Zimmermann’s telome theory of megaphyll leaf evolution: a molecular and cellular critique
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Megaphyll leaf evolution was a critical event in Earth history that had major consequences for the biotic regulation of the global environment. Zimmermann’s telome theory has been widely accepted for over seventy years as the leading explanation for this evolutionary innovation. According to the telome theory, megaphylls evolved from the three-dimensional lateral branches of early vascular land plants in a hypothetical series of three transformations; first, the formation of determinate lateral branches (overtopping); second, the development of ‘flattened’ branch systems (planation); and third, the fusion of planated branches with lateral outgrowths of photosynthetic mesophyll tissue to form the leaf blade (webbing). A critical review of the molecular and cellular evidence identifies plausible genetic, cellular and physiological mechanisms in extant higher plants for overtopping and planation but more limited evidence for the process of webbing (lateral outgrowth fusion). We highlight key outstanding questions concerning the telome theory that are likely to be resolved when gene identification and functional analysis techniques are applied to photosynthetic organisms that have different evolutionary histories.

Introduction
Megaphyll leaves, with their flat blades and complex vasculature, are fundamental light-capture organs formed as determinate lateral outgrowths from the flanks of the shoot apical meristem (SAM). Today, the vast majority of euphyllophytes (i.e. ferns, gymnosperms and angiosperms) utilize the megaphyll leaf form to harvest solar energy, and this underpins the net annual primary production of the contemporary terrestrial biosphere of around 56 billion tonnes of carbon (C) (56.4 × 10¹⁵ g C year⁻¹) [1]. This situation contrasts dramatically with that in the late-Silurian (~420 Myr ago) when the earliest tracheophytes, such as Cooksonia, had neither lateral branches nor leaves but consisted of naked dichotomized branching stem systems [2]. The subsequent origination and spread of megaphyll leaves throughout terrestrial floras did not take place until some 40 Myr later, from the close of the Devonian (Famennian; 359 Myr ago) onwards. It profoundly altered the evolutionary trajectory of plant and animal life, as well as the exchange of energy and materials between the land surface and the atmosphere [1]. In particular, by accelerating the chemical weathering of Ca-Mg silicate rocks, the long-term sink for CO₂, the evolutionary diversification of land plants appeared to create a network of feedback cycles that regulate the long-term geochemical carbon cycle and climate on a multi-million-year timescale [3].

The telome theory was first proposed seventy years ago by the German palaeobotanist Walter Zimmermann in his 1930 book entitled ‘Die Phylogenie de Pflanzen’. In this book, Zimmermann describes the evolutionary sequence of modifications leading up to the appearance of megaphyll leaves on ancestral early axial vascular land plants [4]. Zimmermann’s ‘theory’ was really a description of three fundamental steps — overtopping, planation, and webbing — for transforming a stem (a telome) into a laminated leaf blade by the fusion of lateral branch systems or telomes (Figure 1). Each step was presumably underpinned by modification of the regulation of the genetic networks in those descendent organisms that acquired it, and (presumably) also conferred ecological or physiological advantages on them. It also seems likely, given the independent evolution of megaphyll leaves in all major clades of the Euphyllophytina [5], that each of the three transformations has been recruited multiple times during the evolutionary history of land plants.

Here, we critically review and discuss insights gained from recent advances in molecular and cell biology that contribute towards a fundamental understanding of the telome theory. Our aim is twofold. First, to determine what molecular biology can say about how each step might have arisen. This information addresses one of the long-standing criticisms levelled at the telome theory, that it lacks a developmental mechanism. It might also shed light on other issues, including why certain morphological transformations occur as opposed to others, and why the particular sequence of processes foreshadowed the appearance of leaves [6,7]. Our second aim is to highlight future areas of investigation that might address some of the outstanding issues.
Zimmermann’s telome theory

