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Klaus Winter – the indefatigable CAM experimentalist

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Background In January 1972, Klaus Winter submitted his first paper on crassulacean acid metabolism (CAM) whilst still an undergraduate student in Darmstadt. During the subsequent half a century, he passed his Staatsexamensarbeit, obtained his Dr. rer. nat. *summa cum laude* and Dr. rer. nat. habil., won a Heinz Maier-Leibnitz Prize and a Heisenberg Fellowship, and has occupied positions in Germany, Australia, USA and Panama. Now a doyen in CAM circles, and a Senior Staff Scientist at the Smithsonian Tropical Research Institute (STRI), he has published over 300 articles of which about 44 % are about CAM.

Scope I document Winter's career, attempting to place his CAM-related scientific output and evolution in context of factors that have influenced him as he and his science progressed from the 1970s to the 2020s.

Key words: Biography, crassulacean acid metabolism (CAM), facultative CAM, inducible CAM, Klaus Winter, *Mesembryanthemum crystallinum*, Smithsonian Tropical Research Institute (STRI).

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THE STUDENT YEARS

Klaus Winter was introduced to the international scientific community, and the CAM community in particular, with his first publication, now a CAM classic with over 230 citations. 'NaCl-induzierter Crassulaceensäurestoffwechsel bei *Mesembryanthemum crystallinum*' (Winter and von Willert, 1972) was submitted to Zeitschrift für Pflanzenphysiologie on 11th January, 1972, when Klaus was still an undergraduate student at the Technical University of Darmstadt (Winter, 1972). An account of his discovery of what is now considered the archetypal facultative-CAM species is given in Winter (2023).

Examination of chapter topics and methods of his Staatsexamensarbeit and his subsequent Dr. rer. nat. dissertation, which began in early 1973, illustrates well advantages afforded early career ecophysiologicalists investigating CAM. His analyses of the interactions between salinity and photosynthetic pathway in halophytes, particularly CAM induction in *M. crystallinum*, involved studying under a range of conditions, plants growing in soil or hydroponics in pots, controlled climate cabinets, glass-houses, and in the field in Israel. He performed a wide range of techniques including gas-exchange, enzyme assays, ¹⁴C-labelling, leaf anatomy, determination of malate, Na⁺, K⁺, and Cl⁻, water relation parameters, and microclimate measurements. This corpus of techniques, and mastering the theoretical practical understanding required to use them well, has underpinned many of Klaus' subsequent publications in laboratory- and field- ecophysiology of both CAM and non-CAM plants.

A capacity for prolific publication was quickly evident. Still a doctoral student, Klaus was a co-author on a CAM Nature paper submitted in April 1973 (Osmond *et al.*, 1973), the first of many collaborations with antipodean scientists, and subsequently submitted five

manuscripts, including four of which were single-authored, on salt-induced CAM in 1973 (Winter, 1973a, 1973b, 1973c, 1973d; Winter *et al.*, 1974) and a further four papers in 1974 (Winter, 1974a, 1974b, 1974c, 1974d). He submitted his Dr. rer. nat. dissertation in May, 1975 (Winter, 1975). It was graded *summa cum laude*, of course!

THE FIRST POST-DOC

In 1976 and 1977, Klaus remained in Ulrich Lüttge's lab in Darmstadt under the auspices of a Deutsche Forschungsgemeinschaft (DFG) Wissenschaftlicher Mitarbeiter position. Two themes dominated his research output during this period – pursuing his biochemical and physiological mechanistic investigations of CAM halophytes and a return to the field in Israel for seasonal studies of CAM plants in their natural environments (Figure 1; Winter *et al.*, 1978).

Klaus' antipodean connections continued in Darmstadt when he met and collaborated with Hank Greenway, a gifted critical- and lateral-thinking Australian-based plant physiologist who was visiting under the auspices of a DFG Richard-Merton Guest Professorship (Greenway *et al.*, 1978; Winter and Greenway, 1978). Hank's unalloyed enjoyment of the thrill of science and his preparedness to share and debate ideas particularly impressed Klaus, as indeed it affected many other colleagues and students throughout Hank's career (Atwell *et al.*, 2021).

