

Leaves and Ramification

Astrid Herbig and Ulrich Kull (Stuttgart)

Abstract

Leaf veins have two main functions: they constitute the mechanical reinforcement system and the transport system. To analyse the vein pattern it is necessary to have a - as far as possible - quantitative description of the vein system of real leaves. Quantities used in modern plant anatomy have to be completed by measurements of the fractality of the ramification system (as grid dimension and as exponent of scaling) and by a measure for the partition of the leaf area and the complexity of the patch pattern which we call the supply coefficient.

The leaf venation pattern is a result of the evolutionary process. To find out criteria of a relative optimization during this process, we used simple models of the ramification of leaves. By computer methods such models were tested regarding their quality as a reinforcement system. In real leaves, there must be compromises between reinforcement and transport functions.

The quantities used to describe the leaf vein systems can be applied to other reticulate systems. We selected street nets of towns, and some comparisons between the ramification systems of leaves and of towns show similarities and differences which are discussed.

Introduction

A plant leaf is traversed by a system of veins. The median vein, which is a continuation of the petiole, is the midrib. From the midrib arise lateral veins which branch and anastomose to all parts of the leaf and in this way produce a system of ramification. This system of venation is known as reticulate. Where the main veins run more or less parallel to one another, the venation is said to be parallel.

Leaf veins have two different functions:

- They constitute the system of the mechanical reinforcement of the leaves. The midrib and the main veins contribute to this function to a greater extent than veins of second order and so on. This is the mechanical function of the vein system.
- Leaf veins constitute the system of water supply and of dispatch of the organic substances produced in leaf cells. This is the transport function of the vein system.

The pattern of the veins of plant leaves is very variable. Even species of the same genus, which show a similar pattern of the coarse veins, often exhibit remarkable differences regarding the thin veins and veinlets.

Material and Methods

We selected different types considering different systematic groups of higher plants and the ecological variability within one genus. *Acer* (the sycamores) was used as the latter from which we chose species adapted to different environments but growing in the Botanical Garden under the same artificial conditions. The present interim-report is mainly concerned with data from the *Acer* species; for reasons of comparison some results obtained on *Tropaeolum majus* (nasturtium) are included.

To get information on the details of the venation system, the leaves were made translucent by mazeration and then stained (by 1% safranin in ethanol). But even then, the finest veins and their dead ends only can be identified unambiguously on the microphotographs by the biologist and not by a scanner. Also trichomes interfere in the evaluation of microphotographs. Therefore it appeared that the vein system had to be traced over from the photographs of different magnification. Then, the veins of different diameters could be well distinguished and investigated. Some drawings of vein systems are shown in fig. 1.

For reasons of comparison with other branching systems we used the street systems of Paris of the 19th century and of Rome of the 18th century (fig. 2). Where necessary (e.g. for image processing) town plans were normalized in such a way that the narrowest

