

Progress in Botany 82

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Progress in Botany

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Progress in Botany

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Editors

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Curriculum Vitae



Christian Körner was born in 1949, grew up in Salzburg, Austria (1949) and enrolled at the University of Innsbruck (Austria). In 1973, he received a Master's diploma qualifying him for a teacher's career in natural history. Yet, in the same year, he started teaching undergraduates in botany in Innsbruck and received a PhD in 1977 for his thesis on plant–water relations of alpine plants. In 1982, he became a senior lecturer ('habilitation' for botany), and in 1989, he was appointed full professor for botany at the University of Basel, Switzerland (retired in 2014).

Academic memberships and awards: Austrian Academy of Sciences, German National Academy of Sciences Leopoldina, Honorary Membership of the Ecological Society of America, Marsh Award of the British Ecological Society, Dr. h.c. Illia University Tbilisi and University of Innsbruck.

Academic services: 25 years editorial board and editor in chief for *Oecologia*, editorial boards of *Science* magazine, *Trends in Ecology and Evolution*, *Global Change Biology*, and others. Chair of Global Mountain Biodiversity Assessment (GMBA), task leader in GCTE/IGBP, Chair of Proclim, the Swiss climate change platform, and of the Forum Biodiversity, both at the Swiss Academy of Sciences. Various academic functions at the University of Basel, with that as an ombudsperson on-going.

Publications: c. 400, several edited books, textbook on Alpine Plant Life and Alpine Treeline, and the plant ecology part of the major university text 'Strasburger's Plant Sciences' around 60,000 citations in Google scholar.

Major research fields: alpine ecology, forest ecology, influences of temperature, water, and CO₂ on plants and ecosystems.

For more details see: <https://duw.unibas.ch/en/koerner/>

Tools Shape Paradigms of Plant-Environment Interactions



Christian Körner

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Abstract The direction of science is often driven by contemporary theory, and theory emerges from consolidated empirical knowledge. What we know emerges from what we explore, and we explore what we have technical tools for. I feel that

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technical opportunities contributed strongly towards what is held as a contemporary, widely accepted theory. However, the presumed causality may become reverted, if one accounts for those less explored questions, for which tools are missing. Here, I will reflect on decades of research experience in empirical plant sciences, mainly plant water relations, plant carbon relations and biogeography, during which some mainstream paradigms became challenged. Scientific theory passes through waves and cycles and is even linked to fashion. Insight that seemed established at one time may become outdated by novel concepts facilitated by novel methods, and as time progresses, old concepts may find a revival. In the following chapter, I will illustrate such shifts in awareness and misleading paradigms that were driven by the contemporary availability of methods rather than stringent logics. Examples include plant responses to drought stress; the drivers of plant growth in general, as well as in the context of rising atmospheric CO₂ concentrations; and how physiological plant ecology can contribute to resolving biogeographical questions such as range limits of plant species and plant life forms. My résumé is that explanations of plant responses to the environment are predominantly below ground and require an understanding of developmental and meristematic processes, whereas available tools often lead to attempts at above-ground answers based on primary metabolism (e.g. photosynthesis). Further, well-understood processes at the organ (leaf) level are losing relevance at the community or ecosystem level, where much less understood mechanisms come into action (e.g. stand density control). While the availability of certain convenient methods can open new research arenas, it may also narrow the scope and may direct theory development towards easily measurable parameters and processes.

Keywords CO₂, Drought, Elevation, Growth, Hydraulics, Limitation, Low temperature, Meristems, Nutrients, Photosynthesis, Productivity, Stomata, Water potential, Xylem

1 Prologue

My parents took us, my brother and me, to wild places, such as unspoiled lakeshores or Mediterranean sand dunes where we camped for 3 weeks away from civilization. This was in the 1950s. I had my own garden plot when I was 7, but we never could afford a car with the post-war income my father earned as a community engineer in Salzburg (Austria) and my mother as a freelance professional photographer. I decided to become a biologist at 10. At that age, I entered the 8-year science-oriented gymnasium, with subject-specific teachers, some of whom stayed with class for all 8 years till final exams. One of them was my biology teacher. For a 10-year-old, it was almost unbelievable that talking about plants and animals can be a profession. No question, this was going to become my job. After graduation and founding a

family in Innsbruck, my school teacher career became very brief, however. Walter Larcher, my later doctor father, felt I should better teach undergraduates at the University, and he offered me a job which also paid me through my PhD years from 1973 to 1977, a rather fortunate situation, because in those days, doctoral students were not paid and project money was scarce, a situation explained so well by Erwin Beck in his reflections (Beck 2016).

My graduation project in 1972 had already paved the path towards empirical plant biology. I was given the task to develop and test a so-called leaf diffusion porometer. Today an indispensable instrument to assess plant-water relations (specifically, the degree of stomatal opening in leaves), there was no trustworthy technical solution on the market in the early 1970s. The mechanical, electronic and aerodynamic challenges were substantial. It so happened that W. Larcher had just employed the young physicist Alexander Cernusca to establish environmental physics at Botany. In the post-war years, his father built the first automatic, biometeorological station for the federal high-elevation forest research group that was based in Innsbruck as well (Aulitzky 1961). They worked on treeline questions, a field I wrote a book on, many years later (Körner 2012). Growing up, academically, door to door with a physicist with such interests and skills (e.g. Cernusca 1976), helped me in developing this porometer but also exposed me to micrometeorology and physical solutions to plant science questions, which shaped my thinking till today. With a brand-new design of an electronic humidity sensor made in Switzerland (the country that should later become my academic home), my instrument not only worked very well (Körner and Cernusca 1976) but also made it a hot seller by the then German company Walz. They produced a semi-automatic version and sold 14 instruments in 2 years, before LI-COR stepped in with their null-balance porometer around 1978. I was proud that LI-COR adopted my absolute calibration routine with capillary evaporimeters, the readings of which revealed the amount of vapour that entered the chamber per unit of time and caused the humidity sensor to produce a signal as if a leaf were releasing vapour to the chamber. With these experiences, I was set to become an *experimental plant biologist* or *physiological ecologist*.

