R E V I E W

Evolution and Function of Leaf Venation Architecture: A Review

A N I T A   R O T H - N E B E L S I C K * †,   D I E T E R   U H L ‡,   V O L K E R   M O S B R U G G E R † and H A N S   K E R P ‡

†*Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Sigwartstr. 10, D-72076, Tübingen, Germany and* ‡*Abteilung Paläobotanik, Geologisch-Paläontologisches Institut, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, D-48143, Münster, Germany*

The leaves of extant terrestrial plants show highly diverse and elaborate patterns of leaf venation. One fundamental feature of many leaf venation patterns, especially in the case of angiosperm leaves, is the presence of anastomoses. Anastomosing veins distinguish a network topologically from a simple dendritic (tree-like) pattern which represents the primitive venation architecture. The high degree of interspecific variation of entire venation patterns as well as phenotypic plasticity of some venation properties, such as venation density, indicate the high selective pressure acting on this branching system. Few investigations deal with functional properties of the leaf venation system. The interrelationships between topological or geometric properties of the various leaf venation patterns and functional aspects are far from being well understood. In this review we summarize current knowledge of interrelationships between the form and function of leaf venation and the evolution of leaf venation patterns. Since the functional aspects of architectural features of different leaf venation patterns are considered, the review also refers to the topic of individual and intraspecific variation. One basic function of leaf venation is represented by its contribution to the mechanical behaviour of a leaf. Venation geometry and density influences mechanical stability and may affect, for example, susceptibility to herbivory. Transport of water and carbohydrates is the other basic function of this system and the transport properties are also influenced by the venation architecture. These various functional aspects can be interpreted in an ecophysiological context. © 2001 Annals of Botany Company

Key words: Review, leaves, leaf venation, evolution, network, transport, flow, mechanical stabilization.

INTRODUCTION

Ramified structures represent a common constructional concept in plants which is realized, for example, in the plant axis system, the root system and in the arrangement of conducting bundles in macrophylls (microphylls will be not considered here). In contrast to the three-dimensional axis and root systems of plants, leaf venation can be considered as a two-dimensional ramifying structure. Owing to its importance for systematic classification, attention is paid largely to the architectural properties of leaf venation (e.g. Zetter, 1984; Köhler, 1993). In palaeobotany, macrofossils showing leaf venation patterns are extensively utilized in identifying fossil taxa (e.g. Melville, 1969; Alvin and Chaloner, 1970; Cleal, 1981; Walther, 1998). Few investigations deal with the functional properties of the leaf venation system (Nelson and Dengler, 1997). Ramifying structures are, however, a common phenomenon in living, non-living and anthropogeneous systems, being associated with transport (of mass, energy, forces) (e.g. Bejan, 1997). Well-known examples are the circulatory systems in vertebrates, the tracheidal system of insects, the branching pattern of a river delta or the arrangement of streets in a city. Recently, Pelletier and Turcotte (2000) demonstrated the statistical similarity between geological river drainage networks and the venation pattern of an angiosperm leaf (*Sorbus hybrida*).

It is therefore to be expected that the architectural properties of leaf venation are related to functional aspects. The high interspecific variability of leaf venation patterns indicates strong selective pressures acting on the architectural arrangement of the conducting bundles of a leaf. High variability is also demonstrated by the venation density which shows strong differences on the intraspecific and individual level (Uhl and Mosbrugger, 1999). However, the functional background of this variation is not well understood. An improved knowledge of the influence of architectural properties on the various functional features of leaf venation patterns is thus desirable. Investigations of biological transport phenomena in branching systems which provide for internal fluid flows to maintain vital functions are dominated by the consideration of zoological problems (Canny, 1993).

In this paper, we summarize current knowledge of the evolution of different leaf venation patterns and possible interrelationships between form and function of leaf venation systems. Since functional aspects of architectural features of different leaf venation patterns are considered, the review also refers to the topic of individual and intraspecific variation. Emphasis will be placed on angiosperm leaves due to the great variation and the elaborate architecture of their conduit systems. The article is subdivided as follows: (1) a short introduction of possible

* For correspondence. Fax 0049-7071-949040, e-mail anita.roth@uni-tuebingen.de

topological descriptions of ramifications, followed by a short summary of the current classification system of angiosperm leaf venation patterns; (2) the evolution of basic constructional principles of leaf venation patterns, as known to date; and (3) various functional aspects of the leaf venation system, comprising mainly mechanical stabilization and transport of water and solutes, are discussed with respect to architectural properties of leaf venation patterns, their evolution and their interspecific variation and individual plasticity.

FORMAL DESCRIPTION OF THE VENATION ARCHITECTURE

Topological descriptions

Topology is a subdiscipline of geometry and considers the positional relationships of geometric objects without referring to the angles or distances occurring between them. This section describes briefly topological principles used to describe characteristics of venation patterns. Using topological aspects to characterize leaf venation patterns is beneficial because the definitions of architectural features are then unambiguous.

A ramified pattern may be analysed topologically by describing it as a graph. The underlying mathematical approach is termed graph theory (e.g. McDonald, 1983). A graph is a structure consisting of vertices or nodes and edges connecting the nodes (Fig. 1). A continuous series of edges is termed a path; a cycle is a path which repasses a node (thus introducing an anastomosis). Describing a branching pattern topologically implies a reduction of its structure to its node-edge-interrelationships. Two types of graphs can be distinguished: graphs without cycles (Fig. 1A) and with cycles (Fig. 1B). The presence of cycles in a graph is equivalent to the presence of anastomoses or meshes in the ramifying structure under consideration and distinguishes a network from a 'tree-like' pattern (McDonald, 1983). Figure 1A shows a 'tree' and Fig. 1B shows a network. Bejan (1997) termed ramifying structures without meshes 'tree networks'. Another term for this kind of geometry is 'dendritic structure' (Schulz and Hilgenfeldt, 1994). As 'dendron' is the greek word for 'tree', the term 'dendritic structure' uses the same natural entity for describing a mesh-free ramified system. Dendritic structures

represent the optimal solution to the problem of exploiting an area or a volume with a ramified system (McDonald, 1983), and new approaches to the problem of optimization of transport paths in a finite-size area or volume yield tree systems as solutions (Bejan, 1997). The network in Fig. 1B is derived from the 'tree' in Fig. 1A by introducing a cycle. The degree of reticulation in network patterns can be described by a quantity termed 'redundancy'. Redundancy is a parameter used to describe the path architecture in a network by quantifying the presence of alternative pathways (Strang, 1986). For example, the network shown in Fig. 1B has a redundancy of one because, due to the presence of the mesh, two possible routes lead from one point in the network to another.

Kull and Herbig (1995) investigated several leaves topologically. They determined the numbers of edges (=valency) leaving a node and the number of neighbour meshes adjacent to a mesh. For example, a simple square grid has a valency of four and each quadratic mesh has four quadratic meshes as neighbours. Kull and Herbig (1995) found that leaf venations preferably show tri-valent nodes with six neighbours. This geometry is, for example, represented by honeycombs and is typical of self-generating structures like bubble floats. Kull and Herbig (1995) interpreted this result as an indication of self-generating processes during leaf venation ontogeny.

A ramified structure with cycles will be termed 'network' or 'closed' throughout this paper. A ramified structure without meshes will be termed 'dendritic' or 'open'.

Other principles of formal description

Another descriptive approach to ramified structures is given by the fractal dimension (Peitgen and Saupe, 1988). This rather popular parameter describes the self-similarity of a system which means that a certain geometric structure is repeated on contiguously smaller scales. The fractal dimension is scale independent. The remarkable aspect of this parameter is that it is a rational number and not an integer. Such a structure is not one-, two- or three-dimensional but something 'in between'. The fractal dimension of a two-dimensional ramifying structure describes how 'effectively' this linear—or approximately linear—system exploits an area. The efficiency of a self-similar structure in covering an area increases as the fractal
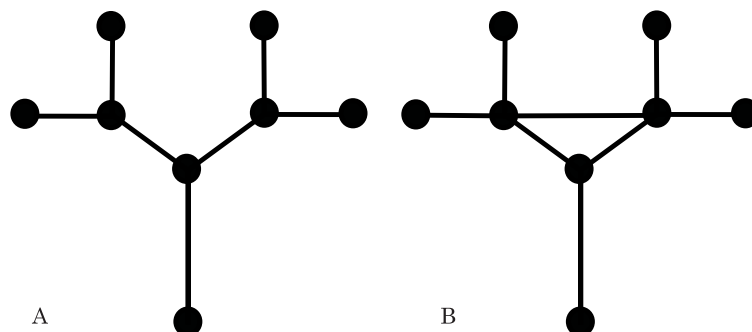

FIG. 1. Diagrammatic representation of two ramifying structures. A, Graph represents a tree or a dendritic system. B, Graph represents a network which is developed from graph A by insertion of a cycle. —, Edge; ●, vertex. For further details see text.

dimension approaches two. Corresponding studies were carried out by Herbig and Kull (1991) and by Mosbrugger (1992). They found that certain leaf venation patterns do indeed approximate fractal geometry. For example, *Acer trautvetteri* shows a fractal dimension of 1·522 (Herbig and Kull, 1991) and *Macropeplus ligustrinus* shows a fractal dimension of about 1·4 (Mosbrugger, 1992). These formal descriptions of leaf venation architecture demonstrate that leaf venation patterns exploit the area in a rather effective manner in order to correspond to functional demands (Herbig and Kull, 1991).