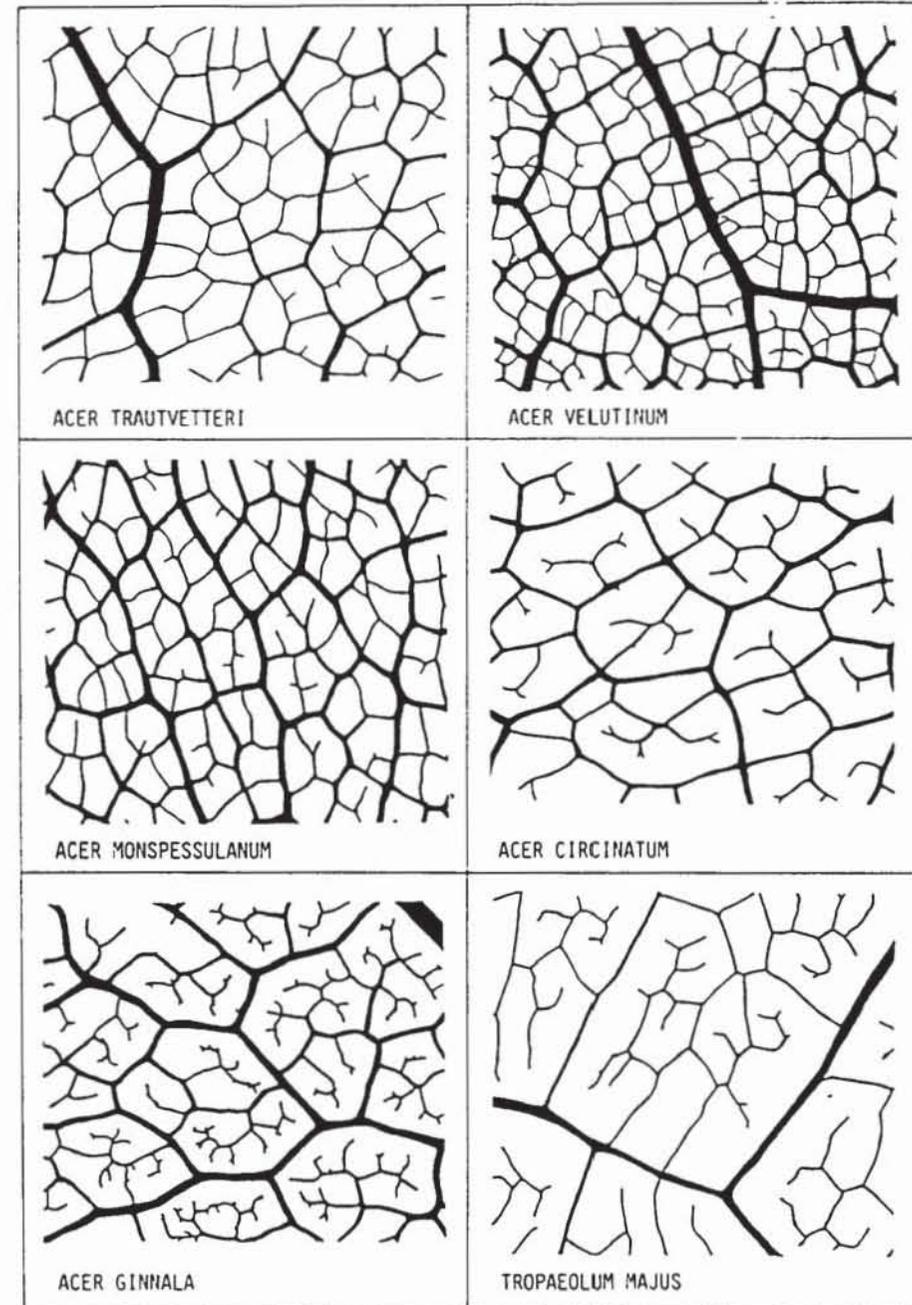


Fig 1 Vein systems of five *Acer* species and of *Tropaeolum majus*

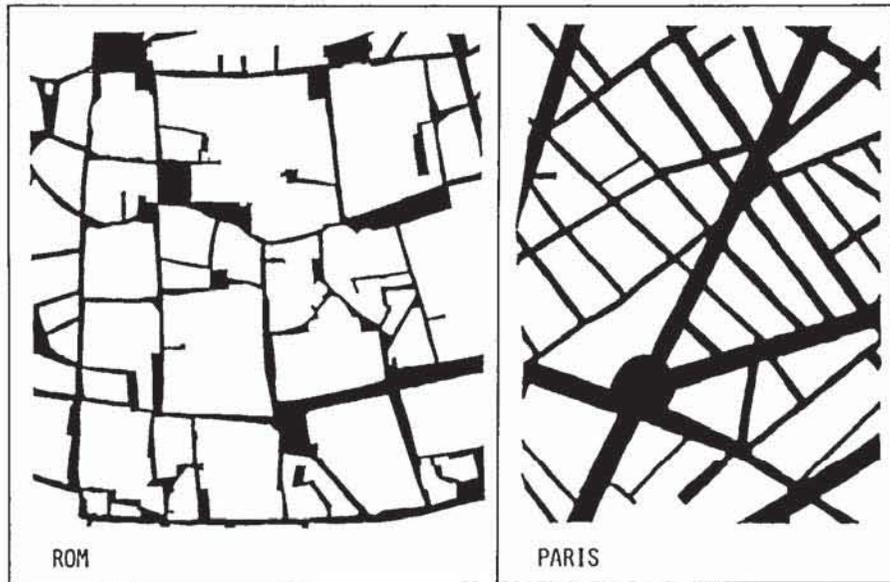


Fig 2 Town maps of quarters of Rome of the 18th century and of Paris of the 19th century

streets had about the same diameters as the smallest veins. This means a shift of the linear scale of about $1 : 10^6$ (or $1 : 10^{12}$ for the plane).

Results and Discussion

Quantitative plant anatomy

Differences in the vein systems can be seen from fig. 1. Species of *Acer* from very dry, steppe like habitats (e.g. *Acer ginnala*) have more dead vein ends than species of mesic and damp forests, the vein system of which shows more meshes (areoles). On the other side, *Tropaeolum*, a rather hygic species (but with a higher degree of succulence than *Acer* leaves) also has many dead ends.

It is known that many species of the families belonging to Magnoliidae have vein systems with many dead ends (SEILACHER, pers. comm.; KLUCKING 1986). The Magnoliidae are thought to be a group of Angiosperms with many rather primitive characteristics, so perhaps also a vein system with many dead ends and a weak reticulation is primitive.

For a more precise characterization of the vein system it is necessary to have criteria of classification which allow a quantitative description of the vein pattern of real leaves. Some quantities

are used in modern plant anatomy (NAPP-ZINN 1974). They are included in table 1:

- Number of dead ends in a defined area, This value is called the veinlet termination number and is also used in pharmacology. Alternatively, the number of areoles relative to the leaf area may be used. This value is low when the vein system has many dead ends. A system with few dead ends has a small mesh-size, which leads to a better mechanical reinforcement.
- Density of the veins, that means length of veins relative to the leaf area.
- Area of veins relative to the leaf area. This is a crude measure of supply of a leaf area and therefore of the effectiveness of the transport. It is a scale-independent measure which enables comparisons with any other branching system without normalization.

Table 1: Values of the quantitative measures of the vein system of the *Acer* species, *Tropaeolum maius* and for comparison of the branching systems of streets in Paris and Rome.