In the late 1960s, Botany at Innsbruck had joined the International Biological Program, IBP, that aimed at assessing the biological productivity of terrestrial ecosystems and explaining its main drivers. The Innsbruck team led by W. Larcher belonged to the so-called ‘Tundra-Biome’ module, contributing to alpine heath productivity and its climatic drivers and carbon, nutrient and water relations (Larcher 1977). I became the ‘water man’ and learned to appreciate the added value of multi-thematic approaches and international comparisons and cooperation. So, my second academic heritage from those years was the *comparative approach* in field-oriented plant sciences.

I was very fortunate that I could meet in person, both pioneers of comparative physiological ecology, Otto Stocker (Darmstadt; Lüttge 1979; see Stocker 1956, 1976 as examples) and Arthur Pisek (Innsbruck; Larcher 1975). I believe my entire work was in their tradition that was so elegantly developed into the modern era by Walter Larcher, a student of Pisek (see Larcher 2003). I still remember the occasion when I explained my porometer to the ca. 80-year-old Arthur Pisek who had already

played with the idea to measure directly what he was exploring indirectly (Pisek et al. 1970). His way of a comparative, ecophysiological characterization of as broad as possible a spectrum of species belonging to a specific habitat type was novel but also timeless and guided much of my alpine research (examples in Pisek and Cartellieri 1934, Pisek 1960, Pisek et al. 1973). When I decided to work with W. Larcher, it was for this conceptual framework that always aimed at the ‘big picture’, the overarching pattern. Species always differ, and these differences matter and need to be accounted for. In a modern phrase, this would be addressed as *functional biodiversity research*, the third legacy from that period.

And then, in 1989, it happened that I was offered a full professorship at the University of Basel, Switzerland. My inauguration lecture at Botany in 1990 was entitled ‘The Art of Asking Small Questions’, meaning that very elaborate methods may consume so much time and energy that the work becomes restricted to one species or even one genotype. Hence, to cover diversity and obtain a big sample and eventually arrive at a ‘big picture’, the challenge is rather to ask cleverly designed ‘small questions’ tied to simple but meaningful traits that can be explored in many species and locations (discussion in Körner 2018a). Leaving Austria, I brought with me the history of 100 years of alpine research in Innsbruck, mostly published in German, which, I felt, deserves wider visibility, complemented by more recent data and insights I took from travelling many other mountain regions during the 1980s. In 1995, I decided to wrap this up in what became *Alpine Plant Life* (Körner 1999a, 2003a, 2021). I started my professional life in Basel with a sense for multidisciplinary work, a reasonable foundation in environmental physics, and an open mind for new methods and alternative explanations of plant responses to the environment. The following four sections summarize ideas I gained over almost half a century of empirical work with plants (see Körner 2018a).

2 Plant-Water Relations Revisited

As water moves from the soil to the atmosphere through a plant, it passes through a series of resistors. In analogy to Ohm’s law, the drivers, resistors and resulting fluxes can be identified and measured (including the variable stomatal diffusive resistance as defined by Gaastra 1959; see also Cowan 1965). My porometer permitted to quantify and monitor the diffusive resistance of the leaf epidermis (or the reciprocal, the leaf diffusive conductance, g) – a tool and new concepts for leaf gas exchange that emerged in these days that shaped my early approaches to plant-water relations.

2.1 Stomatal Conductance Correlates with Photosynthesis

In the 1970s, it was still possible to know almost everything about a subject. Within a very short period of time, porometers had produced hundreds of data sets from

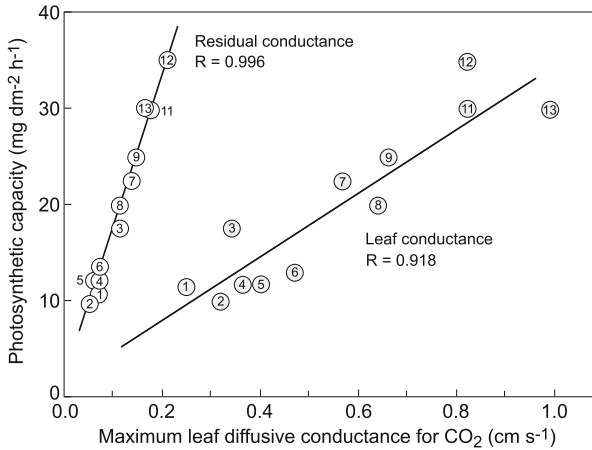


Fig. 1 Maximum leaf diffusive conductance (g) and maximum rate of net photosynthesis (A) of leaves of C3 plants correlate linearly across the major plant functional types across the globe (Körner et al. 1979). 1 succulents, 2 evergreen conifers, 3 deciduous woody plants, 4 herbs from shaded habitats, 5 evergreen broadleaved wood plants, 6 desert and steppe shrubs, 7 deciduous orchard trees, 8 wild-growing graminoids, 9 cultivated C3 grasses, 10 cultivated C4 grasses (not shown; g similar to 11, but A twice as high), 11 herbaceous crop plants, 12 wild herbs from open habitats, 13 plants from aquatic habitats and swamps

around the globe. How do they compare? What are the patterns across the plant kingdom? While IBP was clearly after ‘big global patterns’, my stomata world was ready for a search for big patterns as well. Indeed, maximum stomatal conductance turned out to correlate linearly with the maximum rate of photosynthesis (then called photosynthetic capacity) across plant life forms (Fig. 1; Körner et al. 1979). So, the conductance for gas diffusion turned out to be tightly associated with the capacity of the mesophyll to absorb CO₂. The regression shown in Fig. 1 was strongly driven by plant functional groups with low and high extremes of g_{max} . Years later, a closer look at the central range of the regression, where almost all tree taxa are nested, revealed a surprisingly narrow range of maximum leaf diffusive conductance, averaging at $218 \pm 24 \text{ mmol m}^{-2} \text{ s}^{-1}$ across all 151 taxa examined from different climatic regions (expressed in the molar units that became more popular since then; Körner 1994). While still allowing for some interspecific variation, such a unifying number is rare in plant ecology. What made the variation to condense was the application of a common projected leaf area reference, even when leaves had a strong three-dimensional shape such as in some conifer needles.