The current classification system of angiospermic leaf venation types

The particularly wide variation in leaf venation patterns of angiosperms has been classified by, for example, von Ettingshausen (1861), Melville (1976) and Hickey (1979). In the following, the widely used system of Hickey (1979) and its terminology is adopted. Whereas von Ettingshausen (1861) only considered leaf venation, the scheme of Hickey (1979) also uses other elements of leaf architecture in the classification process, such as leaf shape or the structure of the leaf margin. The classification of an angiospermic venation pattern starts with the primary vein, or, if more than one primary vein is present, with all primary veins entering the leaf from the petiole and the secondary veins branching off the primary vein(s). Primary and secondary veins are termed the major vein class and represent lower order veins. The classification proceeds with progressively higher order veins until the areolation which terminates the vein system. This procedure implicitly utilizes a basic feature of angiospermic leaf venation patterns: the hierarchical organization of veins which is reflected by vein diameter ('. . . the recognition of vein orders is essential in describing leaf architecture'; Hickey, 1979, p. 32). The vein diameter at the point of origin of the vein represents the basic criterion in determining the vein order.

This classification system does not only consider the geometric arrangement of different vein classes. The arrangement of veins of a certain order in relation to other architectural features of the leaf is also important in identifying a certain venation type. This is shown by the following examples. Figure 2 shows three different types of lower order vein arrangement in the case of a single primary vein: a brochidodromous (Fig. 2A), a craspedodromous (Fig. 2B) and a eucamptodromous (Fig. 2C) leaf venation. The brochidodromous arrangement of lower order veins is closed whereas the craspedodromous and the eucamptodromous arrangements of lower order veins are both open. The basic difference between the latter two types is represented by the spatial relation of the lower order veins to the leaf margin. The venation arrangement is termed eucamptodromous (Fig. 2C) if the secondaries diminish towards the leaf margin. If the secondaries reach the leaf margin then the leaf venation is termed craspedodromous (Fig. 2B).

Comparing systematic and topological-geometric descriptions

The latter section dealt implicitly with dicotyledonous leaf venation patterns. This is necessary because Hickey's classification scheme refers to dicots. Topological principles, however, may be applied to both dicotyledonous and non-dicotyledonous and even non-angiosperm venation systems, because only the pure structural patterns of the ramifications are described without any reference to leaf shape, other leaf tissues or vein diameters. Whereas the current classification schemes are necessary as descriptive tools for classifying and identifying taxa, topological and geometric principles may be valuable for analysing leaf venation types in a formal way to detect functional aspects. Both the open and dichotomous venation of a fossil pteridosperm of, for example, the genus *Alethopteris* (Fig. 3A) and a cladodromous arrangement of lower order veins of a dicot leaf (secondaries ramify freely toward the leaf margin) which is realized in, for example, the extant genus *Buxus* (Fig. 3B), represent dendritic structures.

At this point, the current multitude of different terms which are used to describe the various properties of ramification patterns in leaf venation systems will be considered. The terms 'dendritic' or 'open' structure were previously introduced as synonymous and described a
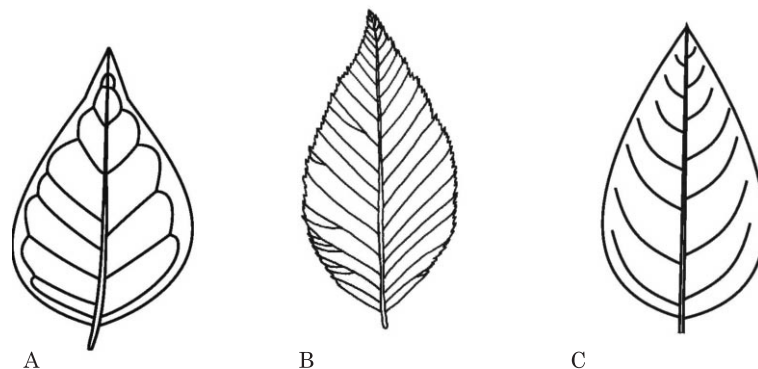

FIG. 2. A, Brochidodromous leaf venation: second order veins are joined. B, Craspedodromous leaf venation: second order veins terminate at the margin. C, Eucamptodromous leaf venation: second order veins diminish and terminate within the leaf blade. All examples redrawn from Hickey (1979).
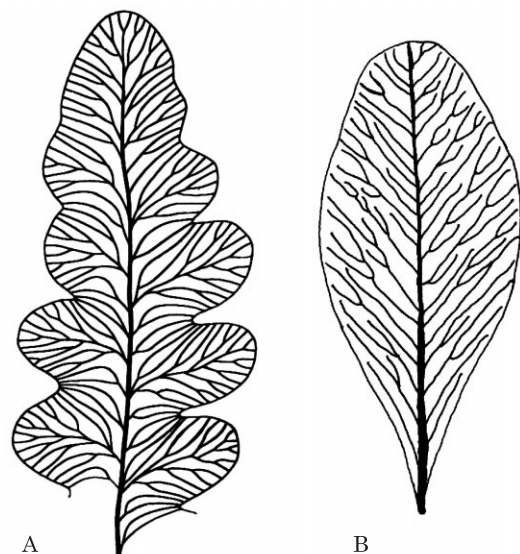
FIG. 3. A, The venation pattern of *Alethopteris quadrata* (redrawn from Wagner, 1968). B, The venation pattern of *Buxus macowani* (redrawn from Köhler, 1993).
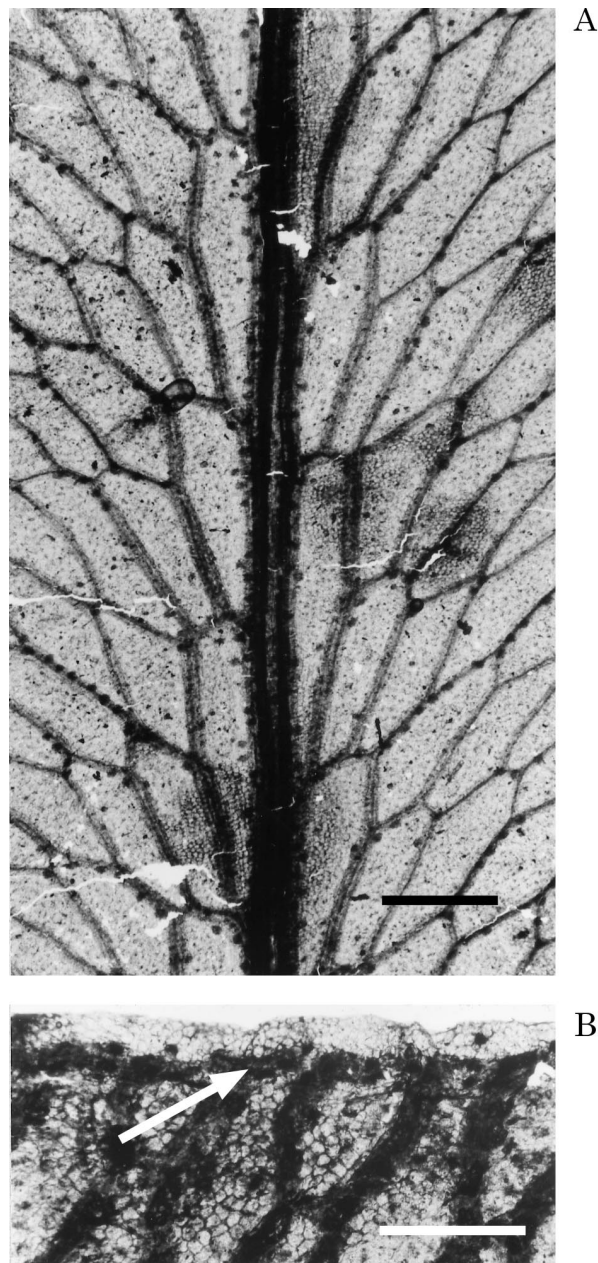

FIG. 4. A, Cuticle of *Barthelopteris germarii* showing the venation pattern near the midvein. Bar = 1 mm (from Krings and Kerp, 1998). B, Detail of a pinnule margin of *Barthelopteris germarii* showing the 'surrounding vein' (indicated by arrow) (from Krings and Kerp, 1998). Bar = 0·4 mm.

ramifying system without anastomoses. The term 'open' as well as the term 'free' is established in the botanical literature as describing a leaf venation without anastomoses (e.g. Wagner, 1979). The term 'dichotomous' refers to a special open branching mode in which a vein splits into two daughter branches. Another term for dichotomous branching is 'bifurcation'.

The term 'cycle' is the topological term for a mesh or an anastomosis. If the ramification pattern shows anastomoses, it is termed 'network' or 'closed' system, as discussed above. The term 'closed' is established in the botanical literature as denoting an anastomosing leaf venation pattern. Also widely used is the term 'reticulate' which is used synonymously with 'network' (e.g. Trivett and Pigg, 1996). The terms listed above are not associated with the description of any hierarchical ordering of the venation pattern. To describe the presence or absence of hierarchical ordering, an additional term is introduced, such as 'simple reticulate pattern' or 'hierarchical reticulate pattern'. One basic feature of angiosperm venation patterns is, as noted above, their hierarchical character (regardless of being open or closed). A simple reticulate pattern is expressed by ferns and pteridosperms showing a network arrangement of their leaf conduit system. An example is the fossil species *Barthelopteris germarii* (Fig. 4).

EVOLUTION OF THE LEAF VENATION ARCHITECTURE

In this section, some basic evolutionary events and trends concerning the evolution of leaf venation patterns are briefly summarized. For a more detailed description and discussion of this topic see, for example, Trivett and Pigg (1996) or Kull (1999).