Species	L	A	VM	SC	GRD	PO	TRA	THI
<i>A.trautvetteri</i>	7.27	0.138	12.9	19.8	1.54	18.5	6.1	0.075
<i>A.velutinum</i>	8.28	0.273	27.5	19.9	1.61	26.7	8.7	0.092
<i>A.monspessulanum</i>	8.80	0.217	23.3	20.8	1.55	21.8	5.0	0.111
<i>A.circinatum</i>	5.31	0.164	6.2	17.6	1.52	17.2	6.7	0.051
<i>A.ginnala</i>	7.27	0.204	6.7	19.4	1.56	22.0	x	0.068
<i>Tropaeolum</i>	5.21	0.086	4.2	21.2	1.43	11.3	23.6	0.105
Paris	23.72	0.405	266.0	10.0	1.74	36.7	---	---
Rome	12.56	0.249	63.7	12.6	1.64	23.2	---	---

L: length of veins/leaf area (mm/mm^2)

A: area of veins/leaf area (mm^2/mm^2)

VM: vein-meshes/leaf area ($1/\text{mm}^2$)

SC: supply coefficient (mm/mm)

GRD: grid dimension

PO: pixels occupied (area of veins) (%)

TRA: maximum of transpiration-rate ($\mu\text{g}/\text{s} \cdot \text{cm}^2$)

THI: thickness of leaf (mm)

x: not yet available

The number of areoles relative to the leaf area shows a very low value for *Tropaeolum* (table 1). In this hygrophytic plant the turgor (the pneu-character) of the cells is more important for the mechanical stability of the leaf than in the *Acer* species. For the density of veins the data in literature (collected by NAPP-ZINN, 1974) vary between about 1

(hydrophytes) and 11 to 12; they depend on the ecology of the plant and also on its life shape. The mean value of several species with oval leaves and of mesic habitats is about 9 to 11; for the *Acer* species investigated we obtained values from 5.3 to 9.

Grid dimension

These anatomical qualities do not sufficiently describe the ramification system. So we had to develop and to test further measures. It is obvious to check if the vein system is self-similar or fractal. As for all real systems, fractality only can be expected in a limited range. For laymen, fractality often seems to be somehow connected with living things. For example, dendrites are often thought to be plant fossils - this is because of their fractal character. But it is long known that they are inorganic products.

The fractality of the ramification pattern is a scale independent measure and should allow a direct comparison to other branching systems as, for instance, wings of insects, public traffic systems, nets of paths and roads and so on. The fractal character of a branching system can be measured in different ways. A rather simple method is the determination of the grid-dimension according to PEITGEN and SAUPE (1988). Because it is used frequently, comparisons to other systems are easily possible

To determine the grid-dimension grids of different mesh-size are laid on the branched structure and the number of occupied meshes is counted. fig. 3 shows the logarithm of these numbers plotted against the log of the mesh-width. If the points form a straight line, the ramificated structure is fractal and the slope of the straight line is the fractal (grid) dimension. From fig. 3 it may be seen that the branching system is fractal in a very good approximation. This investigation is accomplished using a program developed by FRANK-HAUSER and SADLER, which could be established after scanning the drawings of the leaf vein systems. From methodical reasons until now mainly the system of thin veins was investigated, but for two examples it was shown that inclusion of the coarse-veins provide the same fractal dimensions in a good approximation. This seems important to us, because grid dimension values are also measured by MOSBRUGGER using primarily the coarse veins, because he has to include fossil materials in which only the coarser veins are recognizable or preserved.

Fig. 4 shows that the grid-dimension is well correlated with the area of the veins relative to the leaf area. But this only is true within the branching system of leaves and not when other ramification systems are considered.

As already mentioned, we can compare the results from the leaves with the the street-systems of Paris and of Rome. For these systems we find higher grid-dimensions and relative large areas of the streets (fig. 4). When modern towns were included, the areas

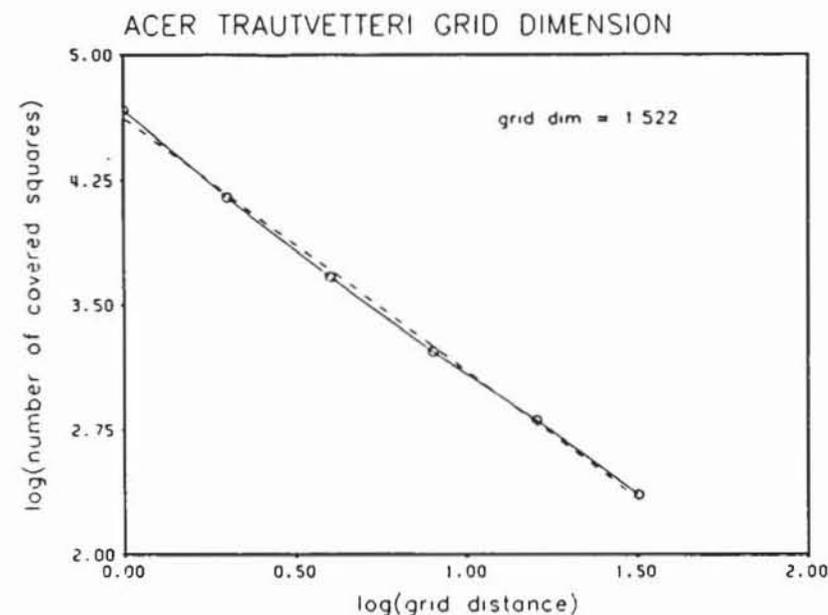


Fig 3 Determination of the grid dimension (example. *Acer trautvetten*)