The 1979 *Photosynthetica* paper took more than a year to become printed after acceptance. By pure coincidence, the mechanism of this interrelationship shown in Fig. 1 was explained by a group in Canberra at the Australian National University in a paper by Wong et al. (1979) that appeared at the same time. Both studies illustrate that plants optimize the gain in C for the unavoidable loss of water, solving the eternal compromise between ‘hunger and thirst’ in plants. Known for authorities like

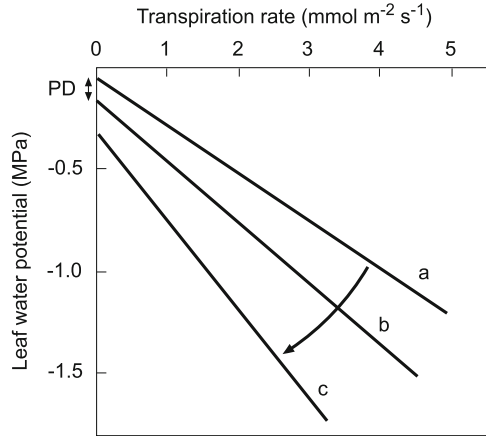
Ralph Slatyer, Barry Osmond, Ian Cowan and Graham Farquhar, this was the place to go for a postdoc. The time in Canberra became most influential in several respects.

I started in Canberra, by testing stomatal response theories along an elevation gradient in the Australian Snowy Mountains. Although the idea that stomata should respond to evaporative forcing (ambient humidity) in a way that minimizes water loss for a given amount of carbon captured was around for several years (Cowan and Troughton 1971, Lange et al. 1971, Schulze et al. 1972), the field evidence was still scarce. *Eucalyptus* in Australia and *Nothofagus* in New Zealand should be ideal objects to test this hypothesis in regions with contrasting humidity. Indeed, both taxa exhibited a clear-cut stomatal response to ambient humidity that could *not* be explained by drought stress (critically reduced leaf water potential as assessed with a pressure chamber; Körner and Cochrane 1985, Körner et al. 1986). Once a threshold of vapour pressure deficit (vpd) was passed, g declined almost linearly. For *Eucalyptus pauciflora* in a dry atmosphere, the vpd threshold for stomatal control of transpiration was twice as high (c. 15 hPa) as for *Nothofagus menziesii* in a humid environment (c. 8 hPa). So, stomata clearly control vapour flux even in well-watered trees, and there was adaptation to the regional climate. Later it was shown that such vpd responses also relate to both photosynthetic capacity and xylem hydraulics (Franks and Farquhar 1999).

2.2 *Transpiration Drives Shoot Water Potential*

A second observation during this field work with *Eucalyptus pauciflora* in the Snowy Mountains made me rethink the contemporary plant-water relations concepts. Counter to widely held assumptions, leaf water potentials became reduced as the rate of transpiration rose, as long as soil moisture was not severely limiting (pushing leaf water potential beyond a critical threshold). The popular view was (and still often is) that a declining leaf water potential should affect stomata and these should reduce flux. In reality, vpd and g jointly determine transpiration, with the inevitable consequence that the leaf water potential must fall across the given hydraulic resistances as long as the water tension remains subcritical for stomatal action (for most trees less than -1.6 to -1.8 MPa). Except when the water potential falls below such thresholds (when deep roots fail to reach adequate soil moisture), leaf water potential is a result of transpiration and not the other way round (Fig. 2; for an early account see Landsberg et al. 1975). At any point in the hydraulic capillary continuum from the root cortex to the leaf mesophyll, the drop in water potential is the consequence of a flux across resistors, with the atmospheric evaporative forcing ‘pulling’ the inelastic water capillaries across all these resistors. This hierarchy of causalities is still not widely appreciated.

Fig. 2 Unless soils are severely dehydrated, the rate of transpiration determines the reduction of shoot water potential (not the other way round). A conceptual diagram based on works by Körner and Cochrane 1985, published in a standard textbook. PD pre-dawn water potential (Körner 2013a)



2.3 A Water/Carbon Relations Proxy: Stable Carbon Isotope Discrimination

For me as the ‘water man’ from Innsbruck, the time in Canberra (1980/1981 and 1989) opened an arena of new topics: stable carbon isotopes in plants (thanks to Graham Farquhar) and plant nutrient relations and plant carbohydrate storage (thanks to Suan Chin Wong). They had a new mass-spectrometer lab there, the CSIRO Department of Forestry next door had an automated nutrient analysis facility, and Chin Wong developed a new enzymatic assay for non-structural carbohydrates in plants (see Sects. 3.2.1 and 4.2). With new tools and new paradigms in sight, my attention gradually moved away from stomata and water potential. Having worked in the Tyrolean Alps, the Great Caucasus, the Andes, the Australian Alps and the mountains of New Zealand and Papua New Guinea, lots of samples waited to become ground and analysed for global patterns related to elevation, complementing measured stomatal and mesophyll properties.

And the global patterns did emerge: provided a large enough sample of species was collected and elevation-related drought was avoided (drought is not an intrinsic feature of mountains), stable carbon isotope discrimination declines with elevation globally. Hence, the photosynthetic efficiency in capturing CO_2 increases relative to constraints by stomatal diffusion (Körner et al. 1988, 1991). This is a clear-cut proof that atmospheric pressure and, thus, the partial pressures of CO_2 and O_2 were the main drivers, confirmed many years later from exploring the Basel herbarium for a large set of congeneric samples from contrasting elevations and latitudes (Zhu et al. 2010). So, high-elevation plants cope extremely well with reduced CO_2 partial pressure, as photosynthetic gas exchange studies confirmed in the high Alps (Körner and Diemer 1987, see Sect. 3). An increased photosynthetic efficiency goes hand in hand with higher leaf nutrient concentrations in high-elevation plants (Körner 1989). With an on average thicker leaf mesophyll, a higher stomatal density is required (when compared in congeneric species from different elevations; Körner et al.

1989a, b). Thus, water relations and carbon relations remain connected at leaf level as one moves to high elevations.

