $|2|$ for leaf vein systems. The calculation by an image-processing program developed by Pfeil could be accomplished after scanning leaf-vein drawings of different magnifications. Over special sets of sizes of veins with a diameter larger than that of the maximum length a scaling exponent can be determined (fig. 8). However, the main veins do not fit into a linear presentation of log-transformed data, because they have a different pattern and usually contain a higher proportion of sclerenchymatous tissue. Variations of the scaling exponent

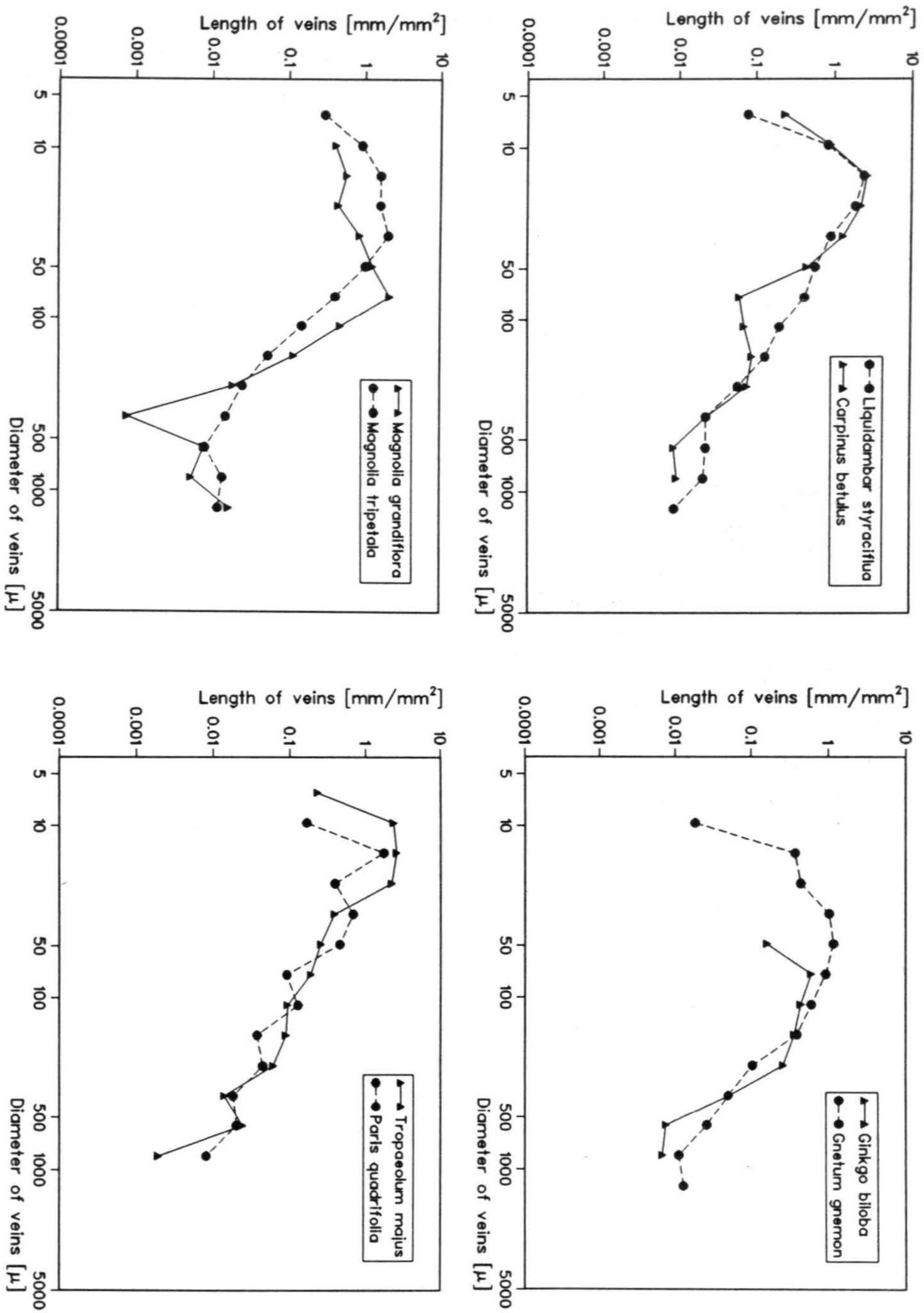

**Fig. 8:** Graphs for determination of scaling exponents of the leaf vein systems. An exponent can be deduced from those parts of the graphs which are by approximation linear. The localization of the graph yields information on the vein system: the higher the ordinate values reached are, the more biomass is used to build up the vein system; the higher abscissa values are found, the thicker are the major veins, which point to a higher effectivity of mechanical reinforcement.
a *Liquidambar* shows one scaling exponent over most diameter classes (except veinlets); *Carpinus* exhibits characteristic differences for different classes of vein diameters. b The gymnosperms *Ginkgo* and *Gnetum* have low maximum values (a thin vein system) an three (resp. four) ranges of scaling exponents. Despite a very different vein pattern of the two species the graphs show much similarity. c *Magnolia tripetala* (decidous) and *M. grandiflora* (evergreen) both show one clear scaling exponent value over a variety of vein diameters, pointing to simplicity in development. d *Tropaeolum* and *Paris* are shown as examples of herbs.