Klaus published the first of what was to become a career-long intermittent series of carbon isotope and titratable acidity studies of succulent and non-succulent plants in the wild (Winter *et al.*, 1976a, 1976b; Winter and Troughton, 1978a, 1978b; Holtum *et al.*, 2016; Pachon *et al.*, 2022). Among these was another CAM classic that traced the seasonal change of isotopic composition and nocturnal malic acid increase in *M. crystallinum* switching from

C₃ to CAM photosynthesis in its natural environment (Winter *et al.*, 1978). He also published his first non-CAM publication, the first report of C₄ photosynthesis in the Polygonaceae (Winter *et al.*, 1977), a discovery initially made during his doctoral research. Included in the latter paper was a reference to Volkens (1887), “Die Flora der aegyptisch-arabischen Wüste”, in which Kranz-anatomy was illustrated around the time that Haberlandt (1884) coined the now-popular linguistically-mixed term, Kranz anatomy.

A SOJOURN DOWN-UNDER

In 1978, Klaus accepted a postdoctoral fellowship in Canberra with Barry Osmond in the Department of Environmental Biology, Research School of Biological Sciences (RSBS) at the Australian National University (ANU). A progressive funding model, by which RSBS was funded directly by a block grant from the Australian federal government, coupled with astute hiring and management by the School's director, Sir Bob Robertson, and Head-of-Department, Ralph Slatyer, had resulted in RSBS being at the cutting-edge of multiple important expanding areas of international photosynthetic and ecophysiological research, all of which Klaus could tap into and from which he could gain experience. George Lorimer, John Andrews and Murray Badger were unravelling the chemistry of the oxygenase reaction of Rubisco and establishing the biochemistry of photorespiration. Ralph Slatyer, Ian Cowan and Grahame Farquhar, with students Suan Chin Wong, Marilyn Ball, Steve Powles and Susanne von Caemmerer, were using sophisticated gas-exchange systems to explore the biophysical and mechanistic bases of plant water movement and its control, and extrapolating their observations to explore components of plant isotope fractionation, photodamage and photoprotection. Barry Osmond's group was at the forefront of research into CAM and photosynthetic nitrogen metabolism (Sutton, 1975; Osmond, 1978; Woo and

Osmond, 1982). The mass-spectrometry unit, managed by Roger Summons and subsequently Zarko Roksandic, was on top of emerging new techniques of stable isotope analyses. Les Watson and Ph.D. student Paul Hattersley were cataloguing Australia's C₄ variety (Hattersley and Watson, 1976) while across campus, at CSIRO Plant Industry, Hal Hatch with post-doc Jim Burnell and students Bob Furbank and Stuart Boag were unlocking the biochemistry of the C₄ pathway.

The calibre of plant scientists in Canberra, and the freedom of academic pursuit there, fostered scientific exchange and attracted overseas visitors (Figure 2; Osmond, 1995, 2014). In 1978-1979 alone, the who's who of eminent overseas visitors to Environmental Biology included Andy Benson, Joe Berry, Olle Björkman, Dave Canvin, Heinrich Fock, Heinrich Krause, Otto Lange, Malcolm Nobbs, Marion O'Leary, John Raven and Irwin Ting. It was in Canberra that Klaus, rather stylish in dress and retiring, first met and collaborated with Joe Holtum, a hirsute scruffy rugby-playing PhD student supervised by Barry Osmond (Figure 2). By 2022 the unlikely pair had co-authored 39 manuscripts on CAM.