In the Devonian and early Carboniferous almost all plants with fern-like leaves (ferns, progymnosperms and gymnosperms) appear to have had an open venation (by definition, venation patterns can only be observed in macrophylls, and therefore taxonomic lineages that usually show microphylls, such as lycopods and sphenopsids, are not considered here). The open venation pattern, formed by bifurcation of veins, represents the primitive architecture which served as a starting point for modern network patterns. An example of such an open venation pattern is the dendritic branching mode of the venation system in *Alethopteris quadrata* (Upper Carboniferous) (Fig. 3A).

These dendritic branching patterns are a characteristic feature of extant ferns and gymnosperms.

Many species of ferns and gymnosperms, fossil as well as extant, show anastomosing venation patterns (Trivett and Pigg, 1996). According to the fossil record, simple network patterns appeared during the Upper Carboniferous (Kull, 1999). They occurred in such groups as seed ferns, cycads, gigantopterids or gentopterids (Trivett and Pigg, 1996). Corresponding taxa are, for example, *Lonchopteris* or *Reticulopteris*, probably belonging to the pteridosperms (see Trivett and Pigg, 1996; Kull, 1999). Obviously, network patterns evolved repeatedly from open venation patterns in different lineages (e.g. *Neuropteris–Reticulopteris*, *Alethopteris–Lonchopteris*). Wagner (1979) suggested that network patterns developed independently in the fern group more than 50 times. Extant fern species with open or closed patterns can be found, for example, in the fern genera *Adiantum*, *Asplenium* or *Polypodium* (Wagner, 1979). However, all these patterns are less complex than angiosperm venation patterns (Wagner, 1979). Ferns show no distinct hierarchical structure in veins of different orders (Kull, 1999). An example of a pteridosperm foliage with anastomosing vein pattern without hierarchical ordering, *Barthelopteris germarii* (Upper Carboniferous-Lower Permian) is shown in Fig. 4. The repeated anastomosing of veins leading to a regular network and the absence of an hierarchical structure is clearly visible.

An exceptional and well-known example of a gymnospermic network pattern which shows an hierarchically structured venation type similar to typical dicot patterns is that of *Gnetum* (Rodin, 1967).

The plant group with the most distinctly and pronounced hierarchical network patterns is represented by the angiosperms, especially the dicotyledons. According to the fossil record, the oldest unequivocal angiosperms existed in the Lower Cretaceous. However, older fossil remains exist which show angiospermic characters. Leaves from the Upper Triassic, for example, show the characteristic network patterns of angiosperm leaves (Taylor and Hickey, 1990). The hierarchical organization of the veins in these leaves is, however, not as distinct as in leaves of modern angiosperms. Similar venation patterns can be found today in extant primitive taxa (belonging to the Magnoliopsida) (Kull and Herbig, 1995). As the origin of angiosperms is still obscure, a clear documentation of the evolutionary development of early angiosperm leaf venation patterns is not yet possible. Hickey (1971) and Hickey and Doyle (1972), for example, suggested that the brochidodromous venation (=second order veins are joined; Fig. 2A) represents the primitive pattern of angiosperms, whereas other patterns, such as the craspedodromous venation (=second order veins branching off the major vein, ramify toward the margin and terminate there; Fig. 2B) represent derived patterns. The evolutionary transition from one pattern to another may be reversible, as pointed out by Takhtajan (1980). An interesting case is *Circeaster agrestis*, a small plant endemic to the Himalayan region. It is an angiosperm with an open, simply dichotomizing venation pattern. Whether this plant is a highly reduced member of an advanced family or simply a member of a very primitive family is still not clear (Oxelman and Liden, 1995; Ren *et al.*, 1998).

Whereas an hierarchical network pattern is characteristic of dicotyledons, the prevailing venation type of monocotyledons is represented by lower order veins which run in parallel and are connected by cross-linking higher order veins. In grass leaves, for example, the conspicuous veins running in parallel from the base to the apex of a leaf are interlinked by small higher order veins which are oriented more or less perpendicularly to the parallel lower order veins (Altus and Canny, 1985; Nelson and Dengler, 1997). The typical leaf venation of monocotyledons is thus represented by a grid-like network. However, patterns which are similar to those of dicotyledons do occur, and evolved independently in several monocot lineages e.g. vanilloid orchids (Cameron and Dickison, 1998). The circumstances that favour the evolution of these dicot-like network patterns in monocotyledons are not yet clear. Some authors have found significant correlations between the structure of anastomoses and the evergreen, climbing habit in monocotyledons (e.g. Conover, 1983), while others have found that this venation pattern is particularly common in shaded forest environments (Cameron and Dickison, 1998).

FUNCTIONAL ASPECTS OF LEAF VENATION PATTERNS

There are two main functions of leaf venation. The first is the transport of substances. The venation system supplies the leaf lamina with water and solutes via the xylem. Additionally, hormones are transported in the xylem. Carbohydrates, which are produced in the assimilating tissue of a leaf, are exported via the phloem. Other substances, such as hormones, are also transported in the phloem to a limited extent. The other function, mechanical stabilization, is based on the lignified xylem (=all xylem elements which contain lignin) and sclerified elements which can be associated with the conducting bundle system of a leaf. The high E-modulus (=ratio between stress and strain of a material; the higher the E-modulus the 'stiffer' the material) of lignin makes the leaf venation system suitable as a stabilizing structure (Niklas, 1992). It is to be expected that the architectural structure of leaf venation influences these main tasks and other functional properties. Functional aspects of leaf venation architecture will be discussed in the following sections.

Mechanical aspects

Most commonly, a leaf is a flat structure that maximizes the surface-to-volume ratio. It is then adequately described as a flat lightweight structure which is spread by mechanically stabilizing structures, usually the veins (as is the case in, for example, insect wings). The leaf lamina can thus be viewed as a stress-skin panel or a polylaminated sandwich which is stiffened and stretched by interconnecting stringers represented by the leaf veins (Niklas, 1999). Such structures exhibit a high flexibility and reconfigure or fold readily under mechanical loading (Vogel, 1989; Niklas, 1999).

Besides the leaf venation and (if present) additional sclerenchymatic elements, other components of a leaf also act as stabilizing agents. In a well-hydrated leaf, the turgor of the living cells makes a significant contribution to stability. There is evidence that the epidermis and the cuticle also represent stiffening agents in leaves (Niklas and Paolillo, 1997; Wiedemann and Neinhuis, 1998). Inherent folding or curling can also contribute to the structural stiffness, as was shown by King *et al.* (1996) for monocot leaves.

Givnish (1979) postulated that large and mechanically stiff midribs were favourable, because the greatest mechanical stress occurs along the longitudinal axis of a leaf. Parallel arrangement of the lower order veins is characteristic of monocot leaves. The mechanical properties of grass leaves were studied by Vincent (1982). He compared the grass leaf to a fibre reinforced material with a parallel arrangement of the fibres, and demonstrated the high stability of this natural construction. The parallel arrangement of veins thus leads to very efficient stabilization of the grass leaf. Mechanical properties of different leaf venation systems were studied using computer simulations by Kull and Herbig (1995). As mechanical reinforcement of the leaf lamina is primarily due to lower order veins (Kull and Herbig, 1995), only veins up to the third order were considered. Kull and Herbig (1995) simulated deformation caused by the net weight of elliptically shaped leaf models with different arrangements of the lower order veins. Their results showed that broad leaves may be stabilized optimally by a set of major veins running in parallel. The highest stabilization of narrow and mid-sized leaves was achieved by a central midrib with rectangularly branching laterals. In real leaves, however, an angle of 90° between secondaries and the major vein is not usually realized. This may be due to the fact that other structures (some of which are mentioned above) also contribute to the reinforcement and that the real branching angles in leaves are related to other functional factors (for example, the unfolding process, see below). Other strategies for increasing mechanical stability which were demonstrated by the simulations carried out by Kull and Herbig (1995) are (for a given venation pattern) (1) decrease in leaf size; (2) increase in the *E*-modulus of leaf tissues and; (3) additional stabilization of the leaf margin.

Mechanical loading may in fact influence leaf size as was demonstrated in studies of leaves of *Acer saccharum* individuals growing in wind-protected and wind-exposed sites (Niklas 1996). Plants from wind-exposed areas tend to develop smaller leaves than plants from protected sites. Additionally, plants from exposed sites develop less stiff petioles than plants from protected sites. Since more flexible petioles and smaller leaf size represent appropriate strategies for drag reduction and reconfiguration, these two features are discussed within the context of adaptive modifications (Niklas 1996). Leaf size is, however, not only of biomechanical but also of general ecological significance (Ackerly and Reich, 1999), because this parameter is related to environmental factors such as nutrient and moisture availability (Givnish, 1987; Körner *et al.*, 1989; Niinemets and Kalevi, 1994) or canopy architecture (White, 1983). This is partly due to the

dependence of the boundary layer thickness on leaf size. If an object is placed in an airstream, the air nearest to the object 'sticks' to it. This causes a stream zone characterized by a velocity gradient with the velocity increasing with increasing distance from the object. The corresponding fluid layer is termed boundary layer (see, for example, Vogel, 1994). In geometrically similar objects, the thickness of the boundary layer increases with the size of the object (for a given fluid and a given flow velocity). Thus, under a given wind velocity, a larger leaf has a thicker boundary layer than a smaller leaf (other factors, such as onset of turbulence due to surface irregularities, are, of course, also significant; see Monteith and Unsworth, 1990). The boundary layer is of great significance for a leaf because its thickness influences heat transfer and gaseous exchange (Monteith and Unsworth, 1990; Schuepp, 1993). The exchange rate of heat or gas decreases with increasing thickness of the boundary layer. Thus decreasing the leaf size not only affects mechanical properties but also heat dissipation and gaseous exchange (i.e. transpiration).