and deviations are shown better in a diagram (fig. 9) according to Hastings and Sugihara (1993). In most cases at least three main ranges of different scaling exponents can be observed: the major vein system, the vein-network and the smallest veinlets with dead ends.
Self-similarity is characterized by constant scaling exponent values over some sets of sizes; it economizes the genetic information: less information is necessary for building up a complicated pattern and probably the same realization process is used during morphogenesis to generate different grades of the hierarchical vein system.

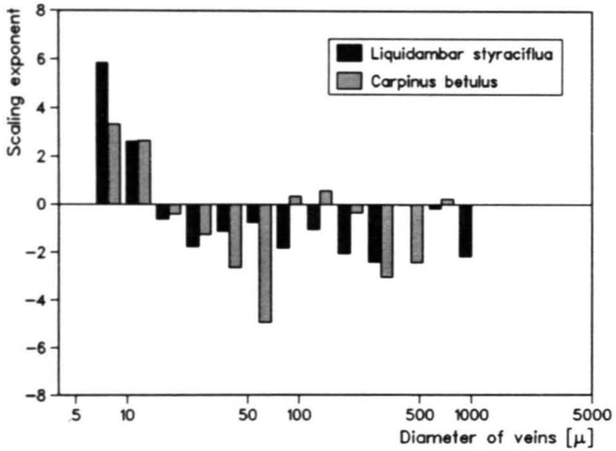

**Fig. 9:** Variations of scaling exponents of leaf vein systems for different vein diameters.

## Function

Physiological anatomy of the vein pattern: A functional characterization of the vein system demands criteria of classification which allow a quantitative description. We chose species according to geometric and ecophysiological criteria to cover a variety of types. The quantities used in physiological anatomy to describe the vein systems are shown in table 3:

- l: density of veins (length per unit leaf area)
- a: area of veins per unit leaf area
- A: average area of areolae
- N: veinlet termination number = average number of dead ends per areole
- N/A: quotient: veinlet termination number/average areole area

Only some important results are described; the details are of primarily ecophysiological interest.

Table 3· Quantitative anatomical and ecophysiological data of the leaf vein systems