In its general form, the telome theory proposes that, by combining and modifying simple multicellular telomes through one or more developmental processes, it is possible to explain all extant and extinct plant morphologies [7]. In the case of leaves, Zimmermann essentially envisaged the transformation of a stem into a leaf by modification of existing organs rather than through a major change in body plan. He postulated that the evolution of a megaphyll leaf proceeded through a series of hypothetical transformations that were based on modifications to a lateral branch of a dichotomized three-dimensional branching stem system, as typified by early Psilophyton- and Rhynia-like plants. The telome module is the distal portion of the axis, the proximal portion is known as a mesome. The first step, ‘overtopping’, occurs when one branch of a dichotomous pair overgrows another to allow the main axis to become a stem and the sub-ordinate stem (i.e. the overtopped branch) to branch out in three dimensions. In the next step, ‘planation’, neighbouring lateral branch systems of terete (cylindrical, tapering) stems become orientated into a single plane, i.e. the branch system is ‘flattened’ not the stem. Finally, lateral outgrowths of photosynthetic tissue (a ‘webbing’) evolved to join the segments of the planated lateral branches to form a laminate leaf blade. It is interesting to note that no single plant lineage has been found to exhibit all three crucial steps in its fossil history. Instead, each one is recognized independently in several different fossil lineages, with putative intermediate stages documented in many early fossil taxa [5].

In the succeeding sections, we summarize the fossil data supporting each hypothesized transformation of the telome theory, and attempt to relate each phase to the molecular developmental and physiological mechanisms identified to date in present day plants (mainly angiosperms).

Transformation one: overtopping

Overtopping, the formation of determinate lateral branch systems, is the limited elongation of branch tips. According to the telome theory, overtopped branches are the necessary precursors to megaphyll leaves [4]. In overtopped branches, vascularisation is primarily channelled into a single or a few vein branches. Determinate three-dimensional lateral branching systems became widespread following the rapid evolutionary radiation of plants during the Early Devonian (Pragian-Emian) [8]. The dichotomizing axial forms remained common during this period but were confined to the rhyniophytes such as Horneophyton lignieri (Kidston and Lang) Barghoorn and Darrah [9]. Caution is required in interpreting the ‘proto-leaves’ of Early Devonian fossils as lateral appendages because the natural orientation of the axis can be difficult to ascertain and because compression during fossilization could artificially flatten branch systems [10]. Nevertheless, the morphology of Early Devonian branched axial systems is thought to have been diverse, with some axes terminating at sterile tips and others with sporangia. The ‘overtopping’ of branched systems, and the appearance of determinate laterals, is recognized as a genuine evolutionary innovation within the Early Devonian.
trimerophytes. In this group, branching was nearly always consistently three-dimensional, as seen in *Pertica quadrifaria* [11] and *Psilophyton* Dawson [12]. There is also anatomical evidence in permineralised proto-leaves of *Psilophyton conicum* that the vascular traces were markedly differentiated from those of the main axis, indicating that they developed laterally [13].

In developmental terms, overtopping requires, first, the initiation of branches, and second, the control of the relative growth rate of different branches. Extant plants exhibit two types of overtopping: sympodial branching where overtopping is combined with reduction, which is typical of (but not exclusive to) lycopsids and some ferns, and monopodial branching, which is typical of the main branching system of the majority of higher plants today.

Branching in angiosperms requires the formation of lateral secondary meristems, termed axillary meristems. These are distributed along the stem proximal to the primary SAM. Although there is some debate as to whether axillary meristems represent pockets of cells that are left behind by the primary SAM or are formed *de novo*, molecular markers for axillary meristems have been identified and mutation in such genes (e.g. LATERAL SUPPRESSOR [LAS]) leads to loss of axillary branching [14]. Thus, at least some of the transcription factors that are involved in defining potential branch points in angiosperms have been identified and their evolutionary history can be investigated.

Once formed, an axillary meristem might grow out or remain dormant. A host of environmental and endogenous signals have been identified that lead to species-specific branching patterns. Nevertheless, a central role for the growth factor auxin in controlling axillary meristem outgrowth (i.e. apical dominance) is a long-standing tenet in plant physiology (reviewed in [15]). More recently, a novel carotenoid-associated signalling system that is involved in axillary branch outgrowth has been identified [16–19]. An interesting idea arising from this research is that many of the factors that control axillary meristem activation converge on auxin transport, and that the relative growth of a branch might be dependent on its relative ability to transport auxin [20*].

The evolution of axillary meristems is not explicitly invoked in the telome theory, yet they clearly represent the major mechanism for branching in angiosperms. Thus, whether the mechanisms identified to date in the control of angiosperm axillary meristem formation support or refute the telome theory is a moot point. As will be seen later, the involvement of auxin flux is a recurring theme in the mechanisms relating to leaf development. The investigation of auxin flux in non-angiosperm species with respect to branch growth would shed light on its potential role in leaf evolution.