Increasing the *E*-modulus of various tissues by sclerification improves the stability of the leaf and primarily affects the mechanical properties, especially fracture toughness. Fracture toughness describes the work needed to add a unit fracture area to an existing crack (Lucas *et al.*, 1991). Fracture toughness is mainly dependent on sclerophylly, and because sclerophylly is commonly due to an increase in the proportion of sclerenchyma within the vascular system or associated with it, is mainly coupled to the venation system (although in some sclerophyllous leaves strands of sclerenchyma are not associated with the vascular bundles) (Choong *et al.*, 1992). However, not all parts of a leaf venation system are equally sclerified in these cases and this effect mainly concerns the arrangement and structure of the lower order veins. It is suggested that the fracture toughness of a leaf has a negative effect on attacks by herbivores (Choong, 1996). As a result of their high fracture toughness, lower order veins are the parts of leaves which are least often consumed by caterpillars (Choong, 1996). Sclerophylly does not only influence the mechanical properties of a leaf. Studies on Mediterranean evergreen species have demonstrated that sclerophyllic leaves can recover from xylem cavitation more readily than non-sclerophyllic leaves (Salleo *et al.*, 1997). This indicates that sclerophylly can be coupled to the water relations of a plant.

A shortcoming of stress-skin panels is their susceptibility to tearing at the margins (Niklas, 1999). The edges of anthropogenic products, such as fabrics, are strengthened by special structures such as selvedges, hems or other appropriate devices to prevent marginal tearing (Niklas, 1999). Leaves, in fact, often show stabilizing structures which run along the margin. These structures may be conducting intramarginal veins or non-conducting structures, such as the tough tissue running along the margin of *Ulmus* leaves (Niklas, 1999). A non-conducting structure also occurs in ferns (Pray, 1962) and is termed a 'false marginal vein'. Similar structures are also present in fossil ferns and pteridosperms (Krings and Kerp, 1998) (see Fig. 4B).

As noted above, stress-skin panels are prone to folding. This feature is of special significance as the leaf unfolds as it

emerges. Kobayashi *et al.* (1998) studied the unfolding of leaf models of *Carpinus betulus* and *Fagus sylvatica*, and investigated the effect of the branching angle of the secondary veins. In both species, the secondaries show a branching angle of 30–50° (in the case of the unfolded leaf). Higher branching angles allow for a more compact folding of the leaf in the bud. The time for expansion, however, increases with increasing branching angle. A leaf with a small angle attains a relatively large deployed area in the early phases of unfolding. Additionally, the kinetic energy needed for the unfolding process increases with the branching angle. The authors suggest that the effects of branching angle on unfolding may be relevant in an ecophysiological context. The branching pattern of the lower order veins may be important for optimizing timing, energy and geometric details of the unfolding process. This can be especially significant for deciduous plants. The craspedodromous venation pattern of many deciduous species, such as *Carpinus betulus* and *Fagus sylvatica* may thus be related to the unfolding of freshly emerging leaves.

On the whole, the mechanical properties of leaves are still poorly understood (Niklas, 1999). From a mechanical viewpoint, leaves represent composite materials. The mechanical behaviour of leaves is thus influenced by the different structural components forming the whole structure including water content (Vincent, 1983). It is also to be expected that the contribution of individual structural components to the mechanical properties is different in various leaf types (for example, mesophytic leaves *vs.* xeromorphic leaves) and the mechanical significance of the leaf venation will vary accordingly. More detailed information about the mechanical construction and constraints of angiosperm leaves and their interrelationship with ecophysiological aspects is thus desirable.

Water transport

Besides mechanical aspects, the transport and efficient distribution of substances is the second main task of the vascular bundle system of a leaf. The transport properties of the vascular bundle system in leaves have been mostly investigated from the point of view of water flow. Altus and Canny (1985) and Altus *et al.* (1985) demonstrated and analysed the global and local distribution of water by different vein types of wheat leaves. The venation system consists of large longitudinal veins (termed lateral veins) which run more or less in parallel, smaller longitudinal veins (termed intermediate veins) also running in parallel, and cross-linking veins (termed transverse veins) connecting the different longitudinal veins (Altus and Canny, 1985). The apparently parallel leaf venation of grasses (and other monocots) thus fulfils the conditions of a network. Using dye tracers, Altus and Canny (1985) and Altus *et al.* (1985) demonstrated that a 'division of labour' exists between the different vein classes. The longitudinal displacement of water from the leaf base to the tip occurs via lateral veins. The local dispersion of water occurs via the intermediate veins which are supplied by lateral veins via transverse veins. Therefore, the architecture of the transport network

matches the structural demands of an efficient irrigation system.

In the case of dictotyledonous leaves, corresponding studies were carried out by Jeje (1985) who observed the water velocity inside the vein system of *Populus balsamifera* leaves using fluorescent dyes. He demonstrated the flow of water entering the leaf via the midrib, the distribution of water to the secondaries and the lateral dispersion of water. The pressure values became more negative with increasing distance from the point where the petiole entered the leaf lamina. In general, highest flow velocities were observed in the basal part of the midrib and the flow velocities decreased with increasing distance from the midrib and with decreasing order of the vein.

The direct observation of the flow occurring in real leaf venation patterns revealed that the different hierarchical orders of the leaf veins are coupled to certain tasks of the supply function. These different transport properties of different conduit orders are due to the fact that, for a given pressure gradient, mass flow per unit time increases with the fourth power of the conduit radius, and the mean velocity of the flow increases quadratically with the conduit radius (Hagen-Poiseuille's law). Lower order veins provide for fast, long-distance transport while local dispersion is carried out by higher order veins. This division of labour based on the hierarchical organization of a ramifying transport system is a common principle in both technical and biological systems (Vogel, 1994). A general quantitative relationship concerning geometry and flow in a ramifying transport system is Murray's law (Murray, 1926). Due to its wide applicability, it will be introduced here together with its physical basis.

Murray's law describes the relationship between radii before and after a branching point in a ramifying transport system: the sum of the radii cubed of the daughter vessels is equal to the radius cubed of the parent vessel ($r_0^3 = r_{1a}^3 + r_{1b}^3$, where r_0 is the parent vessel and r_{1a} and r_{1b} the daughter vessels). The physical background of this relationship is minimization of the energy necessary to drive a given flow through the system and of the energy necessary to maintain the transport system itself. An exponent of three is expected to be valid under the following conditions: if the flow is based on Hagen-Poiseuille's law and if maintenance energy is based on r^2 (Sherman, 1981). If these conditions do not hold true, then this relationship has to be varied or it may fail completely. For example, if the flow is not laminar but turbulent or if diffusion instead of bulk flow occurs, the exponent differs from three (Sherman, 1981). Although this law was first formulated for biological transport systems (e.g. for arterial systems), it is a general relationship that holds true for ramifying biological and non-biological transport structures.

Is Murray's law valid for leaf venation? According to LaBarbera (1990), Murray's law should generally not be valid in the case of plants because of several special features of plant water transport. The most important feature is that the plant does not expend any energy in water transport, because water flow from roots to leaves is driven by transpiration and is thus 'solar-powered'. Thus minimization of energy input should be of no selective value.

Another reason discussed by Canny (1993) is the fact that xylem conduits are leaky, i.e. that lateral outflow takes place via the pits (Altus and Canny, 1985). The conducting bundles of different hierarchical levels (e.g. first order vein, second order vein and so on) differ not only in vessel diameter but also in the number of vessels. With increasing order of the vein, its vessel number as well as the diameter of its largest vessel tend to decrease, as was shown by Wang (1985) and Canny (1993) for sunflower leaves. Murray's law was tested for the largest vessel radii of veins of different orders of sunflower leaves (Canny, 1993, using data of Wang, 1985). Canny (1993) showed that Murray's law appears to be valid in this case. However, more data are needed to draw final conclusions about the interrelationship between pipe dimension, branching behaviour and water transport properties of leaf venation patterns. Despite its importance for ramifying transport systems, the general validity of Murray's law for the leaf venation system is unclear. Additionally, the transport structures which are demonstrated to obey Murray's law are dendritic transport systems (LaBarbera, 1990). However, the evolutionary development of leaf venation systems led, in numerous cases, to anastomosing systems. They deviate from 'plumbing systems' not only in representing leaky capillary bundles but also with respect to their architectural structure.

The various hierarchical levels of leaf venation patterns often show different degrees of reticulation. If the arrangement of the lower order veins of dicotyledonous leaves is considered, then the two possibilities, 'closed' and 'open', are reflected by, for example, the venation types brochidodromous and craspedodromous (Fig. 2A and B). An open or closed architecture of the lower order veins may then be connected to a higher order vein system with a higher or lower degree of reticulation (i.e. the major veins may be arranged in an open manner while the minor veins form a network). The angiospermic venation patterns thus reveal a differentiation between open and closed architectures on different hierarchical levels. The entire venation structure of a dicotyledonous leaf is usually not totally closed, because veinlets often terminate freely in areoles. It is to be expected that different basic patterns of the leaf venation system should exhibit differences in their transport behaviour. The principal network structure of angiosperm leaves and the numerous cases of anastomosing venation patterns in ferns and other gymnosperms (see above) indicate that the presence of meshes in the leaf conduit system is of adaptive value. Thus the possible functional traits of closed and open patterns require special attention.