| | species | l mm/mm² | a mm²/mm² | average areole area A mm² | average number of dead ends per areole N | quotient N/A | maximum transpiration rate µg·cm⁻²·s⁻¹ | diffusive resistance s·cm⁻¹ |
|---|---|---|---|---|---|---|---|---|
| pteridophytes | Selaginella | 0.7 | 0.02 | no areolae | | | | |
| | Osmunda | 2.0 | 0.11 | • | | | | |
| gymnosperms | Ginkgo | 1.4 | 0.14 | • | | | 9.1 | 1.4 |
| | Gnetum | 4.9 | 0.21 | | | | | |
| evergreen | Myrothamnus | 10.5 | 0.28 | 0.012 | 0.3 | 25 | | |
| | Magnolia grandifl. | 5.8 | 0.28 | 0.085 | 1.3 | 15.3 | 5.5 | 2.5 |
| deciduous trees | Magnolia tripetala | 7.3 | 0.17 | 0.120 | 1.4 | 11.7 | 7.4 | 1.0 |
| | Liriodendron | 5.4 | 0.12 | 0.522 | 3.5 | 6.7 | 7.3 | 1.4 |
| | Carpinus | 7.0 | 0.14 | 0.049 | 0.4 | 8.2 | | |
| | Fagus sun leaves | 9.5 | 0.33 | 0.026 | 0.4 | 15.3 | 8.1 | 1.2 |
| | Fagus shade leaves | 9.0 | 0.28 | 0.031 | 0.2 | 6.5 | 3.7 | 2.8 |
| | Liquidambar | 7.7 | 0.15 | 1.275 | 25.5 | 20 | 5.8 | 2.2 |
| | Acer ginnala sun | 11.5 | 0.27 | 0.082 | 3.5 | 43 | 8.6 | 1.6 |
| | A. ginnala shade | 7.7 | 0.14 | 0.209 | 4.3 | 20.6 | 6.6 | 1.4 |
| | A. rubrum | 6.3 | 0.12 | 0.081 | 0.6 | 7.4 | 6.5 | 1.8 |
| | A. saccharinum | 8.5 | 0.17 | 0.034 | 0.2 | 5.9 | 11.7 | 1.2 |
| | A. platanoides | 8.2 | 0.25 | 0.036 | 0.8 | 22.2 | 8.9 | 1.3 |
| | A. campestre | 6.3 | 0.24 | 0.097 | 1.2 | 12.4 | | |
| | A. monspessulanum | 8.1 | 0.22 | 0.032 | 0.1 | 3.1 | 7.4 | 1.5 |
| herbs | Bupleurum | 8.6 | 0.16 | 0.228 | 5.6 | 24.6 | 26.5 | 0.5 |
| | Tropaeolum | 5.7 | 0.07 | 0.155 | 0.8 | 5.2 | | |
| | Oxalis | 1.9 | 0.06 | 1.219 | 0.5 | 0.4 | | |
| | Paris | 1.5 | 0.08 | >5.97 | - | - | | |

The values of vein-densities and their variations are similar to what is already known: in general, the density is higher in sun-leaves than shade-leaves, higher in xerophytes than meso- and hygrophytes, higher in trees with great amplitudes of water supply than in those with balanced water-budgets. A comparison of density values between different species is of only limited value as vein-extensions - if present - take over reinforcement functions.

The area of veins per unit leaf area is a dimensionless number which can be taken as a rough measure of supply. The supply is better in xerophytes than mesophytes, in evergreen than deciduous leaves and better in trees than in herbs. Again, this is primarily important regarding water conditions of the leaves.

The average areole area is not only a question of supply, but also of local mechanical reinforcement. Small veins may be more effective in this reinforcement than is deducted from the amount of their xylem, because a small tensile strain is brought about by the rather negative water potential values ($\Delta\psi$-effect) in the tracheid(s). If vein-extensions are present, they work as a mechanical system and the areolae may be larger than expected. To get similar supply, the areolae may be larger if the distances are equalized by more dead-end veinlets. The quotient of both (N/A) characterizes the supply system. Xerophytes and sun leaves have small areoles or high veinlet termination numbers (or both) and therefore high values of the quotient. Within the genus *Acer* the varying density of the vein extensions in different species seems to be important.

From further correlations of some of the values among one another, some more regularities may be recognized. Fig. 10 shows that the larger the leaf area, the higher is the vein density. Larger leaves perhaps need more veins (per area!) for mechanical reinforcement. But the leaves with very high densities are in most cases small leaves. This probably is caused by an ecophysiological constraint: the very high vein lengths are found in leaves needing under certain circumstances an extremely intense water supply - and these used to be leaves of xerophytes.