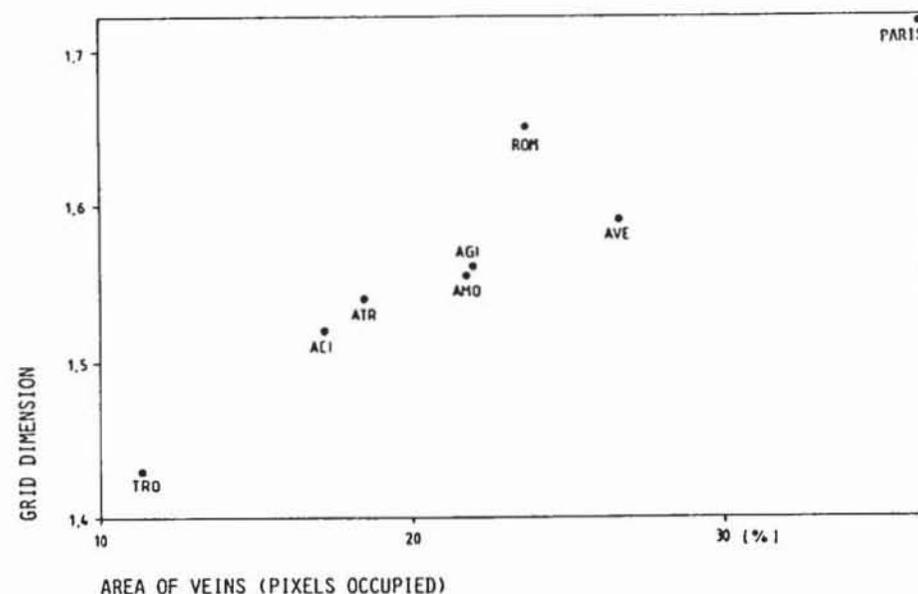


Fig. 4 Correlation of the grid dimension values with the values of the areas of the veins/unit leaf area. The values of the grid dimensions of Paris and Rome are also included.

of the street-systems would be still more spacious. Therefore we can say that leaf venation systems are "slimmer" than the street systems of modern towns. According to FRANKHAUSER, the grid dimension of the Stuttgart railway system (S-Bahn) is 1.56. This value of a slim (and very effective) system fits well when compared with the values of *Acer*.

Scaling exponent

The grid dimension does not contain information on the diminution of the veins. Therefore another measure was developed in which the diameter of the veins is included. Fig. 5 shows the length of veins (per area unit) against the corresponding diameters of the veins, both in logarithmic scales. If there is a relation

$$\text{length} = \text{diameter}^d$$

the points must be situated on a straight line and its slope d then is a fractality measure which we call the exponent of scaling. In this case the fractal dimension can go beyond 2. The calculation was possible by a program of image-processing developed by PFEIL. Leaf vein drawings of different magnifications were scanned. Only a small part of the material available could be evaluated until now; so it is premature to draw general conclusions.

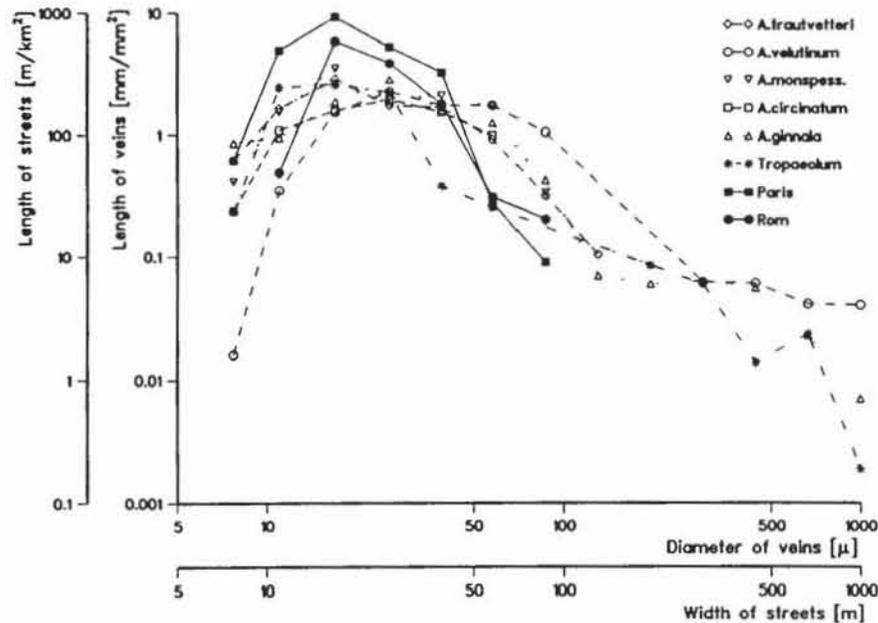


Fig. 5: Determination of the exponents of scaling of the leaf vein systems.