The formation of an axillary meristem is intimately linked with leaf initiation at the primary SAM. The SAM is distinguished by being developmentally indeterminate, that is, it has the potential to form a large number of leaves and associated axillary meristems. The angiosperm leaf, on the other hand, is distinguished by being determinate, i.e. the extent of leaf growth is limited. This difference in determinacy between angiosperm meristem and leaf is set by the expression of a developmental module of transcription factors, the KNOX (*KNOTTED*-like homeobox)/ARP (*AS1-RS2-PHAN*) module (reviewed in [21]). Thus, most angiosperm SAMs are characterised by the expression of KNOX genes and by the lack of ARP gene expression, whereas leaves are characterised by the expression of ARP genes and the consequential suppression of KNOX gene expression. Within the eudicots, the KNOX/ARP regulatory module has been conserved, but the timing and positioning of the switch within the leaf from a KNOX ‘ON’ to KNOX ‘OFF’ state (mediated by ARP gene expression) appears to have shifted in evolution. A delay in switching to a KNOX ‘OFF’ is associated with the acquisition of more complex leaf forms (e.g. compound rather than simple and palmate rather than pinnate leaves) [22**,23]. Moreover, the KNOX/ARP module appears to have been recruited in the acquisition of lateral (leaf) organs on more than one occasion over evolutionary time. For example, the pattern of KNOX/ARP gene expression in microphyll leaf formation (e.g. by *Selaginella kraussiana*) is highly reminiscent of that observed in angiosperms, i.e. KNOX is ‘OFF’, ARP is ‘ON’ [24**]. In *Selaginella*, both ARP and KNOX genes are expressed within the SAM itself, and it has been suggested that this expression pattern is linked with the ability of these meristems to bifurcate, although the mechanism by which this might occur is unclear [24**]. Nevertheless, it is possible that the KNOX/ARP module might have played an important role in the initial acquisition of branching upon which overtopping is theoretically based (Figure 2).

The evolutionary importance of the KNOX/ARP module is also suggested by comparison of its functions in *Arabidopsis thaliana* and the closely related *Cardamine hirsute* [22**]. The switch from the simple leaf morphology of *Arabidopsis* to the compound leaf morphology of *Cardamine* can be linked to an altered timing of KNOX gene expression, probably through alterations in promoter sequences that control the timing and/or position of expression. This is in contrast to the situation for the evolution of the LEAFY (*LFY*) gene (which encodes a transcription factor that is important in the control of flowering). Homologues of *LFY* are present in non-flowering plants, and it seems that the incorporation of this transcription factor into flowering gene networks has been associated with mutation of LFY’s DNA-binding domain rather than with elements that control gene expression [25*].
These emerging molecular genetic data support the concept of bricolage: that ‘evolutionary diversification involves a constant tinkering with a highly conserved set of molecules to produce the most diverse organismal forms’ [26]. KNOX/ARP would seem to represent such a conserved module in leaf evolution.

**Transformation two: planation**

Planation is the flattening of the three-dimensional terete stem segments into a single plane. When overtopped morphologies are combined with planated lateral branches, computer model simulations indicate that they might function to maximize spore dispersal, light interception and possibly also to offer greater mechanical stability [6]. As with the fossil evidence regarding overtopping, caution is required in the interpretation of this innovation from fossils because the compression of initially terete structures during preservation can confer the appearance of planation and lamination [10].

Non-laminate proto-leaves are more commonly planated in Mid than in Early Devonian fossil plant assemblages, although three-dimensional branching structures are retained by many species, such as the progymnosperms.
Tetraxylopteris schmidtii [27] and Actinoxylon banksii [28], and the cladoxylalean Pseudosporochrus nodosus Leclercq and Banks [29]. Typical examples of planated branched systems include those of the cladoxylalean Cladoxylon scoparium Kräusel and Weyland [30] and the putative sphenophyte Ibyka amphikoma [31]. In the Late Devonian, the finely branching non-laminate ‘fronds’ of the putative primitive fern Rhacophyton ceratangium are a particularly noteworthy example of planation, reaching lengths in excess of 30 cm [32].