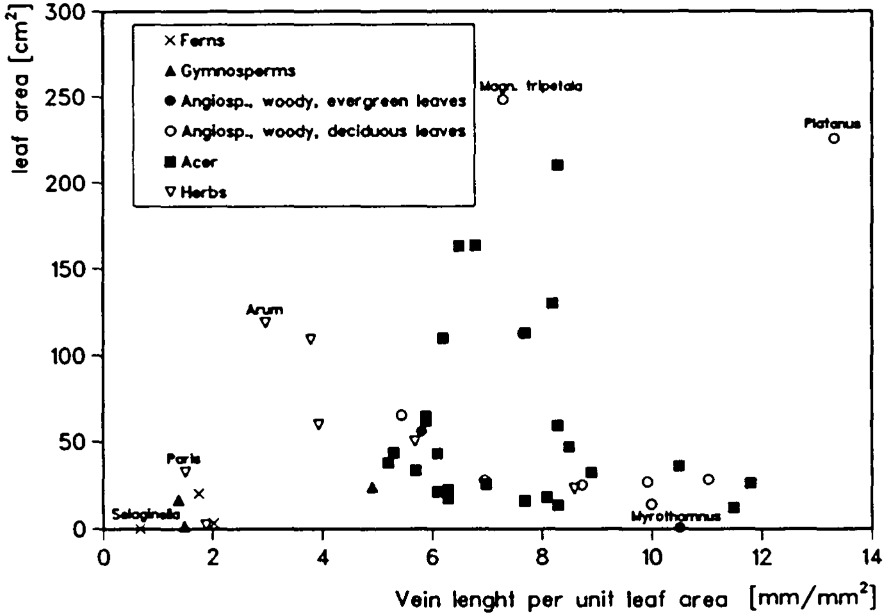

**Fig.10:** Correlations between leaf area and vein density.

Ecophysiological investigations: In mesophytic *Acer* species with rather large leaves (as e.g. *A. platanoides*) one can see with the unaided eye that leaf lamina areas between the thick secondary veins are stretched like slightly curved shells. When loss of turgor causes wilting, the strain of the laminal areas is lost. Because of the water potential differences effective when the stomata are open, all the small veins have negative water potentials and their tracheids surrounding the areolae are under weak tensile strain ($\Delta\psi$-effect). This probably causes local stretching. When the stomata close, $\Delta\psi$ reaches zero and the local reinforcement by stretching is lost (but reinforcement by turgor potential in the cells is maintained).

Information on the capacity of the leaf veins as a water transport system and its "success" is gained from measuring the maximum transpiration rates (measured with a LI-COR-1600-porometer under optimal conditions) and the drought-resistance. The measured transpiration rates are higher than those reported by Larcher (1980), but in several cases similar to the data in Kaufmann (1976), probably because only maximum values were recorded. Maximum transpiration rates were obtained with optimal photosynthetic active radiation and medium values of water potential differences between leaf and air (fig. 11; table 3). If this $\Delta\psi$ rises further (e.g.