From fig. 5 it may be seen that the greatest length (per area) is found for thin, but not the thinnest, veins. The maximum value is found at lower diameters for *Tropaeolum* than for the *Acer* species. For very thin veins (veinlets) no scaling exponent results, but for veins with diameters more than those of the maximum length (diameters 10-30 μm) such a value of fractality can be determined as an approximate value. It is not a fractal dimension in a strict sense because it can go beyond 2. What that means in a biological sense we at present could only speculate of. The scaling exponent seems to be lower for *Tropaeolum* than for the *Acer* species. Significant differences between these latter species are not clear, because the statistical computing is not yet available.

The street-system of towns can be included into such a view without problems as shown in fig. 5 for Paris and Rome. The scaling exponent in these cases is higher than for the investigated leaves.

It is well comprehensible that the veinlets do not fit into the general image; they differentiate at the end of the growth process of the leaf and therefore irregularities may be expected. It is not yet sure whether the main veins really fit into a straight line; because they have a higher proportion of sclerenchymatous tissue linearity cannot be expected by all means.

One may ask what self-similarity (fractality) of the vein system of leaves does mean in a biological sense. Self-similarity economizes the genetic information: the same information may be used for the generation of the vein pattern of all orders and by the same morphogenetic realization process during the early growth of the leaf - at least when the fractal dimension is lower than 2.

Supply coefficient

Another quality independent of scale is what we call a supply coefficient. It is a measure for the partition of the leaf area and the complexity of the patch pattern. Normalized by PFEIL this coefficient SC is defined by the formula

$$SC = \frac{U}{2\sqrt{\pi A}} - 1$$

where U = perimeter of the vein system
 A = area of the vein system

A higher value of SC means a more complex patch pattern. For the species of *Acer* the SC-values are in the range 17 - 20.

Again, the computing also can be used for street systems; in our examples of Paris and Rome the SC-values are much lower. This means that the towns have simpler patch patterns, which is obviously true. The value would be higher for an Islamic town with its many dead ends. When more transport-systems are developed, the supply coefficient rises, as may be seen for *Tropaeolum* with its greater proportion of very thin veins. Regarding the mechanical reinforcement the main veins are much more important, but they are few and therefore their influence on the SC-value is rather low.

Mechanical reinforcement

Employing SEILACHERS principle (SEILACHER, 1970) for our investigations, we can say that the leaf vein pattern depends on mechanical constraints, on the ecophysiological adaptation of the plant and on its phylogenetic history. The latter subject is investigated by MOSBRUGGER. Data on the environmental conditions and on the ecological tolerance of the species can be drawn from literature and own experiments to find out the maximum value of the transpiration as a measure for the transport capacity of the leaf vein system complete these data. Because the leaf venation results from the evolutionary process, the hypothesis of a relative optimization during evolution may act as a theoretical background. To find out criteria of optimization it is advantageous to use simple models of leaves and their vein systems. Then by computer methods it should be possible to figure out favourable constructions for the mechanical system and - separately - for the supply system. Real leaves always must be compromises. From a comparison of real leaves with the artificial models perhaps it will be possible to see in which cases the mechanics and in which the transport systems have more influence upon the shape of the vein system.

Leaf models

The models of the mechanical reinforcement system were calculated with the help of BLETZINGER with a finite-element program used in statics. Different vein pattern were preset (fig. 6). In the model leaves the mass of the veins was arranged in different ways approximating real patterns and varying leaf-form, leaf-area and Young's modulus of the veins and of the leaf-tissue considering the data from literature. Applying Young's modulus is a simplification, but it is necessary to be able to use the methods of statics. Using the program, the deformation of the leaf under its dead weight is calculated. Physiologically, this makes sense, because under great loads the leaves move out of the way. With this method it is possible to find out the strategies which allow the construction of a rather plane leaf. For narrow and middle-sized leaves the best pattern is a medium number of