Evidence for functional differences between open and closed arrangements of the lower order vein system of dicotyledonous leaves is indicated by the frequency of their occurrence which depends on climatic factors. In extant arborescent floras, the brochidodromous pattern prevails in tropical floras whereas non-brochidodromous patterns prevail in northern temperate floras (Bailey and Sinnott, 1916). This climate-dependent variation of venation patterns can theoretically be used in the determination of paleoclimates (Dolph and Dilcher 1979; Wolfe, 1993). In the case of the higher order vein system, a high ratio between number of free endings of veinlets and areole area

appears to be exhibited by xerophytes and is thus interpreted as a xeromorphic character (Holländer and Jäger, 1994; Kull and Herbig, 1995). This character can, however, also vary within an individual according to environmental factors. Sun leaves can show a higher ratio of free endings of veinlets to areole area than shade leaves (Kull and Herbig, 1995).

Direct observation of flow in real leaves (as summarized above) reveals the water transport which occurs in a venation pattern. It does not, however, allow for direct comparisons of the hydrodynamic properties of different leaf venation types. If certain architectural features such as, for example, the presence or absence of anastomoses represent adaptive aspects of water transport capacity, then this may be demonstrated by comparing water transport inside standardized models of basic venation patterns using computer simulations. As a leaf vein represents a bundle of porous capillaries, it can be considered a porous medium according to Darcy's law (see for example Jeje, 1985; Nobel, 1999). This macroscopic approach describes the volume flow of water per area in a porous system being dependent on the hydraulic conductivity of the material and the pressure gradient. While this approach is straightforward in the case of xylem, the situation is more complex for all kinds of parenchymatic tissue due to the presence of different components (for example cell walls and intercellular spaces) and membranes separating apoplast and symplast. Parenchyma can, however, also be treated as a porous medium (Roth et al., 1994).

A numerical study considering the hydrodynamic behaviour of three different arrangements of lower order veins supplying a mesophyll area is given by Roth et al. (1995). The results primarily demonstrate effects caused by the vein arrangement at the leaf margin. At the marginal region, high fluid pressure differences develop if no intramarginal vein, e.g. a vein running parallel and near to the margin, exists.

A quantitative comparison of the results is, however, not possible due to different ratios of lower order vein material to mesophyll. A more elaborate approach is therefore necessary. Figure 5 shows three different leaf venation models. Model A (Fig. 5A) shows a brochidodromous and Model B (Fig. 5B) a non-brochidodromous leaf venation model. The third model leaf (Model C, Fig. 5C) represents the brochidodromous Model A in which interruptions were introduced to achieve a degree of redundancy of zero. Model C thus represents topologically an open system. All model structures have dimensions of 36 cm^2 and the same ratio of lower order vein area to mesophyll area. Figure 5 shows the resulting pressure gradients, depicted as contour plots (Roth-Nebelsick, unpubl. res.). The mean pressure values (over the whole leaf model area) are −734 Pa (Model A), −858 Pa (Model B) and −810 Pa (Model C). The brochidodromous and redundant venation pattern achieves the least negative mean pressure of all three models. The pressure contour plots (Fig. 5) reveal that in the cases of Model B (Fig. 5B) and Model C (Fig. 5C) (both with a degree of redundancy equal to zero) the areas adjacent to the second and third order veins which are located furthest away from the fluid entrance region show highly negative fluid
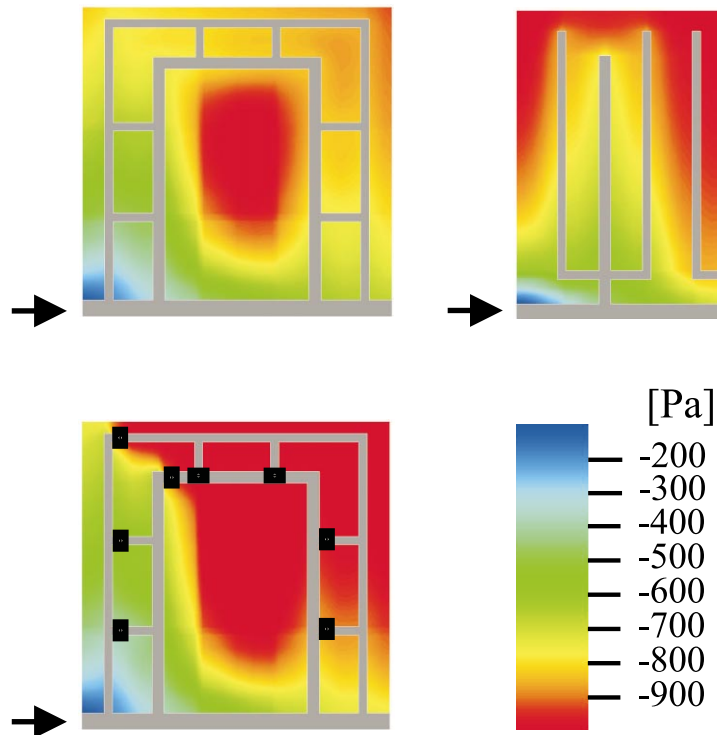
FIG. 5. Distribution of fluid pressure differences (shown as contour plots) over different leaf model structures. Leaf venation is shaded grey to make the pattern visible. The flow is generated by a constant outflow from the leaf lamina. The legend of the pressure values is included. Arrows indicate the site of fluid inflow (= fluid entrance). A, Brochidodromous Model A. B, Non-brochidodromous Model B. C, Brochidodromous Model C with interruptions of the venation system which lead to zero redundancy. The local interruptions of flow are achieved by defining small vein areas as material with zero permeability. These areas are indicated by black rectangles. The size of the rectangles is not identical to the original size of the zero permeability material (Roth-Nebelsick, unpubl. res.).

pressure values when compared to areas located closer to the fluid entrance region.

The resulting fluid pressure value at a mesophyll point in the leaf models depends on (*a*) the distance from the nearest vein and (*b*) the pressure at that nearest vein region. In the case of a zero redundancy system, the fluid pressure value of a certain point in a vein depends on (*a*) the path length between the fluid entrance region and the considered location and (*b*) the fluid pressures due to water withdrawal rates integrated over the entire vein locations passed when 'travelling' between the entrance region and the considered vein location (see Jeje, 1985). For a redundant closed system, however, several routes exist and the water can take the shortest path to a certain mesophyll location. Open and closed systems will thus differ in their transport behaviour. This difference results in less negative fluid pressure values and in a more homogeneous fluid pressure distribution in the case of the interconnected structure of the venation system of Model A compared to Models B and C. A homogeneous pressure distribution due to different possible routes was suggested by Altus *et al.* (1985) in the case of the wheat leaf venation and by Skalak and Özkaya (1989) in the case of meshed microvascular blood vessels.

Another interesting aspect is represented by the pressure values at the marginal regions of the model. As stated above, a marginal vein guarantees a sufficient water supply to the leaf margin, which is prone to high water stress. The

fluid pressure distribution of Model A (Fig. 5A) does in fact show moderate fluid pressure values at the marginal region in contrast to Model B which has no marginal vein (Fig. 5B). In Model C (Fig. 5C), however, the marginal region also shows highly negative fluid pressure values compared to Model A. Obviously, a marginal vein is only able to guarantee moderate fluid pressure values at the marginal regions if the system is redundant and if the marginal vein branches off the major vein at the leaf base. A marginal vein is thus beneficial for both mechanical stability (see 'Mechanical aspects') and water supply.

Another important aspect of redundancy in a transport network is the improvement of its safety, as compared to an open structure. In the case of a network, elimination of one or more vein paths due to injury is compensated for because fluid can reach the regions beyond the damaged site by numerous bypasses. This is not the case with completely open structures. Networks with a high degree of redundancy should be correspondingly resistant to vein damage. This idea is well-established (Wagner, 1979, see above). The safety aspect of a closed structure is demonstrated by Models A and C (Fig. 5A and C). The interruptions which were introduced in Model A and lead to Model C caused an increase in fluid pressure without blocking the transport flow. How relevant is this effect for real leaves? Plymale and Wylie (1944) tested the wound tolerances of several species with different venation architectures by introducing severe

interruptions into their venation systems. They showed that in many cases leaves were still well supplied with water that reached the regions of the lamina beyond the damaged points via numerous bypasses including the minor venation. The survival rate of leaves did not appear to be dependent on the architecture of the major veins. Survival of leaves in these experiments does not, however, provide evidence of other negative effects of the damage. For example, one can speculate that the water use efficiency is decreased by such interruptions and that the degree of its decrease may be dependent on leaf architecture. The aspect of improved safety may be especially important for evergreen species. Ensuring long-term functioning of evergreen leaves is certainly of adaptive value for these plants, because the degree of leaf damage due to, for example, herbivory, increases with increasing leaf age (Coley, 1980). The function of carbohydrate transport is, of course, also affected by the quality and safety of the venation. This will be considered in a later section.

Another advantage of closed networks may be seen in the case of different transpiration rates at different lamina locations. According to Van Gardingen *et al.* (1989) and Beyschlag *et al.* (1992), the degree of stomatal opening can vary over a leaf. A closed network would be able to provide for a homogeneous pressure distribution by re-routing the water flow to sites with higher rates of water loss.

Whereas open systems are able to exploit an area most efficiently, closed systems obviously have many advantages. It is thus not surprising that closed venation systems appeared repeatedly during land plant evolution.