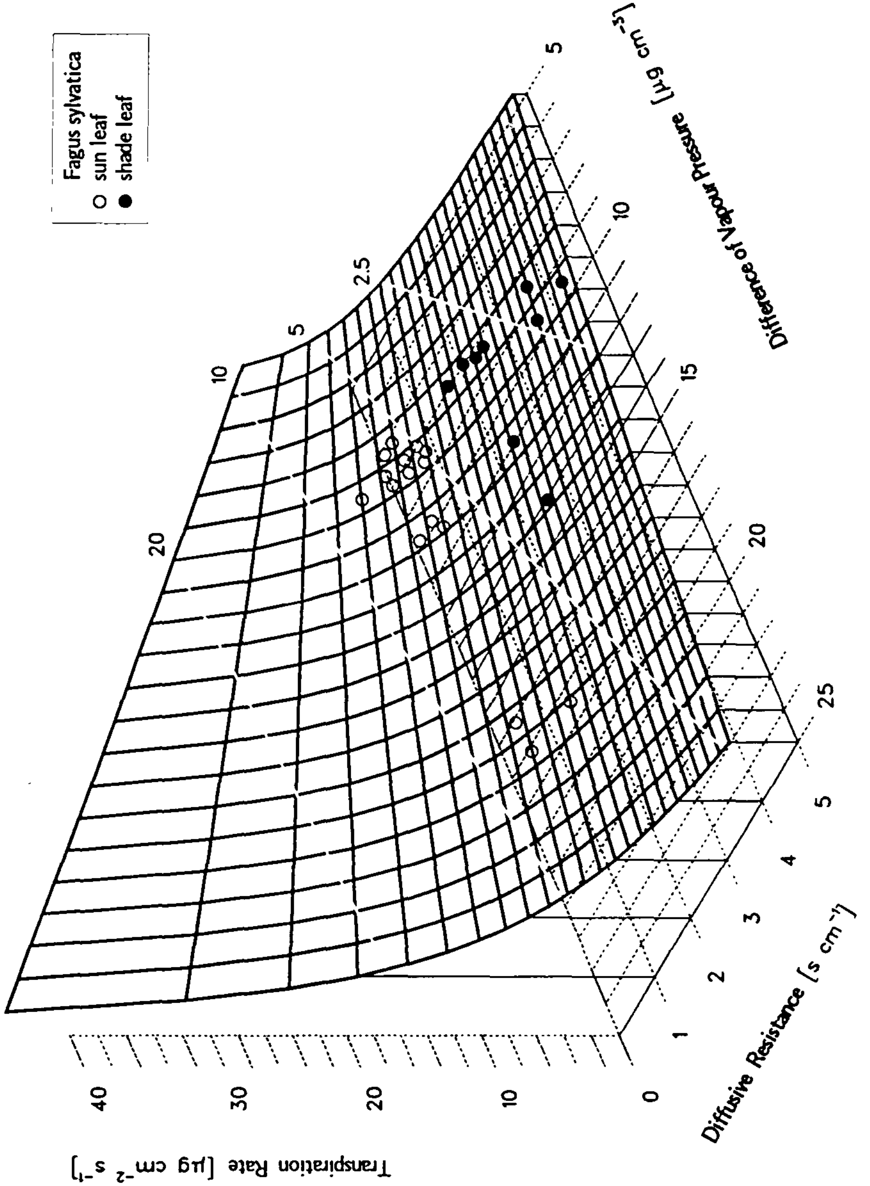

**Fig.11:** Maximum transpiration rates of sun- and shade-leaves of *Fagus sylvatica* (beech). The transpiration rates depend on the vapour pressure difference and the opening width of the stomata. The data are presented in a three dimensional diagram. Marks at 2,5, 5, 10, and 20 $\mu g/cm^2s$.

by experimental conditions), stomatal regulation takes place and the transpiration rates are maintained rather constant, which means a continued regulation of the stomata/water state-system in the leaf. As a further relation example the connection between properties of the leaf-vein system and the transpiration rates is shown in fig. 12.

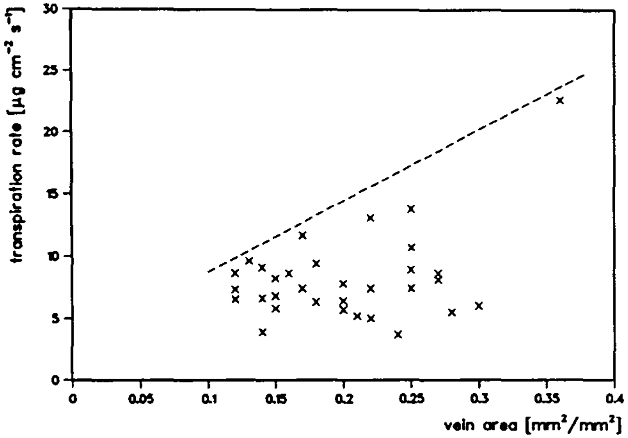

**Fig.12:** Correlation of maximum transpiration rates of leaves with the vein area per unit leaf area. A limiting graph seems to be caused by the limit of water supply.