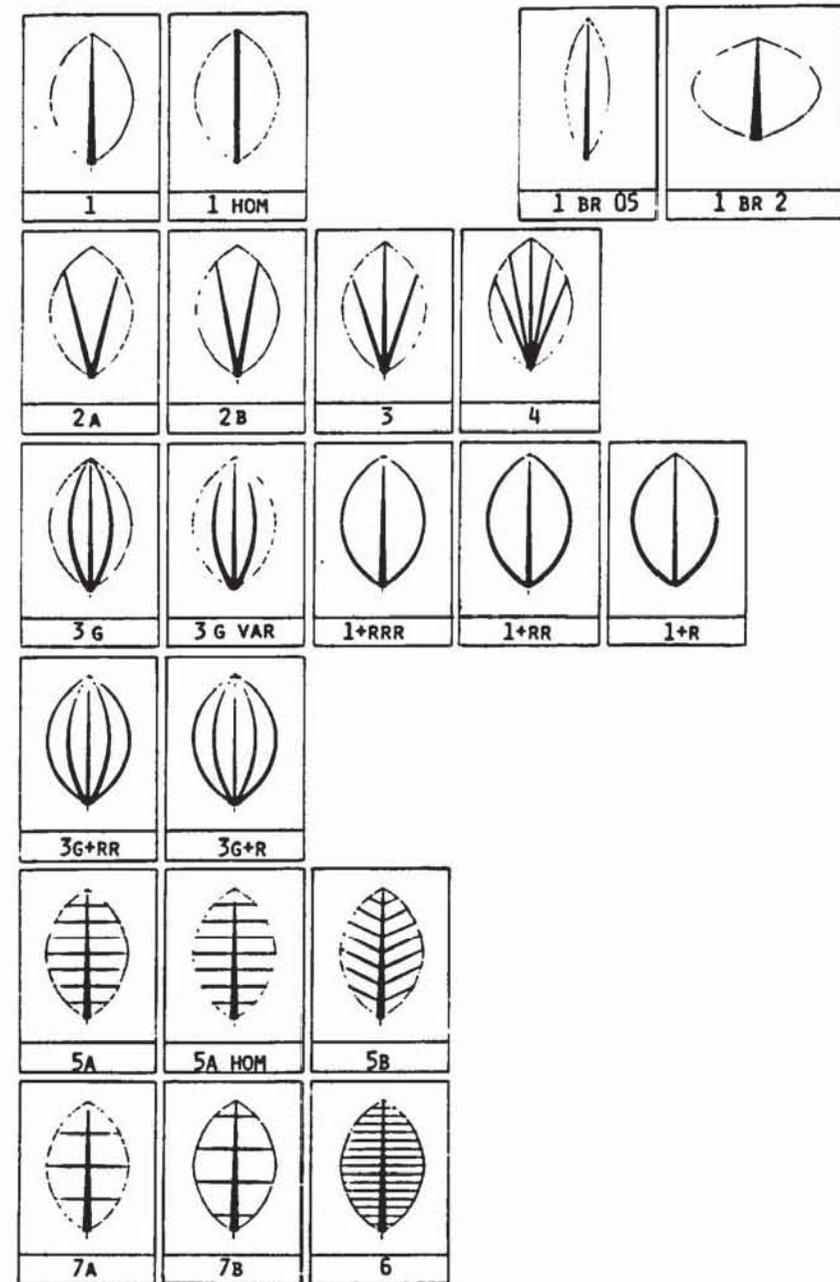


Fig. 6: Variation of models

lateral veins rectangular to the mid-rib (fig. 7). For broad leaves a more or less parallel venation is mechanically more effective. (Grass-like and very narrow leaves were not included in our investigation). Strategies to generate mechanically more stable leaves (fig. 8) can be related to: diminution of the leaf; pattern of reinforcement; increase of Young's modulus (not only of the vein-systems, but also of idioblastic sclerenchyma, epidermis and of the mesophyll-tissues). In a next step the influence of variation of the reinforcement of the leaf margin was tested. The resulting effects for leaves of different width are shown in fig. 9. With the computer program available, it is not yet possible to optimize the system in a strict sense (in our calculation the vein pattern was preset!).

Capacity of the transport system

To get quantitative data on the capacity of the transport system of our model leaves they were covered with a grid (fig. 10) and for all crossing points of the grid pattern the direct way D to the petiole and also the way to the next vein and through the vein-system to the petiole (way K) was measured and the length of this detour calculated as a percentage

$$\frac{U-D}{D} \%$$

The poorest value (17.7%) naturally is found for the model leaves with a rectangular vein system. The number of secondary veins, in this case, has only a minor influence. Better values are obtained when the secondary veins arise with acute angles (12.8%) and even better values are obtained for model leaves with parallel veins (10.5%). Further improvements are to be expected by variation of the angles or by using a denser system of parallel veins. The real leaf of *Acer trautvetteri* was tested for reasons of comparison and a value of 7.6% was obtained. This is the best value at all which we got - nature is better than our simple models!

This calculation is based only on a geometric view of the vein system and therefore cannot include all factors which are effective. We are not yet sure how to incorporate the important effects of higher transport velocities in thicker veins, which in leaves often causes a detour to be more effective and quicker than the direct way.

We have not yet enough data to generalize our results. When the set of data will be more complete, it should be possible to find out which of our several variables show strong (phylogenetic or mechanical) constraints and which vary considerably, e.g. as a consequence of ecological adaptation.