No modern-day representatives of planated branching stems are known, although the sub-tropical gymnosperm genus Phyllocladus has greatly reduced true leaves and phylloclades might represent planated shoot systems [33]. In the Araucariceae, large multi-veined leaves are planated into large compound shoots, and the Cupressaceae and Podocarpaceae leaves with a single vein are re-orientated to produce a two-dimensional flattening of shoots [34].

In developmental terms, planation requires the juxtaposition of branches and hence would involve the positioning of branch initiation points and the co-ordination of relative branch growth. In modern angiosperms, branch points (i.e. axillary meristems) are intimately associated with leaf position. Significant strides have been made in our understanding of the molecular control of leaf initiation and its patterning within the SAM in the past few years (reviewed in [35]). As in axillary meristem outgrowth, auxin plays a central role in the control of leaf initiation and its patterning, with auxin flux through plant tissue directed by the pattern of expression of a series of auxin efflux (PIN-FORMED [PIN]-encoded) and influx (AUXIN1 [AUX]) carriers. With respect to leaf (and, thus, associated branch) positioning, analysis of PIN and AUX expression patterns in the primary SAM indicates that local accumulation of auxin at discrete sites within the meristem dictates the presumptive position of leaf formation [36,37]. On the basis of this system, different patterns of auxin flux can be modelled [38–40], leading to different patterns of leaf initiation. Depending on the extent of internode expansion that occurs between these leaf initiation events (which might be influenced by KNOX gene expression

The potential role of auxin in patterning branching. (a) The site of determinate branch formation (dark blue) is dictated by local accumulation of auxin (AUX) within the SAM (depicted as a light blue circle). (b) The dynamic integration of auxin flux within the SAM leads to the shifting of the local auxin maximum with time so that adjacent portions of the SAM become successively determined to form branches. Recent data based on PIN distribution provide models as to how this might occur. (c) If internode growth between successive branches is limited, a series of adjacent co-planar branches could be formed (i.e. planation could occur). The relative outgrowth of each branch itself might depend on auxin transport within the branch, and the determinancy or indeterminacy of each branch could vary depending on its KNOX/ARP status.
[24**], various constellations of leaves (and associated axillary meristems) could form in three-dimensional space, a pre-requisite for planation (Figure 3).

Transformation three: webbing
The fossil record shows that as photosynthetic branching systems were successively overtopped and planated, closely aligned branches became webbed or infilled by thin lateral outgrowths of photosynthetic mesophyll tissue to produce the broad lamina of a leaf blade. True laminate leaves are atypical of Mid Devonian floras. They appear more frequently only in Late Devonian forest floras dominated by the progymnosperm *Archaepetra* Dawson [41], although these structures were by no means a ubiquitous adaptation among terrestrial plants at this time. Fossil megaphylls vary enormously in shape, size and morphology: from the large laminate leaves of *Archaepetra obtusa* to the finely dissected branches of *Archaepetra fissa* [42,43]. By the Mississippian (Tournasian-Viséan) plants that had megaphyll leaves were confined to the ferns, pteridosperms and sphenophytes, as arborescent lycophytes with long microphyll leaves dominated floras. The leaves of the early sphenophytes, such as *Archaeocalamites radiatus* (Brongniartt) Stur and *Sphenophyllum tenerrimum* Ettingshausen, remained as lateral branches without laminae, with laminate forms only appearing in later groups [44]. In the pteridosperms *Diplopteridium teilianum* (Kidston) Walton and *Rhacoepetra circularis* Walton, and possibly in other members of the same group, leaves were exclusively laminate, closely resembling those of modern ferns. In other pteridosperms, taxa with broad lamina, such as *Charbeckia macrophylla* [45], coexisted with taxa such as *Diplopteridium holdenii* that possessed highly dissected terete forms [42]. Only with the rise of the gymnosperms and the decline of the arborescent lycophytes (from the Late Carboniferous onwards) does the laminate leaf-form become firmly established in floras worldwide.