2.4 *When Leaf-Level Processes Become Overruled by Stand-Level Adjustments*

It is widely held that plant life on land became vigorous, once stomata were ‘invented’. Their control of water loss seems like the ultimate solution for plants to cope with periodic water shortage. Yet, from an investment and amortization perspective, this could mean shutting down an expensive machinery (leaves) for much of the time when water falls short. From a ‘management perspective’, it would be more efficient to install less of that machinery (foliage) per unit land area but keep it running for most of the time. Most physiological plant ecologists do not like this sort of reasoning because there is little to measure with fancy equipment. Hence, the fundamental role of leaf area per unit land area (LAI) or plant spacing (e.g. Whitehead et al. 1984), leaf area per total plant mass (LAR), and the role of rooting depth (e.g. Jackson et al. 1996; our own works in Aleppo pine in Sarris et al. 2013) tend to become neglected. Reduced stand density and LAI and higher investment in roots and species replacement towards specialist taxa are by far the most important long-term biological responses to water shortage (Körner 2013a), with stomata meeting a sort of fire brigade function for rapid intervention. Researchers have repeatedly been surprised that plants keep transpiring and even growing under severe drought as a result of such stand-level adjustments. A good example is *Festuca orthophylla*, the dominant species in the Bolivian Altiplano, at 4,250 m elevation with annual precipitation of c. 300 mm confined to a few months, with hot days and freezing nights during most of the year. We found that these tussocks keep tillering and expanding leaves throughout the long dry season (Monteiro et al. 2011; Monteiro and Körner 2013). The explanation is plant density control (Fig. 3). The root spheres of these tall grass tussocks cover land six times larger than the tussock itself (or clusters of fragmented tussocks), and they do not overlap among neighbours, with the consequence that the water available per unit of tussock area exceeds 1,500 mm, sufficient to make a year-long living. Note the sandy substrate (and, thus, a lack of a capillary continuum) prevents deep moisture from becoming exhausted by evaporation from bare soil. An entirely different strategy is adopted by perennial forbs scattered among these tussocks: tiny leaf rosettes, firmly attached to or even sunken into the ground, resting on huge below-ground structures such as tap roots (Patty et al. 2010). So there are different solutions to the same problem with spacing and plant architecture as the dominant factors.

Plant-water relations came a bit out of fashion in the late 1980s till the early 2000s, with most questions seemingly resolved. As a consequence, most young researchers nowadays had never heard about pressure-volume curves (Körner and Cochrane 1985). Simple diffusion porometers almost disappeared from the market

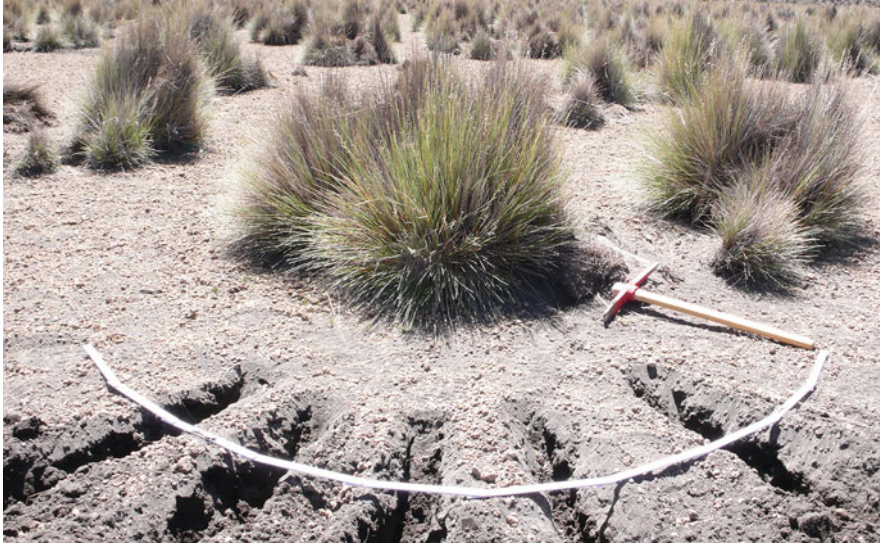


Fig. 3 Wide plant spacing or other ways of reducing leaf area per unit land area is the most important long-term adjustment to drought. Once land cover is tuned to moisture availability, stomatal responses play a minor role. The photograph shows the exploration of the size of the root sphere of tall grass tussocks in the Bolivian Altiplano at 4,250 m asl

and gave place to more abundant and sophisticated CO₂ gas exchange equipment that delivered leaf diffusive conductance as a by-product (see the carbon chapter for the consequences). The use of pressure chambers became largely reduced to student courses. Only a few faculties globally had staff that was able to teach basics in plant-water relations, and only a hand full of labs maintained research in this field, largely on xylem hydraulics.

2.5 Hydraulic Failure in Trees: Cause or By-Product of Tree Mortality?

Big drought waves in the south-western USA and clever instrumentation suddenly changed the mood, and plant-water relations came back to front stage via plant hydraulics. About 90% of all papers that employ the phrase ‘hydraulic failure’ appeared in the last decade (e.g. McDowell 2011, Anderegg et al. 2012, Choat et al. 2012, Urli et al. 2013). Trees are considered dying, because their stem conduits could not meet the demand by foliage. Attracted by those aspects of the soil-plant-atmosphere continuum that can be easily measured (xylem conductivity, fraction of embolized xylem), other aspects that were considered key to plant survival under drought in the early half of the last century received less attention (e.g. tissue dehydration tolerance). While trees that have lost their conduits’ integrity by

xylem embolism are likely to enter problems when it comes to recovery as moisture returns, the currently often implied chain of causalities is quite incomplete (Körner 2019). Trees build stems largely to compete with their neighbours (and, in doing so, manage to resist an hurricane), using the same structures for stability that can also serve water transport. Given the dominant mechanical demand, circumstantial and direct evidence obtained since nearly 50 years ago indicates that the conduit systems' capacity is way oversized. Not surprisingly, most of the conductive rings are taken out of function after a few years, resulting in a narrow, conducting sapwood. In ring-porous oaks, all rings but the last one are deactivated.

Why would evolution select for such narrow, conducting sapwood fractions if conductive capacity was likely to become an existential limitation under drought? People have done 'cruel' things to small stems, cutting them in half, even crosswise (e.g. Mackay and Weatherley 1973), with no effect on leaf transpiration. I got involved in the latest of such attempts, although the biggest in scale ever: we cut 30–40-m-tall trunks in situ in half and observed canopy responses from the gondola of a crane (see Fig. 7): no effect on transpiring leaves under bright summer weather when fluxes peak (Dietrich et al. 2018). While one can question the dummy nature of a cut compared to widespread embolism, it seems obvious that drought is the most unlikely of all conditions during which the capacity of a piping system can become exhausted, when that system can supply crowns at maximum transpiration with only part of it being intact. We found flux rates to double in intact xylem near the edge of the cut (indicating spare conductive capacity), like water flow in a creek narrowed by the walls of a lock. Once stomata are closed in response to a severe drought, the flux will approach zero. As I explained in this recent comment (Körner 2019), xylem embolism is better viewed as a by-product, not the cause of mortality, when roots fail to supply water, once the soil-root capillary continuum became interrupted. That debate will continue, but inevitably, the focus has to turn to roots at one end and dehydration tolerance at the other end (leaves and shoots) within the soil-plant-atmosphere continuum.