Variability of venation density

One parameter of significant importance to the transport capacity of a leaf is the venation density. The effect of venation density on transport is simple: the higher the venation density, the more channels per area are available for conduction (however the reinforcement function of the leaf venation is also affected). Leaves are usually covered by a dense vein system. This is also reflected by the results of the fractal dimension (see 'Other principles of formal description'). The venation density quantifies the amount of leaf venation. This parameter is generally expressed as vein length per area. Other quantities, which are easier to measure, can serve as approximate values for vein density. For example, the mean distance between veins is closely correlated with vein density in a regularly reticulated venation system. However, vein length per area is the more reliable parameter (Uhl and Mosbrugger, 1999).

Vein density shows high individual and intraspecific variability as a reaction to external factors. Studies have revealed a complex interrelationship between venation density and numerous environmental parameters. It is well known, for example, that venation densities increase in a single plant with increasing height of insertion of a leaf (Zalenski, 1904; Manze, 1968; Roth and Yee, 1991). A similar phenomenon is the well-known difference in venation densities developed by sun and shade leaves, with the latter showing a less dense network (Schuster, 1908; Esau, 1965). Other factors that lead to higher

venation densities are reduction of soil water availability (Zeuner, 1932; Keller, 1933; Manze, 1968; Herbig and Kull, 1991) and air humidity (Lebedincev, 1927). This can be observed within plants of a single species growing at different localities (Manze, 1968) or within larger taxonomic groups existing in different environments (e.g. deciduous forest compared to grasslands) (Zalenski, 1902). The common interpretation of these correlations is that for a certain transpiration rate, leaf water potential becomes less negative with increasing venation density (e.g. Kull and Herbig, 1994). Interestingly, plants from tropical rainforests where levels of humidity are high, also show very high venation densities compared to plants from e.g. deciduous forests (Pyykkö, 1979). Another factor, whose influence is not yet clear, is leaf size. Some authors have found that venation density is greater in small leaves (Schuster, 1908; Uhl, 1999), others that it is greatest in large leaves (Gupta, 1961), and yet others found no measurable effect of leaf size (Manze, 1968). There is some evidence that within a single plant, venation density is correlated with leaf size (with smaller leaves having higher densities), but this is not the case if leaves from different individuals of one population are studied (Uhl, 1999).

In addition to these factors, it has been shown that increasing levels of illumination (Maximov, 1929), wind speed (Grace and Russell, 1977) and nutrient deficiency (Philpott, 1956; Beiguelman, 1962) can also cause an increase in venation density. In contrast to these data, however, it seems that the concentration of atmospheric CO_2 does not affect venation density (Uhl and Mosbrugger, 1999), but more data are needed to enable a definitive statement in this regard. It is clear that all the factors that influence venation density interact in a natural stand of plants. From what we know so far it appears that at least in deciduous forests of SW-Germany, humidity is the factor with the greatest influence on venation density (Uhl, 1999).

Carbohydrate transport

So far, only the transport of water has been discussed. Leaf veins also function to export carbohydrates after leaf maturation. All considerations of the effects of venation architecture on transport discussed above are also valid, in principle, for carbohydrate transport. The site of phloem loading is the minor venation whose fine structure is dependent on the type of loading involved (Gamalei, 1989; van Bel, 1993; Flora and Madore, 1996) and where expression of corresponding carbohydrate transporters has been demonstrated (Riesmeier *et al.*, 1993). The flow of carbohydrates is subsequently conducted towards the major veins. The integrity and density of leaf venation is thus expected to be not only important for water influx, but also for carbohydrate efflux. This was also indicated by wounding experiments carried out by Wylie (1938) on *Syringa vulgaris* leaves. The leaves remained alive, demonstrating the retention of a functional water supply. Beyond the wounded sites, however, starch grains developed. This may indicate that the remaining network connections were no longer sufficient for the export of carbohydrates.

Raven (1994) considered the functional consequences of the spatial distribution of leaf veins and observed a correlation between the photosynthetic fixation pathway (C_3, C_4 and CAM) and the maximum vein distances. The mean maximum interveinal spacing decreases in the order C_3, C_4 and CAM. Light-saturated photosynthesis rates increase in the same order. This suggests that the transport of carbohydrates from the assimilating sites to the phloem may be involved in the limitation of the maximum interveinal spacing in leaves.

The possible correlation between carbohydrate transport and leaf venation density appears mainly to concern the minor venation, which determines interveinal spacing. It can be speculated that many of the environmental effects on the venation density listed above are not only influenced by water transport but also by carbohydrate export. The complex and reticulated structure of the minor venation in angiosperms would also be functionally related to a sufficient and safe assimilate transport. However, more studies are needed to improve our understanding of the interrelationships between the geometrical properties of leaf venation and carbohydrate transport.

Evolution of leaf venation and functional aspects

Functional aspects discussed in the preceding sections have often been considered with respect to evolution of leaf venation. In the case of ferns and pteridosperms, for example, taxa with anastomosing venation patterns appeared and vanished after some time (see 'Evolution of the leaf venation architecture'). The evolutionary appearance of network patterns following the primitive open patterns and the numerous cases of parallel evolution of anastomosing architectures encourage attempts to identify adaptive values. Zodrow and Cleal (1993) linked the appearance of plants with closed venation systems (i.e. *Reticulopteris*) with decreasing availability of water: 'It is thus clearly tempting to relate the change from open to anastomosed veining as a response to this climate change' (Zodrow and Cleal, 1993, p.77). Kull (1999) discusses the appearance of network patterns in a similar context. The evolutionary development of closed venation systems is, according to Kull (1999), linked to the decrease in atmospheric CO_2 which resulted in an increase in stomatal density, because stomatal density affects water relations. Thus Kull (1999) also interprets closed venation patterns as advantageous for water supply.

Another evolutionary development of venation patterns supports this notion of an interrelationship between the appearance of anastomosing venation patterns and climate changes (i.e. aridization). During the Permian, anastomosing patterns were widespread. Examples are the venation patterns of the Glossopteridales and Gigantopteridales which are taxa characteristic of Gondwana. Members of these groups exhibit a variety of different and complex network patterns (see, for example, Chandra and Singh, 1992; Li *et al.*, 1994) with some gigantopterids expressing hierarchical ordering of veins. These venation patterns do not, however, show any distinct hierarchical organization

such as that in angiosperm leaf venation patterns (Hickey and Doyle, 1977).

According to Wagner (1979), there is no evidence for a clear adaptive value of network *vs*. open venation patterns in extant ferns. He discusses the ideas of various authors on mechanical stabilization and water supply demands respectively. The notion that closed venation patterns in ferns lead to an improved water transport capacity is not supported by data concerning occurrence of anastomosing patterns in xeric habitats (Wagner, 1979). The safety aspect of closed venation systems is also considered by Wagner (1979). He postulates correlations between the activity of herbivores and the development of closed patterns in ferns, because the presence of anastomoses maintains water supply in the case of local damage.

Bond (1989) argued that the evolutionary success of the angiosperms leading to their dominance in most temperate and tropical vegetation is partly due to the network architecture of their leaf venation systems. According to Bond (1989), this should lead to a more efficient transport through the leaf and contribute to the rapid growth of angiosperm seedlings. This idea is in fact corroborated by the simulation results which are summarized above. To gather evidence for the proposed hypothesis, Becker *et al.* (1999) investigated the hydraulic conductance of leaves, shoots and roots as well as the whole-plant hydraulic conductance of several sapling-sized tropical angiosperms and conifers. The angiosperm species showed a wide variation in leaf size and venation architecture. The results obtained by Becker *et al.* (1999) showed: (1) there was no significant difference in hydraulic conductance between angiosperms and conifers and (2) that the leaf hydraulic conductance was not dependent on venation complexity. There are, however, some factors other than venation architecture that are important for the hydraulic conductance of a leaf. As discussed in the previous section, the density of veins represents the 'venation quantity'. This is the reason why the simulation models presented above show the same amount of vein material: this should allow for a direct quantitative comparison of the developing pressure gradients. Under a given transpiration rate, the developing pressure distribution over a leaf depends not only on the architectural pattern but also on the amount of vein material which is arranged over a leaf. Other factors which contribute to the final hydraulic conductance are the diameter of the vein conduits (Hagen-Poiseuille's law), the number of conduits in a vein and the thickness of the leaf (a thick leaf has a higher mesophyll conductance than a thin leaf). The interrelationship between leaf venation architecture and water supply may thus be obscured in a real leaf by numerous other factors influencing the hydraulic conductance. Another aspect is the high ontogenetic plasticity of angiospermic leaf morphology which balances out, to a certain degree, the effects of environmental factors. Some examples are discussed in the text, such as variation in leaf venation density, ratio between free endings of veinlets and areole area or leaf size.

These considerations do not, however, imply that the leaf venation pattern is insignificant in determining the water supply capacity. If a venation pattern achieves, with a given

amount of xylem material and under a given transpiration rate, a lower mean pressure gradient than other vein arrangements with a comparable amount of xylem material then it represents an economic 'high quality architecture'. This appears to be economically advantageous because lignin is a high-cost material (Larcher, 1997). To obtain information about the efficiency and economy of a certain venation pattern, it may be necessary to investigate conductance of a leaf together with other parameters, such as venation density and fine structures of veins. Since these ideas also concern carbohydrate transport, both xylem and phloem should be considered.