Klaus flourished in this heady academic environment, learning methods, absorbing rapidly evolving ecophysiological/physiological theory, and making important connections. He continued his assault upon unravelling the physiology and biochemistry of *M. crystallinum*, particularly phosphoenolpyruvate carboxylase (PEPC) that he began with Greenway in Darmstadt. "Working the night shift (Black and Osmond, 2003)" for several months with Beethoven cranked up to 11, Klaus produced more CAM biochemistry classics with his demonstration of the changes in the km_{PEP} and ki_{malate} of PEPC from CAM *M. crystallinum* during day-night cycles (Winter, 1981a, 1982). This research demonstrated that PEPC is unlikely to be functional during deacidification in the light as it is maintained in a

state that is highly sensitive to malate inhibition. The experiments were intense: in order to be sure that the form of the enzyme being studied was that in tissue, extraction, desalting and assay of PEPC within two minutes was required. George Lorimer, a biochemist, was not impressed with Klaus blasting plant extracts under non-equilibrium conditions through Sephadex-G25 under pressure but, as demonstrated in an associated methods paper (Winter, 1980), Klaus' system worked.

With John Pate, Klaus continued his field isotopic CAM-exploration studies with the first survey of semi-arid areas of Western Australia (Winter *et al.*, 1981b), showing CAM-type isotopic values in *Calandrinia*, an observation that has been pursued in recent years (Winter and Holtum, 2011; Hancock *et al.*, 2018, 2019).

He expanded his isotopic surveys to include tropical and sub-tropical wet forests for which disparate evidence of CAM in epiphytes was emerging (Nuerenbergk, 1961; Coutinho, 1963; McWilliams, 1970; Medina and Troughton, 1974; Neales and Hew, 1975; Wong and Hew, 1976). In the first survey of epiphytes in the rainforests of eastern mainland Australia Klaus demonstrated CAM in orchids, *Pyrrhosia* ferns and reported CAM for the first time in rubiaceaceous ant-plants, *Mymecodia* and *Hydnophytum* (Figure 3; Winter *et al.*, 1983). The latter observation has been investigated more recently by Tsen and Holtum (2012) and Chomiki and Renner (2016).

In November 1978, Klaus visited Madagascar, sampling Madagascan succulents in the Tsimbazaza Botanic Garden in Tananarive and travelling roughly 750 km to sample in the south-eastern spiny Didiereaceae forests in the vicinity of Fort Dauphin. He noted that the dominance and high biomass of the CAM flora was demonstration that CAM is an ecologically effective photosynthetic process in the semi-arid environments of Madagascar

(Winter, 1979). An aspect of the study not mentioned in the succinct paper in *Oecologia* was the difficulty he faced in exporting his plant samples. Madagascar had been recently liberated from colonialism but was virtually bankrupt. Klaus had to convince sceptical customs officials that he was not a smuggler, that the dozens of small dried plant samples were not of medical value and did not represent an attempt to illegally export Madagascar's sovereign wealth.

OPPORTUNITY IN NORTH AMERICA

In 1980 Klaus moved to a postdoctoral research position in Gerry Edwards' lab in the Horticulture Department at the University of Wisconsin, Madison. Gerry's lab and Hal Hatch's lab in Canberra were the pre-eminent labs investigating C₄ photosynthesis but Gerry's lab also had interests in the mechanisms of CAM photosynthesis (e.g. Spalding *et al.*, 1979). By coincidence, Klaus was able to continue collaborating with Joe Holtum, who also took up a postdoc at Wisconsin but with Marion O'Leary in the Department of Chemistry.

In Madison, Klaus continued his pursuit of the physiology and biochemistry of CAM, producing 12 publications mostly on *M. crystallinum* which, by now, was a model species for studies on CAM (Bohnert *et al.*, 1988). Collaborating with Joyce Foster (Figure 4), Gerry Edwards, Mark Schmitt, Geoff Arron, Tsuzuki Mikio, Hideaki Usuda and Joe Holtum, Klaus published studies included changes of level of PEPC during induction of CAM in *M. crystallinum* (Foster *et al.*, 1982); activity and quantity of PEPC and Rubisco in relation to leaf age, nitrogen nutrition during a day night cycle in *M. crystallinum* and *Kalanchoë pinnata* (Winter *et al.*, 1982b), evidence against a previous hypothesis that in *M. crystallinum* nocturnal accumulation of malic acid occurs in mesophyll tissue with proton transport to epidermal tissue (Winter *et al.*, 1981a); malate decarboxylation by