How does water get through roots? An interesting question as posed by Steudle and Peterson (1998). And how does water get to the root, when the soil passes through critical dehydration? And why did evolution retain tracheids, after the far more efficient vessels had been 'invented'? And why are some trees dying from severe drought with hardly any embolism and others do well after drought with a lot of embolism (Johnson et al. 2018)? The likely explanation is that all this has little to do with hydraulic failure of the stem xylem as such but with the roots' failure to obtain water. When drought tolerance was discussed in the early part of the last century, this was a question of how much tissue dehydration is tolerable. The stem's xylem as such was never considered the bottleneck when people started to quantify the segments of the soil-plant-atmosphere continuum (SPAC; see, e.g. Jarvis 1975, Jackson et al. 2000). A xylem that becomes embolized because the roots fail to replenish crown water loss represents a water reservoir to the tree (with tension relaxed in the broken capillary system), a finite source of apoplastic water for attached parenchyma, from the paratracheal one to that in the mesophyll. How long does that reservoir last under minimum transpiration in order to survive

(Čermák et al. 2007)? How much can a tree reduce such minimum losses compared to its apoplastic stores? What is the role of minor conduits and tracheids for facilitating recovery, when most vessels became dysfunctional? And what is the role of roots in protecting trees from critical dehydration? In my view these are the decisive questions. Stem hydraulics received so much attention in the drought mortality debate because their conductivity had been quantified, and not because they explain mortality. Tools shape paradigms. There is no question that water flux in xylem is still full of unknowns and is a most fascinating research area (e.g. Meinzer et al. 1999, Tyree 2003, Holbrook and Zwieniecki 2005, Mayr and Sperry 2010), but roots are the weakest link between soil and foliage (Jackson et al. 2000), though much harder to study.

3 Plant Carbon Relations in a Source-Sink Context

Since De Saussure (1804) discovered that plants ‘eat air’, it fascinated plant scientists but also the broad public how they do it, and it soon became obvious that the process of CO₂ assimilation is central to life on earth. And so it was to my early career.

3.1 *Photosynthesis Under Low CO₂ Partial Pressure*

If anywhere, I felt, CO₂ assimilation should limit plant growth in ‘thin’, high-altitude air and in cold places. Thus, high-elevation photosynthesis needs to be understood in a broad range of species. With water-cooled triple-walled glass cylinders placed in situ over the dominant alpine sedge species in the Alps (Fig. 4), it became clear that the rate of net photosynthesis at 2,300 m elevation is largely light limited, with temperature playing a minor role because of perfect thermal acclimation (Körner 1982). The reference for this judgement was a fully illuminated, horizontal leaf’s capacity to absorb CO₂ at optimum temperature. Clouds, suboptimal leaf angles and mutual shading in the canopy almost halved potential seasonal assimilation and, thus, presumably also growth. This work was entirely driven by my then assumption that growth in alpine plants (or plants in general) is photosynthesis driven and thus carbon limited. Later works proved this assumption to be wrong.

With a substantial Austrian Science Foundation grant, I could buy the then most advanced technology to study leaf photosynthesis and its response functions to light, temperature and CO₂ concentration in situ. Testing high alpine plants’ photosynthetic response to elevated CO₂ was particularly tempting given the intrinsically low partial pressure of CO₂ at high elevation and the ongoing atmospheric CO₂ enrichment (Körner 1992). This battery and mass-flow controller-operated system worked fast enough, so that it was possible to study replicated response functions of net photosynthesis in 12 pairs of congeneric species at 2,600 and 600 m elevation during

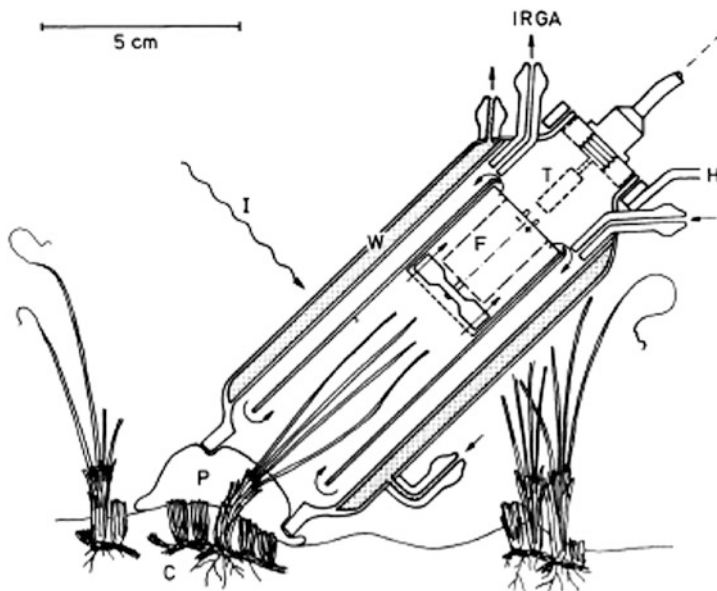


Fig. 4 In situ studies of alpine plant photosynthesis with a three-walled air-conditioned glass chamber mounted to *Carex curvula* tillers (Körner 1982). *F* fan, *W* water jacket, *H* holder, *T* temperature and humidity sensor, *P* plastic silicon rubber, *C* rhizome system

the short alpine summer. The outcome was expected to explain why alpine plants are so small and grow so little compared to their low elevation relatives and how much these high-elevation plants might profit from future atmospheric CO₂ enrichment.

Alpine species turned out to absorb CO₂ far more efficiently than congeneric low-elevation species (in line with the carbon isotope data from around the globe, see Sect. 2). By this efficiency, they not only neutralize the 20% diminished partial pressure of CO₂ at the 2,600 m test site near Innsbruck compared to the valley floor (600 m) but also exhibited higher maximum rates of assimilation (Körner and Diemer 1987). Hence, there was no evidence that these plants faced unit leaf area-based carbon constraints of growth any greater than low-elevation species do. Elevating CO₂ supply caused rates of photosynthesis to strongly increase. When artificially grown under elevated CO₂ in full sunlight, these alpine species retained this high carbon capturing capacity (Körner and Diemer 1994). However, time was not yet mature to question the carbon limitation paradigm that drove all this leaf gas exchange research.