In developmental terms, the webbing of telomes to produce a laminate leaf blade requires, first, the production of lateral outgrowths and, second, either congenital or postgenital fusion of adjacent branches. The lateral growth of lateral outgrowths and, second, either congenital or postgenital fusion events lead to the gradual restriction of plant tissue to form a leaf. Rather, a tissue volume is specified by the pattern of PIN protein, and thus, auxin flux. This patterning process is thought to depend on a complex and not yet fully resolved feedback loop of auxin flux and PIN protein distribution [58]. In this system, there is no evidence of the postgenital fusion of plant tissue to form a leaf. Rather, a tissue volume is formed and, at the same time, patterning processes define a simple vascular network. A feedback system then enables a co-ordination of leaf lamina growth and more complex vascular patterning [57**].

High carbon dioxide: an environmental barrier to leaf evolution?
Large megaphyll leaves became widespread some 40–50 Myr after the origination of vascular land plants. Fossil evidence indicates, however, that at least one group of plants was capable of producing megaphyll leaves millions of years earlier. Early Devonian (Pragian) proto-leaves of rare Chinese fossils of *Eophyllophyton bellum* [59] are tiny, planated and webbed by thin lamina (thickness 40–200 μm) [59]. They occur on lateral branches and are not confined to terminal fertile regions, like similar lamina structures in *Adokophytton subverticillatum* Li and Edwards and *Calathea beckii* Hao and Gensel from the same flora, and so are not thought to have a role protecting the sporangia. Consequently, these proto-leaves have been interpreted as true photosynthetic megaphyll leaves with a distinctive morphology of deeply incised lobes reaching 2.0–4.5 mm in length and 1.4–4.0 mm in width [60]. The

Thus, the *CUP SHAPED COTYLEDON (CUC)* genes (encoding NAC [NAM-ATF1-CUC2] transcription factors) in *Arabidopsis* prevent the fusion of cotyledons [52], and mutation of the *CUPULLIFORMIS* gene in *Antirrhinum* leads to the dramatic formation of fused organs throughout the plant [53]. These genes must be expressed between forming primordia to prevent fusion, and fusion occurs in their absence. In addition to these transcription factors, auxin has also been implicated in the control of lateral organ fusion. Thus, disruption of auxin flux often leads to fused organs, and it is possible to induce collar-type leaves by manipulating auxin patterns around the SAM [54,55]. With respect to postgenital fusion, the cuticle composition of the cell wall is a potential target. Thus, manipulations that lead to loss or disruption of the cuticle lead to postgenital fusion events [56].

The lateral organs of angiosperms can clearly be persuaded to fuse. During angiosperm leaf initiation and development, however, there are no obvious fusion events. Most notably, at the time of initiation, there is no overt vascular differentiation in the angiosperm leaf. Recent data using PIN proteins as markers of auxin flux and thus, by implication, of vascular differentiation, show that the influx of auxin at the site of presumptive leaf formation on the SAM predicts the position at which the primary vascular tissue (i.e. the midrib) will form [37,57**]. Subsequently, the pattern of vascular formation appears to be prescribed by the pattern of PIN protein, and thus, auxin flux. This patterning process is thought to depend on a complex and not yet fully resolved feedback loop of auxin flux and PIN protein distribution [58].
rare occurrence of *E. bellum* megaphylls suggests that the basic molecular ‘toolkit’ for producing and assembling leaves was in place tens of millions of years before this evolutionary innovation became widespread [1], and raises the question of what prevented plants from releasing this morphogenetic potential?

One hypothesis links the inordinately long delay to the high CO₂ concentration in the Silurian atmosphere; large megaphyll leaves only appear and become widespread after a 90% drop in CO₂ concentration during the Devonian and early Carboniferous, which corresponds to a 100-fold rise in the stomatal density of fossil leaves [61]. This inverse response of stomatal numbers to CO₂ concentration on an evolutionary timescale is consistent with the effects of CO₂ seen in extant plants over centuries [62] and might also have a genetic basis [63]. Experimental studies using the C24 *Arabidopsis* accession identified *HIGH CARBON DIOXIDE* (*HIC*) as a gene that is expressed exclusively in guard cells and is putatively linked to long-chain fatty acid synthesis [63]. When the expression of *HIC* was reduced, stomatal density increased by up to 40% when grown at elevated CO₂ concentrations, whereas normal (wildtype) plants showed either a small reduction in stomatal density or no change in response to elevated CO₂ [63]. Gray et al. [63] hypothesized that *HIC* negatively regulates stomatal development in normal plants through the production of long-chain fatty acids that are deposited in the guard cells. These fatty acids block the diffusion of an unknown signalling compound that represses stomatal development. Under conditions of elevated CO₂ concentration, fatty acid synthesis is disrupted and production of the repressing signalling compound inhibited, allowing stomatal density to increase.