mitochondrial NAD-malic enzyme in *M. crystallinum* in the CAM mode (Winter *et al.*, 1986a); and an investigation of malate metabolism in a non-CAM plant that had been incorrectly identified as CAM (Winter, 1981b). It was whilst in Madison that Klaus began publishing non-CAM papers (e.g. Winter *et al.*, 1982c, 1982d, 1982e).

Significantly, it was primarily during his Madison post-doc that Klaus and colleagues established the intracellular localization and activities of CAM enzymes in CAM and C₃ *Mesembryanthemum* (Holtum and Winter, 1982; Tzuzuki *et al.*, 1982; Winter *et al.*, 1982a, 1982d). This information was used to infer the intracellular movement of carbon during CAM, the enzymes required, their compartmentation, the requirements for exchanges of metabolites via membrane transport, and how the system may be regulated (Edwards *et al.*, 1982; Foster *et al.*, 1983). This biochemical model of CAM was studied, not by surveying gene expression, but by enzymatically digesting leaves to obtain mesophyll protoplasts from C₃ and CAM tissues. Intracellular compartmentation and the extent of enzyme activities was established by assaying chloroplast, mitochondrial and cytosolic fractions separated following differential and density gradient centrifugation. The product of this research still forms the basis of our understanding of CAM biochemistry (e.g. Winter and Smith, 1996a, Winter and Smith, 1996b; Holtum *et al.*, 2005) although we now know that CAM has evolved independently at least 67 times (Gilman *et al.*, 2023) and significant variations in CAM biochemistry occur (e.g. Holtum *et al.*, 2005; Moreno-Villena *et al.*, 2022).

A RETURN TO GERMANY

In 1981 Klaus returned to Germany under the auspices of a DFG Habilitation Fellowship at the University of Würzburg where the Botany Department II, under the astute leadership of Otto Lange, was an international hub of plant ecophysiological research. The same year he

was awarded the prestigious Heinz Maier-Leibnitz Prize, a premier DFG award that recognises outstanding achievements of early career researchers and provided a DM 10,000 incentive for support.

Klaus attended the 1982 CAM conference at University of California-Riverside, effectively the first international CAM congress (Ting and Gibbs, 1982) where many prominent CAM researchers from around the world met for the first time and established career-long friendships. For example, at the meeting Klaus first met Clanton Black, Park Nobel and Irwin Ting and remet Andrew Smith, with whom he has frequently published and from whom he has received much sound advice on the vagaries of written English. Among my many memories of the congress is one of a middle-aged Prof Manfred Kluge, dressed in a suit, most perplexed, attempting to convince a bouncer at the local bar that he was indeed over 21 and trying to explain why his German passport, which was all he had to proffer as ID, did not include a local Californian address!

On completion of his habilitation (Dr. rer. nat. habil.) in 1983, Klaus won a 5-year Heisenberg Fellowship, a DFG award for up-and-coming researchers who had published research of high academic quality and originality and who were promising university teachers.

Whilst at Würzburg, Klaus maintained his interest in the tropical diversity of CAM by participating in the 1984 Oakham School Expedition to Papua New Guinea (Figure 5). The expedition enabled Klaus to survey succulent epiphytes along an altitudinal gradient from Lae on the eastern coast through the Chimbu Valley, Kegslug and Kundiawa, to the timberline of Mt Wilhelm (4,509 m), the highest mountain in PNG. Thirty-five years later, the resultant manuscript (Earnshaw *et al.*, 1987) remains the only CAM study of the flora of

New Guinea, the island with the highest plant diversity of any island on Earth (Camara-Leret *et al.*, 2020). In terms of CAM plants, it is estimated that the island supports in excess of 3,000 species of orchids, 100 species of *Hoya* and *Dischidia*, and an essentially unassessed diversity of ant-plants (Simonsson Juhonewe and Rodda, 2017; de Vogel *et al.*, 2022).