Conclusions: A leaf is primarily a system for trapping and transforming light energy and therefore, the main biochemical factory of the plant. Besides $CO_2$, also N, water and appropriate temperatures are necessary for its maintenance. These and some other environmental variables have a major influence on the leaf development during ontogeny as on its (phylogenetic) evolution. The relations are summarized in fig. 13.

In a leaf the cost/benefit ratio must be a maximum in a persistent way. The laminar form of a leaf is caused by the light trapping function, as may be concluded from a simple geometrical consideration. A duplication of the volume of a leaf could theoretically result in very different geometric shapes. By which of these shapes would the different functions of the leaf (light trapping, storage, transport, reinforcement, defence) be optimized? For all functions except light trapping a compact leaf (small surface) would be best, only the utilization of light - and further, if in wet areas an excess of water must be transpired - needs a laminar form. Transport and reinforcement are accomplished by the vein system; its evolution is subordinate to the overriding selection-pressure for light trapping.

During evolution a multicriteria optimization takes place, in which many different strategies are possible as may be concluded from fig. 13. Which of these are favoured by selection cannot be predicted. The selection pressures will modify that organ or tissue, whose ontogeny or shape or previous function can most easily respond (Ganong's principle).

To reach maximum efficiency, long living (evergreen) leaves must adapt to the unpredictable environment to a higher degree than short living leaves, similarly leaves of trees must adapt more than leaves of small herbs. Most successful under such conditions is not a strongly fixed optimal construction, but one allowing a reliable function (and development) under a variety of circumstances. In spite of the many possibilities, the shape of the vein system is primarily caused by water conditions and reinforcement, as confirmed by our ecophysiological data. The data also point to a rather high plasticity of the system of small veins. The question now is: how is this plasticity accomplished during leaf development and in evolution? From our investigations on form we conclude that the vein system in part is destined by genetic determination and in part specified by self organization. This most certainly leads to high plasticity.