3.2 Effects of Elevated CO₂ on Plants and Ecosystems

Through my move to Basel, the CO₂ enrichment experiments with alpine plants discussed above became interrupted. Meetings with the small but growing research

community that had an interest in exploring plant responses to elevated CO₂ at IIASA (Laxenburg near Vienna), Woods Hole (USA) and Lunteren (Netherlands) made it clear that we do need realistic ecosystem-level experiments in this field. The conference dinner of the Lunteren meeting in the artificial jungle at Het Heijderbos was a key experience: during the train ride back to Basel, I designed an experiment with tropical model ecosystems that capitalized on the brand-new experimental greenhouse at the Institute of Botany in Basel.

3.2.1 Tropical Forests

We built four highly diverse, humid tropical plant communities composed of 15 species each, with understory, shrub, tree and liana taxa, planted as small clonal propagules, provided by the Basel tropical greenhouse staff. These complex but exactly replicated communities in a split-plot design were grown on a low-fertility, leaf litter compost-sand mixture. The communities were rapidly filling the 17 m³ air-conditioned containments that either received elevated or ambient CO₂. Hot and humid conditions caused plants to grow so vigorously that the taller life forms

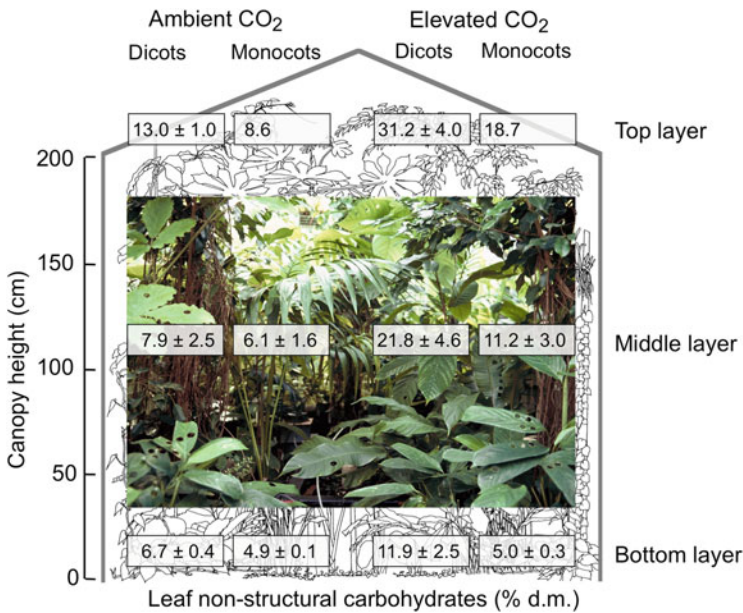


Fig. 5 Model jungles composed of 15 humid tropical species belonging to different plant functional groups and exposed to contrasting CO₂ supply reveal no CO₂ ‘fertilization’ effect on biomass production, but enhanced soil CO₂ release and nutrient leaching. Elevated CO₂ concentrations caused non-structural carbohydrate concentrations in leaves (shown here) to rise dramatically (except for monocots in the understory at 1–2% sunlight), while leaf area index levelled off at 7 (Körner and Arnone 1992)

pushed the roof after 3 months (Fig. 5). The expected CO₂ fertilization effect on biomass production was not found. In what became my first paper in *Science* magazine (Körner and Arnone 1992), we showed massive starch accumulation in the upper canopy, higher root mass, much higher soil CO₂ release and increased nutrient leaching through a lysimeter drainage to the basement of the building. Counter to expectation, LAI levelled off slightly lower under elevated CO₂. In retrospective, this makes sense, given the overabundance of photoassimilates.

These works found a continuation at the Smithsonian Tropical Research Institute (STRI) in Panama under a Mellon Foundation grant in cooperation with Klaus Winter. We grew seedlings of tropical trees and shrubs in situ under elevated and ambient CO₂ concentrations in very deep forest shade on Barro Colorado Island in order to test the hypothesis that low light is the most likely condition to induce a CO₂ fertilization effect. Why? Because elevated CO₂ shifts the light compensation point of photosynthesis, and these plants grew right at the light compensation point, so that the CO₂ concentration became decisive for whether they can grow at all (Fig. 4.1 in Lüttge 2008). And indeed, providing those seedlings with extra CO₂ induced a very strong growth stimulation at otherwise very small absolute growth rates (Würth et al. 1998a). Such deep-shade responses to elevated CO₂ may decide upon later forest structure. Should liana seedlings take a similar advantage, the likelihood of lianas reaching the canopy top would rise. And lianas grown from Yucatan seed sources in deep shade on original forest soil we shipped in from the site of origin to Basel did indeed exhibit exceptional CO₂ responses (in part more than doubling biomass; Granados and Körner 2002). Remarkably the biomass effect from pre-industrial to then ambient CO₂ concentrations was much bigger than that from ambient to similar CO₂ increases in the future. More aggressive lianas would enhance tree turnover and reduce forest carbon stocks (Körner 2004a, b), and indeed tropical lianas have been observed to become more aggressive in recent decades (Phillips et al. 2002, 2004). Thus, a biodiversity effect exerted by a CO₂-enhanced liana growth can shorten the mean residence time of C in the biggest biological carbon reservoir and, thus, reduce its contribution to the global biomass C stock.

Experiments conducted in a temperate zone forest confirmed the CO₂ x shade interaction. When light is reduced to very low levels, elevated CO₂ causes a significant relative stimulation of growth of seedlings (Hättenschwiler and Körner 2000) and lianas (Zotz et al. 2006) irrespective of nutrition, yet again, at otherwise very low absolute rates of growth.

How will a fully sunlit tropical forest canopy respond to rising CO₂ concentrations? Still today, this remains a field of speculation, because it is very hard to estimate or model sink control of carbon capture in late successional forests. Scaling from tree or plot level to net biome responses entails other problems related to stand dynamics (e.g. Phillips et al. 2004; Brienen et al. 2015), which determine the carbon stock: faster growth commonly reduces the mean residence time of carbon, that is, tree longevity (Körner 2017, Büntgen et al. 2019). Whatever the long-term carbon sink capacity of a tropical forest is, one would expect that individual leaves in the canopy, artificially exposed to elevated CO₂, would never show any C-overflow symptoms (that means an accumulation of non-structural carbohydrates, NSC).