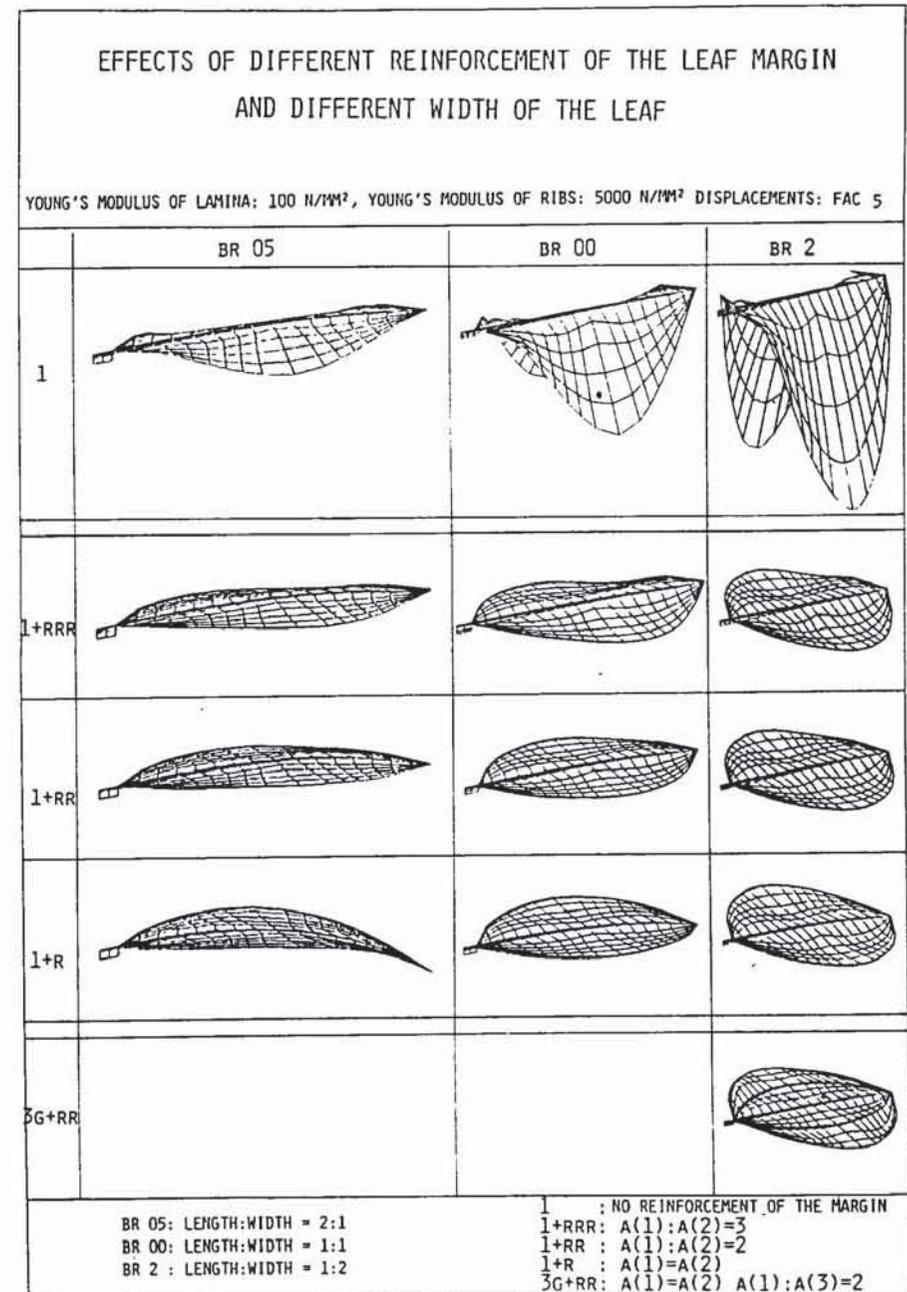


Fig. 7: Effectiveness of different vein systems as patterns of reinforcement (Finite element method).

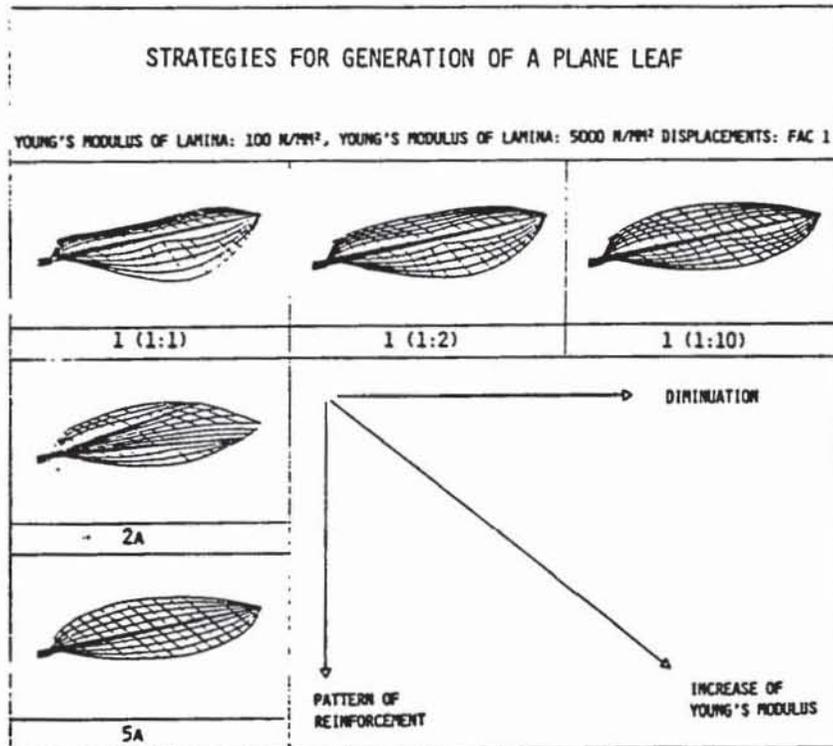
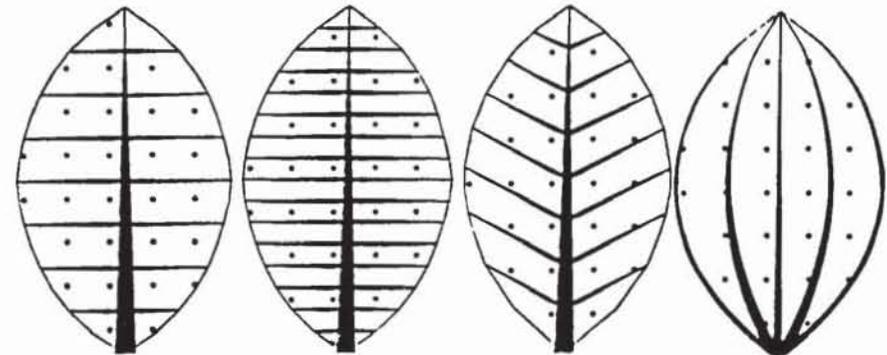