CONCLUDING REMARKS

The principal characteristics of the leaf venation pattern of a species are, in general, genetically fixed (for exceptions see Uhl *et al.*, 2000). This provides the basis for using the leaf venation as a taxonomic tool. Many geometric properties of leaf venation are, however, obviously coupled to functional traits and the evolution of diverse patterns is therefore connected to form-function relationships. Mechanical demands, transport constraints and possibly other aspects, such as ontogenetic factors, are interlinked and form a complex pattern of factors contributing to the functional background of the evolution of leaf venation patterns. The example of another leaf trait, pubescence, demonstrates how diverse the functional features of a structure can be. Leaf hairs have been proposed or shown to have numerous functions, and overlap between the different aspects can occur (Press, 1999). Considerations of (possible) relationships between a structure and its biological performance generally demonstrate that (1) often the real adaptive value depends on the actual environment of the considered species, (2) the functional significance of a morphological structure can be surprising (and therefore non-intuitive) and (3) there is usually more than one constructional solution to a problem (Koehl, 1996; Press, 1999). The identification of a certain function is therefore often not trivial. This is certainly the case with leaf venation in which different functional features interact, such as venation density which improves both transport of water and carbohydrates, or are independent from each other, such as transport which is unaffected by a 'false marginal vein'.

It is, of course, to be expected that functional aspects of these traits and functional properties of the leaf venation remain to be discovered. Sclerification, for example, shows the at first unexpected effect of being involved in xylem cavitation reversal (Salleo *et al.*, 1997). The fact that ramified or network structures represent a common phenomenon in living as well as in non-living systems offers the possibility of using interdisciplinary approaches to improve our understanding of the leaf venation system.

ACKNOWLEDGEMENTS

LITERATURE CITED

Ackerly DD, Reich PB. 1999. Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. *American Journal of Botany* **86**: 1272–1281.

Altus DP, Canny MJ. 1985. Water pathways in wheat leaves. I. The division of fluxes between different vein types. *Australian Journal of Plant Physiology* **12**: 173–181.

Altus DP, Canny MJ, Blackman DR. 1985. Water pathways in wheat leaves. II. Water-conducting capacities and vessel diameters of different vein types, and the behaviour of the integrated vein network. *Australian Journal of Plant Physiology* **12**: 183–199.

Alvin K, Chaloner WG. 1970. Parallel evolution in leaf venation: an alternative view of angiosperm origin. *Nature* **226**: 662–663.

Bailey IW, Sinnott EW. 1916. The climatic distribution of certain types of angiosperm leaves. *American Journal of Botany* **3**: 24–39.

Becker P, Tyree MT, Tsuda M. 1999. Hydraulic conductances of angiosperm versus conifers: similar transport sufficiency at the whole-plant level. *Tree Physiology* **19**: 445–452.

Beiguelman B. 1962. Cerrado: Vegetacao oligotrófica. *Ciencia e Cultura* **14**: 99–107.

Bejan A. 1997. Constructal tree network for fluid flow between a finite-size volume and one source or sink. *Revue generale de thermique* **36**: 592–604.

Beyschlag W, Pfanz H, Ryel RJ. 1992. Stomatal patchiness in Mediterranean evergreen sclerophylls: Phenomenology and consequences for the interpretation of the midday depression in photosynthesis and transpiration. *Planta* **187**: 546–553.

Bond WJ. 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society* **36**: 227–249.

Cameron KM, Dickison WC. 1998. Foliar architecture of vanilloid orchids: insights into the evolution of reticulate leaf venation in monocotyledons. *Botanical Journal of the Linnean Society* **128**: 45–70.

Canny MJ. 1993. The transpiration stream in the leaf apoplast: water and solutes. *Philosophical Transactions of the Royal Society of London Series B* **341**: 87–100.

Chandra S, Singh KJ. 1992. The genus *Glossopteris* from the late Permian beds of Handapa, Orissa, India. *Review of Palaeobotany and Palynology* **75**: 183–218.

Choong MF. 1996. What makes a leaf tough and how this affects the pattern of *Castanopsis fissa* leaf consumption by caterpillars. *Functional Ecology* **10**: 668–674.

Choong MF, Lucas PW, Ong JSY, Pereira B, Tan HTW, Tuerner IM. 1992. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytologist* **121**: 597–610.

Cleal CJ. 1981. A new species of *Neuropteris* from the middle Westphalian of Palencia. *Estudios geologicos* **37**: 77–82.

Coley PD. 1980. Effects of leaf age and plant life history patterns on herbivory. *Nature* **284**: 545–546.

Conover MV. 1983. The vegetative morphology of the reticulate-veined Liliiflorae. *Telopea* **2**: 401–412.

Dolph GE, Dilcher DL. 1979. Foliar physiognomy as an aid in determining paleoclimate. *Palaeontographica, Abteilung B* **170**: 151–172.

Esau K. 1965. *Plant anatomy.* New York: Wiley and Sons.

Ettingshausen von G. 1861. *Die Blatt-Skelete der Dikotyledonen.* Wien: Staatsdruckerei Wien.

Flora LL, Madore MA. 1996. Significance of minor-vein anatomy to carbohydrate transport. *Planta* **198**: 171–178.

Gamalei Y. 1989. Structure and function of leaf minor veins in trees and herbs. A taxonomic review. *Trees* **3**: 96–110.

Givnish TJ. 1979. On the adaptive significance of leaf form. In: Solbrig OT, Jain S, Johnson GB, Raven PH, eds. *Topics in plant population biology.* Columbia: Columbia University Press, 375–407.

Givnish TJ. 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist* **106**: S131–S160.

Grace J, Russell G. 1977. The effect of wind on grasses. III. Influence of continuous drought or wind on anatomy and water relations in *Festuca arundinacea* Schreb. *Journal of Experimental Botany* **28**: 268–278.

Gupta B. 1961. Correlation of tissues in leaves. 1. Absolute vein-islet numbers and absolute veinlet termination numbers. *Annals of Botany* **25**: 65–70.

Herbig A, Kull U. 1991. *Leaves and ramification*. Stuttgart: Mitteilungen des SFB 230 Heft 7, 109–117.

Hickey LJ. 1971. Evolutionary significance of leaf architectural features in the woody dicots. *American Journal of Botany* **58**: 469 (abstract).

Hickey LJ. 1979. A revised classification of the architecture of dicotyledonous leaves. In: Metcalfe CR, Chalk L, eds. *Anatomy of the dicotyledons, 2nd edn. Vol. I, Systematic anatomy of the leaf and stem*. Oxford: Clarendon Press, 25–39.

Hickey LJ, Doyle JA. 1972. Fossil evidence on evolution of angiosperm leaf venation. *American Journal of Botany* **59**: 661.

Hickey LJ, Doyle JA. 1977. Early cretaceous fossil evidence for Angiosperm evolution. *Botanical Review* **43**: 3–104.

Holländer K, Jäger EJ. 1994. Morphologie, Biologie und ökogeographische Differenzierung von *Globularia*. *Flora* **189**: 223–254.

Jeje AA. 1985. The flow and dispersion of water in the vascular network of dicotyledonous leaves. *Biorheology* **22**: 285–302.

Keller BA. 1933. Über den anatomischen Bau dürre- und hitzeresistenter Blätter. *Berichte der Deutschen Botanischen Gesellschaft* **51**: 514–522.

King MJ, Vincent JFV, Harris W. 1996. Curling and folding of leaves of monocotyledons—a strategy for structural stiffness. *New Zealand Journal of Botany* **34**: 411–416.

Kobayashi H, Kresling B, Vincent JFV. 1998. The geometry of unfolding tree leaves. *Proceedings of the Royal Society of London Series B* **265**: 147–154.

Koehl MAR. 1996. When does morphology matter? *Annual Review of Ecology and Systematics* **27**: 501–542.

Köhler E. 1993. Blattnervatur-Muster der Buxaceae Dumortier und Simmondsiaceae Van Tieghem. *Feddes Repertorium* **104**: 145–167.

Körner C, Neumayer M, Menendez-Riedl SP, Smeets-Scheel A. 1989. Functional morphology of mountain plants. *Flora* **182**: 353–383.

Krings M, Kerp H. 1998. Epidermal anatomy of *Barthelopteris germarii* from the Upper Carboniferous and Lower Permian of France and Germany. *American Journal of Botany* **85**: 553–562.

Kull U. 1999. Zur Evolution der Adernetze von Blättern, insbesondere der Angiospermen. *Profil* **16**: 35–48.

Kull U, Herbig A. 1994. *Leaf venation patterns and principles of evolution*. Stuttgart: Mitteilungen des SFB 230. Heft 9, 167–175.

Kull U, Herbig A. 1995. Das Blattadersystem der Angiospermen: Form und Evolution. *Naturwissenschaften* **82**: 441–451.

LaBarbera M. 1990. Principles of design of fluid transport systems in zoology. *Science* **249**: 992–1000.

Larcher W. 1997. *Physiological Plant Ecology, 3rd edn*. New York: Springer Verlag.

Lebedincev E. 1927. Physiologische und anatomische Besonderheiten der in trockener und feuchter Luft gezogenen Pflanzen. *Berichte der Deutschen Botanischen Gesellschaft* **45**: 83–96.

Li H, Tian B, Taylor EL, Taylor TN. 1994. Foliar anatomy of *Gigantoclea guizhoaensis* (Gigantopteridales) from the Upper Permian of Guizhou Province, China. *American Journal of Botany* **81**: 678–689.

Lucas PW, Choong MF, Tan HTW, Tuerner IM, Berrick AJ. 1991. The fracture toughness of the leaf of the dicotyledon *Calophyllum inophyllum* L. (Guttiferae). *Philosophical Transactions of the Royal Society of London Series B* **334**: 95–106.

McDonald N. 1983. *Trees and networks in biological models*. Chichester: John Wiley & Sons.