In Würzburg, Klaus began a fruitful collaboration with Barbara Demmig, a PhD student in Würzburg who, in 1984, undertook a postdoc with Olle Björkman at the Carnegie Institute at Stanford before returning to Würzburg in 1986 to undertake her habilitation. Their initial publications were on the ionic, osmotic and photoprotective nature of chloroplasts of CAM plants, particularly *M. crystallinum* in both C₃ and CAM modes (Demmig and Winter 1983a, 1983b, 1986; Winter and Demmig, 1987).

1984 was the only year during his career in which Klaus did not publish. The reason was that he spent much of 1984 researching and writing a detailed synthesis of CAM plant ecophysiology which was published the following year (Winter, 1985), the year he was appointed Professor of Botany (C3) at Würzburg. Between 1985 and 1987, in a series of mainly collaborative ecophysiological and physiological papers topics from within his review were explored: CAM in the roots of leafless orchids was demonstrated, in effect following up on Klaus' isotopic observations of Australian leafless orchids (Winter *et al.*, 1983; Winter *et al.*, 1985); stomatal patterns and nocturnal acidification in *Welwitschia mirabilis* (a Gnetophyte) were addressed (Winter and Schramm, 1986; von Willert *et al.*, 2005). Also explored were the responses of CAM plants that grew under low light conditions (Winter *et al.*, 1986b), gradients of CAM within leaves of *Kalanchoë daigremontiana* (Winter, 1987), the contribution of respiratory CO₂ as carbon source for nocturnal acid synthesis at high

temperatures (Winter *et al.*, 1986c), and the relationship between turgor pressure and tissue acidity (Rygel *et al.*, 1987).

Twenty-five publications between 1988-91 were primarily non-CAM collaborations with Demmig and colleagues on chlorophyll fluorescence, xanthophyll cycle, photoinhibition and photoprotection. Two CAM-related studies of South and Central American plants, a study of photoprotection in Venezuelan cacti (Adams *et al.*, 1989) and an investigation of the xanthophyll cycle in *Clusia rosea* (Winter *et al.*, 1990; his first *Clusia* publication), were perhaps a harbinger of a major change in his career that was about to occur, a move from Würzburg to Panama.

THE PANAMA YEARS

In 1991, Klaus took up a staff scientist position at the Smithsonian Tropical Research Institute (STRI) in the Republic of Panama. STRI, a well-funded institute with a range of research sites (e.g. a lowland rainforest station at Barro Colorado Island, a montane rainforest station at Fortuna, Pacific and Atlantic forest canopy cranes) and good technical support, is an excellent platform for tropical lab-based and field studies. The move from a research and teaching position in Würzburg to an essentially research position at STRI may have surprised some European colleagues but was certainly not out of character. Effectively his new job was to study tropical plant ecophysiology and to communicate. Of course, although not specifically employed to investigate CAM plants, many CAM plants are plants of the tropics!

After three decades, Klaus remains at STRI, having been promoted to senior staff scientist in 1998. His outstanding performance has been supported by collaboration with a series of talented graduate students, post-docs and visitors, and by the availability of

research infrastructure at STRI, particularly the acquisition in 1993 of land adjacent to the Panama Canal at Gamboa of which 1 ha was developed into a plant ecophysiology research site. The space, affectionately known as 'Winterland' to the international CAM community, is home to the Tropical Domes project (Figure 6). The domes provide replicate controlled experimental spaces within which plants can be grown in soil under altered concentrations of CO₂ (or other gases), temperatures and water supplies.

The high Winter-lab productivity has been significantly accelerated by the expertise of the long-serving 'engine room' of Dr Aurelio Virgo, Milton Garcia and Jorge Aranda (Figures 7a, b and c), who have cultured plants, constructed and maintained and updated physical and physiological infrastructure (such as enabling the transfer from paper to digital recording of gas-exchange output, Figure 8), undertaken laboratory analyses (including thousands of acid titrations) and who have been co-authors on 44 articles with Klaus.