Fig. 8: Strategies for the generation of a plane leaf



ACER TRAUTVETTERI

Fig. 10: Model leaves and real leaf of *Acer trautvetteri*: crossing points of the grid pattern for which the detours were calculated.

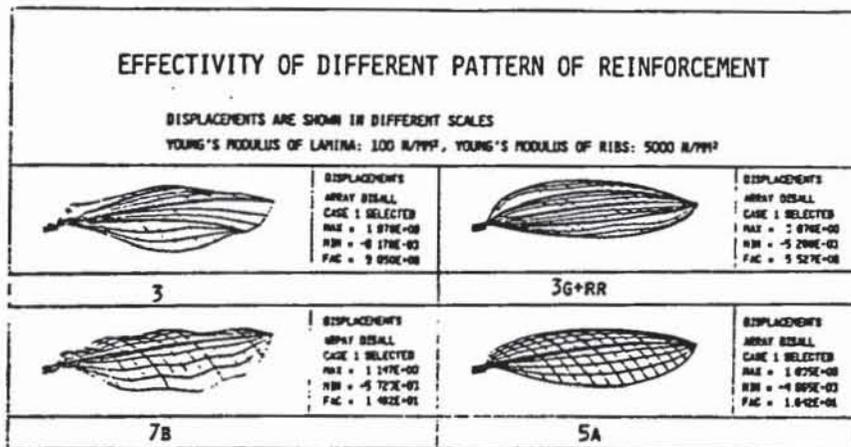


Fig. 9: Effects of different reinforcement of the leaf margin and different width of the leaf on the mechanical stability of the lamina.

Comparison with road systems

Finally, the problem of the comparability of the ramification system of leaves with that of road systems shall be discussed. The thin veins of the leaf form a reticulate supply system just like the streets in a town. The grid dimensions of the street systems of Paris and Rome were already mentioned. They are higher than those found for leaves, the supply coefficient is lower, the length of streets and their area per unit area are much higher and also the number of meshes per unit area is higher when normalized as mentioned (compare table 1). What is the reason for these differences? Leaves are supplied by a system which has three dimensions; the coarse veins and also thinner veins usually are thicker than the mesophyll tissue between them. A town has houses with several floors, but the supplying system (streets) is developed mainly in two dimensions. In botanical terminology: the mesophyll (houses) is thicker than the veins (streets). Only some additional supply-units (water, gas) and in modern time the underground-railway systems turn into the third dimension. A second reason may be the following: for leaves it is important that all cells are connected with the petiole and, additionally, that sufficient safety in the vein system against disruption of transport by local damage is warranted. In a town, it is necessary to reach much more places without great detours than in a leaf. Therefore, the network of streets must have smaller meshes and less dead ends.

The area which is necessary for supply is higher in Paris of the 19th than in Rome of the 18th century (table 1; A). For modern towns the values would be still higher and the fractality of the street system would be broken because of the establishment of large new thoroughfares.

Our results show that a leaf is much more economical and more effective regarding the "good of area" and this is achieved by an effective use of the third dimension. But the comparability of the ramification in a leaf and in a town is limited. A leaf grows to a final size according to a genetic program and influenced by the environmental conditions. A town never gets ready and never reaches a final size. When we see street-works and building-grounds in a town, we often erroneously think these phenomena only to be temporal - but they are the normal state in a town. We also cannot anticipate the future development of a town. Therefore it is not possible to simply transfer results of our investigations into town-planning: there is no bionics of town-planning! But perhaps from our results it may be possible to see what in any case would be disadvantageous for a town.

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References

- KLUCKING, E.P. (1986): Leaf venation patterns. Bd. I: Annonaceae. Berlin.
- NAPP-ZINN, K. (1974): Anatomie des Blattes. II Blatt Anatomie der Angiospermen (-Handbuch der Pflanzenanatomie). Berlin, Borntraeger.
- PEITGEN, H.O. and SAUPE, D.(eds.) (1988): The science of fractal image. New York, Springer.
- SEILACHER, A. (1970): Arbeitskonzept zur Konstruktionsmorphologie. *Lethaia* **3**, 393-395