The functional significance that this response holds for leaf evolution has been revealed by theoretical calculations of the energy budgets of various hypothetical and actual photosynthetic structures [61]. For an early axial land plant in the Silurian high CO₂ atmosphere, whose simple structure intercepts minimal quantities of solar energy, stem temperatures remain safely below the lethal temperatures despite having a very restricted transpirational cooling stream dictated (in part) by few stomatal pores. By contrast, such a low transpiration rate is insufficient to prevent the temperature of large megaphyll leaves exceeding the highly conserved thermal limit within the plant kingdom, because of their much greater interception of solar energy. In fact, according to theory, large megaphylls only become a viable option after stomatal density and transpirational cooling capacity increase with the well-documented 90% drop in CO₂ concentration in the late Palaeozoic [61].

The ‘high CO₂’ hypothesis is independently supported by quantitative analyses from the fossil record. These show, first, a 25-fold enlargement in the maximum size of leaf blades that tracks the late Palaeozoic drop in atmospheric CO₂ [43]; second, increases in leaf size in two phylogenetically independent clades (progymnosperms and pteridosperms) [42,43]; and third, the first enlargement of *Archaeopteris* leaves in association with an eight-fold rise in stomatal density [43]. It is possible, therefore, that high CO₂ concentrations acted as an environmental ‘barrier’ that prevented the origination and spread of large megaphylls. Once that environmental barrier was removed, ecological processes, especially competition between species for light, soil water and nutrients, would have driven both the co-evolution of the root and shoot and the well-documented increase in plant height [3].

**Future directions and conclusions**

The first years of this century have seen significant steps forward in the identification of genetic mechanisms that provide a basis for interpreting leaf evolution. Much of this work has concentrated on model angiosperms, in which rapid systems for both gene identification and functional analysis have been established. The next few years will see the application and development of such technologies in an ever wider spectrum of plant species, covering the breadth of distinct extant plant clades. Indeed, for some representatives of mosses and ferns, genomic approaches are well underway [64–66] and have provided insightful data linking *KNOX* gene expression, auxin and organogenesis [67,68]. These approaches will provide the tools with which at least some of the ideas described in this article can be investigated. In particular, hypotheses on the role of environmental factors as driving forces for the selection or adaptation leaf form will become testable.

With respect to the telome theory, several questions remain unanswered (listed in Box 1). At present, over-topping and planation seem, at least conceptually, to be highly plausible mechanisms for leaf evolution. Genetic-based mechanisms have been identified in present day plants that might have been transposed from early plants. With respect to webbing, a mechanism that involves only

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**Box 1 Outstanding questions.**

1. Are the genetic loci that control branching in angiosperms of evolutionary significance?
2. Is the system of auxin flux identified in angiosperms conserved in evolution?
3. To what extent does the *KNOX/ARP* transcription factor module represent a basic mechanism in lateral organ formation? How is the expression of this module integrated with auxin signalling?
4. Is the abaxial–adaxial patterning process and lamina formation an innovation in angiosperms?
5. How widespread are genes such as *HIC* in controlling stomatal responses to CO₂ concentration in plants with different evolutionary origins?
6. What are the physiological or ecological advantages of each transformation?
lateral outgrowth from individual branches seems more likely than a step requiring branch fusion. As a consequence, if the fusion element of webbing is not a requirement for leaf evolution, then the requirement for planation is not obvious. At a more general level, there is also a need to investigate the ecological advantages gained by plants that acquired each transformation, particularly in respect of the interception of solar energy and the efficiency of CO2 uptake in relation to water loss, in the high CO2 of the Silurian atmosphere.

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References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest


58. Analysis of PIN protein pattern within developing leaves indicates that the predicted flux of auxin prescribes the future pattern of vascular differentiation within the leaf, leading to a sequential increase in vascular complexity coupled with leaf growth.


63. Woodward FI: Stomatal numbers are sensitive to CO2 increases from pre-industrial levels. Nature 1987, 327:617-618.