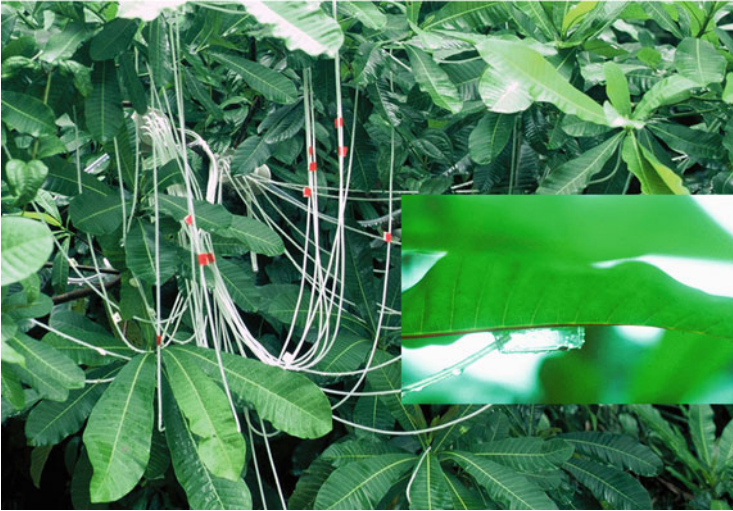


Fig. 6 Providing 12 cm² leaf sections at the top of a humid tropical forest in Panama with extra CO₂ derived from soil: isotopic labelling confined to exposed leaf tissue, carbohydrate accumulation despite a near to infinite carbon sink of such tall trees compared to a small leaf section and no stomatal response to elevated CO₂ (Körner and Würth 1996; Würth et al. 1998b)

Huge trees would always permit dissipating extra C obtained by a single leaf. It seemed worth testing this hypothesis in order to obtain at least a hint at top canopy C relations in the light of rising CO₂.

At the Smithsonian crane site near Panama City, we trapped CO₂ released from the soil under 4 m² of black plastic foil on the ground. Inevitably that CO₂ carries a stable carbon isotope signal ca. 20 permille more negative than in free-air CO₂. We then pumped this isotopically labelled CO₂ to a manifold box in the 40–50 m tall forest canopy. From the crane's gondola, we attached small transparent plastic cups to the underside of big leaves and connected these to the manifold box so that the cups became continuously flushed with extra CO₂ from soil (Fig. 6). After a week only, leaf tissue attached to the cup was packed with extra NSC compared to controls (Würth et al. 1998b), very similar to what we observed in our greenhouse jungles in Basel. Leaf sections under the cup carried a clear carbon isotope signal reflecting the soil-derived CO₂. These data demonstrate that NSC accumulates in foliage in response to elevated CO₂ irrespective of source-sink relationships. Neither NSC nor the ¹³C signal was dissipated within a given leaf blade but remained confined to the exposed leaf section. Another surprising observation was that stomatal conductance was not reduced in leaf sections exposed to elevated CO₂, challenging a common hypothesis. With this rather simple and cheap experimental system, we could demonstrate across different tropical tree species that NSC accumulation is an intrinsic response to elevated CO₂, irrespective of sink capacity. While we do need entire forest CO₂ enrichment experiments, such small-scale studies can illuminate basic questions for this largest of all biological C reservoirs on earth (for a review see Körner 2009).

3.2.2 Alpine Vegetation

Established at my new post in Basel, I received a substantial grant by the Swiss Science Foundation for the first in situ CO₂ enrichment experiment in alpine grassland, using a special design of open top chambers with an excentric air release collar (1992–1995). After four seasons in a high-CO₂ environment at 2,500 m asl, either with or without mineral fertilizer addition, the productivity of this grassland remained unresponsive to elevated CO₂, but a relatively low dose of NPK fertilizer (40 kg ha⁻¹a⁻¹) alone almost doubled above-ground biomass (Schäppi and Körner 1996; Körner et al. 1997).

At that point, the carbon limitation hypothesis was falsified for fully illuminated vegetation, both in a vigorously growing humid tropical model jungle and a slow growing alpine test system. The results for the alpine one were confirmed later in a free-air CO₂ enrichment (FACE) experiment, with glacier forefield vegetation, in which elevated CO₂ even exerted negative effects on plant biomass (Inauen et al. 2012), which we attributed to competitive inhibition of nutrient availability by an exudate-driven microbial community. In a recent experiment, we tested the gradual effect of shading from no shade to half of sunlight for three seasons in the same type of late successional grassland, which had no effect on bulk above-ground biomass (but at maximum shade below-ground biomass became measurably reduced after 3 years), underlining that photosynthesis was not constraining above-ground biomass production (Möhl et al. 2020). These results suggest that alpine vegetation is not carbon limited as I was assuming when studying high-elevation gas exchange in my early career (see Sect. 3.1). Whether the similar results obtained with the tropical model ecosystem reflect real-world responses awaits to be explored in large-scale in situ experiments.

3.2.3 Temperate Forests

How could it be that providing photosynthesis with more CO₂ stimulated its rate per unit leaf area instantaneously but had no effect on growth and biomass accumulation? Were experimental conditions prohibitive for growth in these specific cases? And if so, where did all the extra carbon go? Whatever the explanation, it was clear that larger-scale and more realistic experiments were needed, performed in the field, without interfering with the nutrient cycle, no soil disturbance, no enclosures and preferentially with forest trees, given so many hopes are tied to their ability to capture more carbon in a CO₂-rich future. A site was to be found with as many as possible tree species with adult individuals in a small area that could be surveyed from a huge building crane at the level of tree crowns 30–40 m above ground. After spending 1–2 tons per day of industrial CO₂, cleaned to food quality and released in the forest canopy for eight seasons, using a free-air CO₂ release system, the growth response of the exposed deciduous trees was zero (Körner et al. 2005, Bader et al. 2013). There was a clear isotopic fingerprint of the added CO₂ in tree rings,