Manze U. 1968. *Die Nervaturdichte der Blätter als Hilfsmittel der Paläoklimatologie*. Bonn: Wilhelm Stollfuß Verlag.

Maximov NA. 1929. *The plant in relation to water*. London: George Allen & Unwin Ltd.

Melville R. 1969. Leaf venation patterns and the origin of angiosperms. *Nature* **224**: 121–125.

Melville R. 1976. The terminology of leaf architecture. *Taxon* **25**: 549–561.

Monteith JL, Unsworth MH. 1990. *Principles of environmental physics, 2nd edn*. London: Edward Arnold.

Mosbrugger V. 1992. Constructional morphology as a useful approach in fossil plant biology. *Courier Forschungsinstitut Senckenberg* **147**: 19–29.

Murray CD. 1926. The physiological principle of minimum work. I. The vascular system and the cost of blood volume. *Proceedings of the National Academy of Sciences of the USA* **12**: 207–214.

Nelson T, Dengler N. 1997. Leaf vascular pattern formation. *The Plant Cell* **9**: 1121–1135.

Niinemets Ü, Kalevi K. 1994. Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability. *Forest and Ecology Management* **70**: 1–10.

Niklas KJ. 1992. *Plant Biomechanics*. Chicago: The University of Chicago Press.

Niklas KJ. 1996. Differences between *Acer saccharum* leaves from open and wind-protected sites. *Annals of Botany* **78**: 61–66.

Niklas KJ. 1999. A mechanical perspective on foliage leaf form and function. *New Phytologist* **143**: 19–31.

Niklas KJ, Paolillo DJ Jr. 1997. The role of the epidermis as a stiffening agent in *Tulipa* (Liliaceae) stems. *American Journal of Botany* **84**: 734–744.

Nobel PS. 1999. *Physicochemical and environmental plant physiology, 2nd edn*. New York: Academic Press.

Oxelman B, Liden M. 1995. The position of *Circaeaster*—Evidence from nuclear ribosomal DNA. *Plant Systematics and Evolution* Suppl. **9**: 189–193.

Peitgen HO, Saupe D. 1988. *The science of fractal image*. New York: Springer-Verlag.

Pelletier JD, Turcotte DL. 2000. Shapes of river networks and leaves: are they statistically similar? *Philosopical Transactions of the Royal Society of London Series B* **355**: 307–311.

Philpott J. 1956. Blade tissue organization of foliage leaves of some Carolina shrub-bog species as compared with their Appalachian mountain affinities. *Botanical Gazette* **118**: 88–105.

Plymale EI, Wylie RB. 1944. The major veins of mesomorphic leaves. *American Journal of Botany* **31**: 99–106.

Pray TR. 1962. Ontogeny of closed dichotomous venation of *Regnellidium*. *American Journal of Botany* **49**: 464–472.

Press MC. 1999. The functional significance of leaf structure: a search for generalizations. *New Phytologist* **143**: 231–219.

Pyykkö M. 1979. Morphology and anatomy of leaves from some woody plants in a humid tropical rainforest of Venezuelan Guayana. *Acta Botanica Fennica* **112**: 1–41.

Raven JA. 1994. The significance of the distance from photosynthesizing cells to vascular tissue in extant and early vascular plants. *Botanical Journal of Scotland* **47**: 65–81.

Ren Y, Xiao YP, Hu ZH. 1998. The morphological nature of the open dichotomous leaf venation of *Kingdonia* and *Circaeaster* and its systematic implication. *Journal of Plant Research* **111**: 225–230.

Riesmeier JW, Hirner B, Frommer WB. 1993. Potato sucrose transporter expression in minor veins indicates a role in phloem loading. *Plant Cell* **5**: 1591–1598.

Rodin RJ. 1967. Ontogeny of foliage leaves in *Gnetum*. *Phytomorphology* **17**: 118–128.

Roth A, Mosbrugger V, Neugebauer HJ. 1994. Efficiency and evolution of water transport systems in higher plants—a modelling approach. I. The earliest land plants. *Philosophical Transactions of the Royal Society of London Series B* **345**: 137–152.

Roth A, Mosbrugger V, Belz G, Neugebauer HJ. 1995. Hydrodynamic modelling study of angiosperm leaf venation types. *Botanica Acta* **108**: 121–126.

Roth I, Yee S. 1991. Ökologisch-taxonomische Untersuchungen über Leitbündeldichte und Leitbündelmuster bei Angiospermen-Laubblättern. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **113**: 7–71.

Salleo S, Nardini A, Lo Gullo MA. 1997. Is sclerophylly of Mediterranean evergreens an adaptation to drought? *New Phytologist* **135**: 603–612.

Schuepp PH. 1993. Leaf boundary layers. *New Phytologist* **125**: 477–507.

Schulz H-C, Hilgenfeldt S. 1994. Experimente zum Chaos. *Spektrum der Wissenschaft* **1**: 72–81.

Schuster W. 1908. Die Blattaderung des Dicotylenblattes und ihre Abhängigkeit von äußeren Einflüssen. *Berichte der Deutschen Botanischen Gesellschaft* **26**: 194–237.

Sherman TF. 1981. On connecting large vessels to small. The meaning of Murray's law. *Journal of General Physiology* **78**: 431–453.

Skalak R, Özkaya N. 1989. Biofluid mechanics. *Annual Review of Fluid Mechanics* **21**: 167–204.

Strang G. 1986. *Introduction to applied mathematics*. Cambridge: Wellesley-Cambridge Press.

Takhtajan A. 1980. Outline of the classification of flowering plants (Magnoliophyta). *Botanical Review* **46**: 225–359.

Taylor DW, Hickey LJ. 1990. An Aptian plant with attached leaves and flowers: implications for Angiosperm origin. *Science* **247**: 702–704.

Trivett ML, Pigg KB. 1996. A survey of reticulate venation among fossil and living land plants. In: Taylor DW, Hickey LJ, eds. *Flowering plant origin, evolution and phylogeny*. New York: Chapman & Hall, 8–31.

Uhl D. 1999. *Leaf venation density as a climatic and environmental proxy. Implications for palaeoclimatology*. PhD Thesis, Institute and Museum for Geology and Palaeontology, Tübingen, Germany.

Uhl D, Mosbrugger V. 1999. Leaf venation density as a climate and/or environmental proxy—a critical review and new data. *Palaeoclimatology Palaeogeography Palaeoecology* **149**: 17–30.

Uhl D, Mosbrugger V, Walther H. 2000. Stress-induzierte Aberrationen der Blattaderung in Rotbuchen (*Fagus sylvatica* L.). Kurze Mitteilung. *Feddes Repertorium* **111**: 7–8.

Van Bel AJE. 1993. Strategies of phloem loading. *Annual Review of Plant Physiology and Plant Molecular Biology* **44**: 253–281.

Van Gardingen PR, Jeffree CE, Grace J. 1989. Variation in stomatal aperture in leaves of *Avena fatua* observed by low-temperature scanning electron microscopy. *Plant Cell and Environment* **12**: 887–898.

Vincent JFV. 1982. The mechanical design of grass. *Journal of Material Sciences* **17**: 856–860.

Vincent JFV. 1983. The influence of water content on the stiffness and fracture properties of grass leaves. *Grass and Forage Science* **38**: 107–111.

Vogel S. 1989. Drag and reconfiguration of broad leaves in high winds. *Journal of Experimental Botany* **40**: 941–948.

Vogel S. 1994. *Life in moving fluids*. Princeton: Princeton University Press.

Wagner RH. 1968. Upper Westphalian and Stephanian species of *Alethopteris* from Europe, Asia Minor and North America. *Mededlingen van de Rijks Geologische Diienist, Serie C.* **6** Maastrict.

Wagner WH. 1979. Reticulate veins in the systematics of modern ferns. *Taxon* **28**: 87–95.

Walther H. 1998. Die Tertiärflora von Hammerunterwiesenthal (Freistaat Sachsen). *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* **43/44**: 239–264.

Wang X-D. 1985. *Loading and translocation of assimilates in sunflower*. PhD Thesis, Monash University, Australia.

White PS. 1983. Corner's rules in eastern decidous trees: allometry and its implications for the adaptive architecture of trees. *Bulletin of the Torrey Botanical Club* **110**: 203–212.

Wiedemann P, Neinhuis C. 1998. Biomechanics of isolated plant cuticles. *Botanica Acta* **111**: 28–34.

Wolfe JA. 1993. A method of obtaining climatic parameters from leaf assemblages. *U.S. Geological Survey Bulletin* **2040**. Washington.

Wylie RB. 1938. Concerning the conductive capacity of the minor veins of foliage leaves. *American Journal of Botany* **25**: 567–572.

Zalenski Wv. 1902. Über die Ausbildung der Nervation bei verschiedenen Pflanzen. *Berichte der Deutschen Botanischen Gesellschaft* **Bd. 20**: 433–440.

Zalenski Wv. 1904. Materials for the study of the quantitative anatomy of different leaves of the same plant. *Memoires de l'Institut Polytechnique de Kiev* **4**: 1–203.

Zetter R. 1984. Morphologische Untersuchungen an *Fagus*-Blättern aus dem Neogen von Österreich. *Beiträge zur Paläontologie von Österreich* **11**. Wien.

Zeuner FE. 1932. Die Nervatur der Blätter von Öningen und ihre methodische Auswertung für das Klimaproblem. *Centralblatt für Mineralogie, Geologie und Paläontologie, Abt. B.* 260–264.

Zodrow EL, Cleal CJ. 1993. The epidermal structure of the carboniferous gymnosperm frond *Reticulopteris*. *Palaeontology* **36**: 65–79.