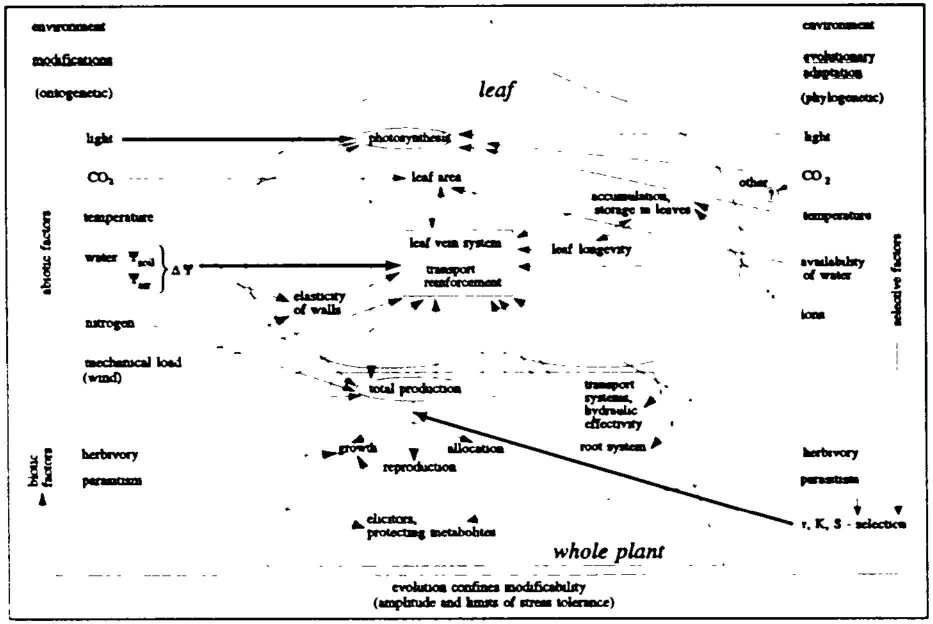

Fig.13: Leaf vein system. ontogenetic and phylogenetic dependence on environmental factors. Not all factors are included (e.g leaf shape, petiole state are omitted). The relations are described primarily on the level of tissues and organs; cellular and physiological aspects are not shown in detail. The mutual dependencies of environmental factors (as e.g temperature/$\Delta\psi$) are not included. - During evolution the leaf vein system is liable to a multicriteria optimization process.

## Hypothesis

Ontogeny of the leaf vein system: The species specific pattern of the major veins is most probably generated in all cormophytes according to the same general principle of the realization of a genetic program. This realization may be described by the Gierer-Meinhardt hypothesis (Gierer and Meinhardt, 1972; Meinhardt 1979), which postulates the operation of an activator and an inhibitor. The pattern of the areolae and veinlets in angiosperm leaves is variable, as may be seen from a comparison of sun- and shade-leaves from one tree. Its variability is limited by genetic constraints, but also chance is important during ontogeny.

The generation of this pattern is probably a process of self organization. During early growth, after initiation of the elements of the major vein system, the plate-meristem is differentiating in the bud. Veinlets are initiated in approximately the largest distance from already differentiating veins, but the accurate locality is determined by chance through small asymmetries. A genetic constraint of this self organization process may be concluded from the development of vein extensions. In leaves with vein extensions the value of their distances divided by the average least vein distances is rather constant (Wylie 1951).

The veins do not only contain xylem, but also phloem elements. This seems to be of major importance for the self organization process. In the closed bud of an angiosperm tree, the problem is not the water supply, but the supply with organic substances for plasmatic growth. The initiation of at least one protophloem element increases transport which is necessary for the construction of the tracheid and perhaps of sclerenchym cells. This leads to an autocatalytic positive feedback for vein development, operating as an "activator". Evans (1976) claimed such a process to be caused by the Matthew-effect ("For unto everyone that hath, shall be given, that he shall have abundance", Matth. 25, 29). If the phloem has to provide organic compounds for a larger area, there will be a stronger sink, inducing a more effective vein growth, which probably is further influenced by the plant hormones. The hormone balance (esp. auxins/cytokinins) seems to be the simplest way to prevent a similar differentiation of meristematic cells in the immediate neighbourhood of a veinlet. This is the inhibitory effect necessary for pattern generation. In this differentiation process phloem elements have the outrider function, which is in accordance with anatomical data regarding ontogeny (Esau 1943). However, after initiation, the xylem elements develop more readily: water supply is a prerequisite for further cell growth and the veinlet-endings finally produced often only consist of one xylem element. In dicot leaves the process may be hierarchical, large meshes of the vein network, the areolae and the free ending veinlets are brought about by the self organization process which comes to an end when the meristematic growth of the lamina finishes. The state reached at this moment is frozen and visible as the pattern of the smallest veinlets.

The genetic fixed major vein pattern thus seems primarily determined by the development of the water transport system, which is evolutionary canalized, as shown by Mosbrugger and Roth (in press). The pattern of small veins in angiosperms very probably is intended by a self organisatory process for which in ontogeny the phloem initiation acts as a pace-maker.

Evolution of the leaf vein system: The self organization of the system of small veins seems to be a key invention in the evolution of spermatophytes. Its ecological and physiological advantages are clear from the previous remarks. The main questions of an evolutionary description are: when, why and how did the key invention appear.

When? Meshes in leaves of ferns and pteridosperms occur from the Westfalian (Upper Carboniferous) onwards. They are similar to what is found in several ferns today in which a primitive form of plate growth participates in their development.Plate growth is a prerequisite for the evolution of a self organizational vein differentiation. Typical areolae are found in *Pannaulika triassica*, a dicot-like leaf from the Upper Carnian, perhaps belonging to a proto-angiosperm (Cornet 1993). Today, the gymnosperm *Gnetum* shows a somewhat similar vein system with areolae.