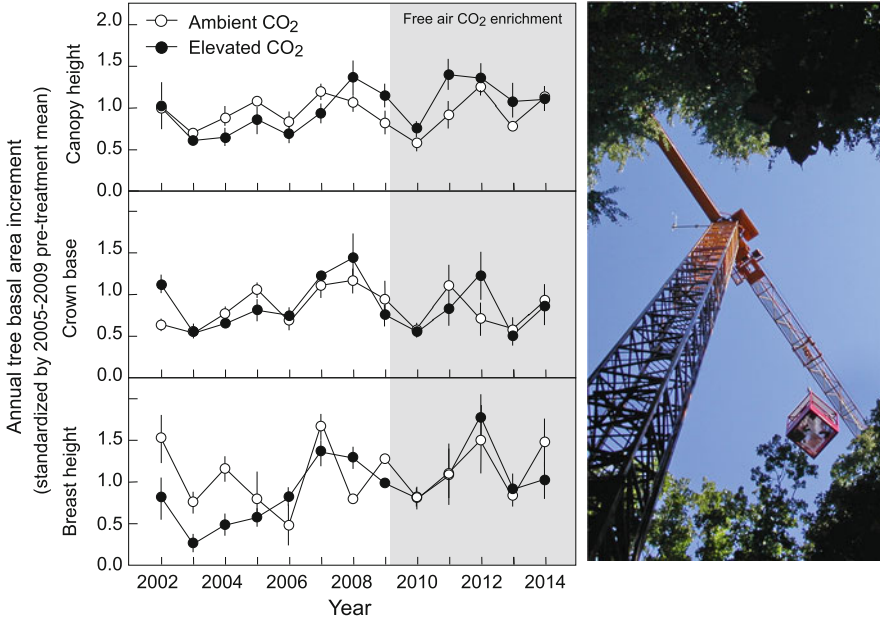


Fig. 7 Mature, 36-m-tall *Picea abies* trees take no growth advantage from five seasons of canopy-scale CO₂ enrichment. The diagram shows standardized tree ring responses for three heights (Klein et al. 2016b). The canopy crane operated for 20 years near Basel facilitated a large number of research works in mature forest trees

confirming efficient CO₂ enrichment (Keel et al. 2006), and per unit leaf area photosynthesis remained stimulated (though somewhat downregulated) by year 8 (Bader et al. 2010).

We repeated the same treatment for 5 years in 36-m-tall spruce trees, with the same result (Klein et al. 2016a; Fig. 7). Other research groups working with test forests under steady state (closed canopy, constant leaf and root turnover) arrived at the same answer (boreal forest, Sigurdsson et al. 2013; temperate forest, Norby et al. 2010; eucalypt forest, Ellsworth et al. 2017), all lining up with the observation that evergreen oaks growing for 30 years around natural CO₂ springs in Tuscany took advantage from elevated CO₂ when they were young, after coppicing, but the signal disappeared at canopy closure (Hättenschwiler et al. 1997). The fate of extra C was suspected to dissipate through a myriad of metabolic leaks, most likely associated with phloem transport and processes in the rhizosphere, each too small to produce a measurable signal, but summing up to a substantial C release (Mildner et al. 2014, Klein et al. 2016b). Very recently that view had been supported by data collected at the Australian Eucalyptus FACE experiment (Jiang et al. 2020).

An exciting by-product of the experiment with tall spruce trees at the Swiss Canopy Crane site was the observation that the stable carbon isotope signal applied to the tree crowns with CO₂ derived from fossil fuel could be traced to roots and stems of neighbouring beech and other tree species, indicating substantial below-

ground interspecific carbon transfer (Klein et al. 2016b). We could show that these mature forest trees share a large number of common ectomycorrhiza taxa, of which the recently discovered, phylogenetically very old Basidiomycota genus *Sebacina* plays a key role for C trafficking (Rog et al. 2020).

3.2.4 Summary of Elevated CO₂ Research

Taken together, none of these experiments provided evidence that carbon was a growth-limiting resource at contemporary CO₂ concentrations and in full sunlight. While climatic conditions varied extremely across these experiments, the remaining common denominator was that the closed nutrient cycle in these test systems did not facilitate enhanced carbon incorporation. When the nutrient cycle was opened in experiments with trees, either by growing saplings in potting mixtures, disturbing the ground, starting with spaced saplings in fertile soils, applying horticultural conditions or allowing the system to recover from a shoot to root imbalance due to recent disturbances, this opens a short-term window for a so-called CO₂ fertilization effect (Körner 2006b).

However, in the long run, soil nutrient limitation is almost inevitable, but it is unlikely that nitrogen supply alone sets the ultimate limit for several reasons. Most importantly, the nitrogen cycle is, in principle, open, with the size of the cycling N-pool adjusting over the years to the availability of other nutrients (e.g. P depending on weathering but, for instance, also Mo if one considers N₂ fixation; Barron et al. 2009; Wurzbürger et al. 2012). Not surprisingly growth and productivity of tropical forests were not found N limited in these and related works. In addition, the forest test site in Switzerland that showed no growth stimulation by elevated CO₂ received substantial rates of anthropogenic N deposition since the 1970s with peaks close to 50 kg N ha⁻¹ a⁻¹ in the test region and rates coming down during the last decades to 20–25 kg N ha⁻¹ a⁻¹, with P, Mg or K more likely candidates for the next limiting resource, similar to what has been concluded for the Australian Eucalyptus FACE, cited above. Accordingly, N/P ratios in tree foliage widened critically in central Europe in recent years (Braun et al. 2010). So, the issue is far more complex and cannot be reduced to N limitation. The only experiment so far that tested growth responses to elevated CO₂ on two different soil types on which the test species *Fagus sylvatica* and *Picea abies* co-occur naturally ended with a surprise: the patterns observed on calcareous soil was the opposite to the pattern on the siliceous soil (Spinnler et al. 2002). Admittedly, these saplings grew on dug-out soils in large open-top chambers, facilitating vigorous growth and, thus, a CO₂-fertilization effect. Yet, had we employed only one of these soil types, we had written two entirely different publications (*Fagus* ‘winning’ over *Picea* on calcareous soil and vice versa on the acidic soil). Quite clearly, soils rule tree responses to elevated CO₂, and responses of young saplings cannot be extrapolated to adult trees.

In summary, these results suggest that we are living in a CO₂-saturated world, with a growth stimulation by CO₂ via photosynthesis restricted to fertile locations and, perhaps, to fresh clearings and young plantations. It is not even clear whether