Why? During the Upper Carboniferous the transition to a cool period of earth history began ("cold store" period of the Late Paleozoic). Much $CO_2$ was fixed in big coal measures and the plate motions led to the estabilshment of pangaea. Plants had to adapt to more severe climatic conditions. The photosynthetic efficiency had to be maintained under lower $CO_2$ concentrations and worse water conditions. Simultaneously, mechanical reinforcement had to be stabilized under an adverse climate. During the period from Uppermost Carbonifeous to Triassic these strong selective forces caused the development of a more adaptable "new vein system". The above mentioned factors determine the genetic constraints of the self organization process of vein until today! From preliminary experiments with a tropical species of the fern *Asplenium* we conclude a significant leakage of water from its veins. According to the literature, the leakage is low in angiosperms. The "new vein system" thus is more effective.

How? As described, the first step - achieved by some ferns - was the evolution of a plate growth,

resulting in a gross mesh system of veins. The key invention of self organization of the system of smaller veins probably was driven by the phloem differentiation (in accordance with the biogenetic rule!) which was necessary for the development of a typical bud. The bud is an adaptation to temporary drought which might be one of the leading factors of angiosperm evolution. The evolution of the angiospermous bud very probably is connected with the development of the "new vein system". The combination of the plate growth with the more effective and more adaptable vein development is a preadaptation for evolution of angiosperm leaves to variable ecological conditions. The system of medium class veins was perhaps originally characterized by vein-extensions as an adaptation to temporary drought. Their pattern is genetically fixed. During evolution these extensions were lost in hygrophythes and many mesophytes, in which the $\Delta\psi$-effect is sufficient for local reinforcement.
The advantages of the angiosperm vein system may be seen from the fact that all ferns which have to survive under severe water stress are poikilohydrous plants but poikilohydrous angiosperms are rare exceptions (e.g. *Myrothamnus*).

Evolution; general implications: The higher plasticity raised by the key invention of the self organized vein system increases fitness in variable environments. It allows optimal partitioning of biomass and functional adjustment during ontogeny. During geological periods of great environmental fluctuations a rather quick adaptation within the limits of the genetic constraints is possible. This may lead to different adaptations of the vein systems of the species of one plant family during geologically short periods.
The self organization hypothesis also may overcome the problem that in some regard cells seem to be only markers of growth and not the source of morphogenesis. Therefore, it makes such efforts as to construct a hypothesis deriving multicellular plants from coenocytic algae (Kaplan and Hagemann, 1991) needless.
A problem not further discussed is the temporal control of the self organization process requiring an elaborate timing system (Romberger et al. 1993), for which according to recent findings the activity of a transcription factor may be central (ffrench-Constant, 1994). This reflection may call to attention that biology still is one discipline -from molecular to ecological level!
Through the key invention of the angiosperm vein system new niches were established, e.g. for many insects which use the ressources in a new mode (leaf-mining, veinlet-sucking ...). So it also serves as an example for the general principle that the number of ecological niches rises during evolution which, therefore, is an infinite and open process.

## Acknowledgements

Thanks are due to our coworkers, the Dipl.-Biol. Susanne Diehl-Rückert, Ute Schubert, Dr. Ulrike Vallon und Gabriele Zauner for assistance, especially in arduous computing. The investigations would not have been possible without the help of many members of other projects, which is gratefully acknowledged. They are Dr. J. Greis (D 6), Dr. Eda Schaur (C 2), Dr. A. Kesel (B 4), Dr. A. Roth (B 5) and the Geschäftsstelle of the SFB. Special thanks are due to Prof. Dr. G. Blind (Math. Institute). For supply with plant material we want to thank Mr. Scheffel (Hohenheim), for correction of the English Mr. Carsten Hoffmann (Irvine) and for typing of the mscr. Mrs. Sabine Pfafferott.

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