The infrastructure and human resource support at STRI has enabled Klaus to investigate not just CAM but to expand his interests in more general ecophysiology of climate change, CO₂ effects, water-relations, light, temperature and nutrients, and functional traits (cf. Winter 2023). Of ca. 209 articles Klaus has authored or co-authored whilst at STRI, ca. 92 (44 %) have been on CAM. STRI support has also enabled Klaus to promote CAM networking, graduate training and information exchange by hosting international CAM congresses in 1993 and in 2010 (a third is planned for March 2023) and fostered scientific productivity by assisted students and colleagues to spend appreciable time in Panama. Klaus' support was also provided through active participation in international CAM meetings at Cape Tribulation (Figure 9), Cambridge (2007), Merida (2012), Illinois (2013), Lake Tahoe (2004, 2014) and Phoenix (2018) (Figures 9 and 10).

At STRI, Klaus continues to publish with long-term CAM colleagues (Table 1), particularly with Joe Holtum and Andrew Smith (Figure 10). Since their first publication (Winter *et al.*, 1981a) Winter and Holtum have co-authored 39 papers, almost all on CAM, of which 35 have been published since Klaus arrived at STRI (see https://stri-sites.si.edu/docs/cvs/CV_Klaus_Winter_Oct_2022.pdf).

An important event in CAM science was the publication in 1996, of a monograph on crassulacean acid metabolism in the Springer Ecological Studies series (Winter and Smith, 1996a). The monograph, which had its genesis during the CAM conference held at STRI in Panama in 1993, documented the 18 years of CAM research since the previous CAM monograph (Kluge and Ting, 1978). Notably the 1996 book included the first list of known CAM plants (Smith and Winter, 1996), 328 genera in 33 families at the time, and a major summative chapter that reconciled contrasting energetic costings for CAM (Winter and Smith, 1996b). The updated list of plants with CAM published in this volume (Gilman *et al.*, 2023), which includes many name changes and newly-recognised C₃-CAM and facultative species, conservatively indicates at least 67 independent origins of CAM in 320+ genera in 38 families.

An important facet of Klaus's tenure at STRI has been an expansion of his scientific footprint from mainly CAM research to examining interactions between tropical plant ecophysiology and climate change. With STRI post-docs, staff and visitors, he has explored in the field and/or under controlled conditions the responses of tropical angiosperms, conifers, pioneer and late-successional species, epiphytes, mangroves and mycorrhiza to soil nutrients, low and high [CO₂], high irradiation, high temperature, water availability, photoinhibition and ozone levels (Table 2).

For 50 years Klaus has been an indefatigable experimentalist, providing plant environmental and photosynthetic ecophysiology data for more than 300 publications. The driver of this productivity is Klaus' natural and perhaps somewhat obsessive curiosity to understand how plants function in the real world. For example, although Klaus reported inducible CAM in *M. crystallinum* in his first publication (Winter and von Willert, 1972) it was not until 2007 that he could demonstrate experimentally that the expression of CAM in *M. crystallinum* was truly under environmental control (Winter and Holtum, 2007). To establish the latter he had to use a career's experience of performing gas-exchange to grow *M. crystallinum* from seed to death without the plants ever performing net nocturnal CO₂ uptake typical of CAM. Experimental skills initially learnt and honed investigating CAM ecophysiology as a student and in his early post-doc years were adapted at STRI to examine the wider world of plant responses to climate change, particularly the readjustments of tropical vegetation. Although trained in a pre-molecular era, he has embraced the molecular revolution, particularly in systematics and phylogenetics (e.g. Brilhaus *et al.*, 2016; Ávila-Lovera *et al.*, 2022; Lujan *et al.*, 2022).

The large number of scientists who have collaborated with him, and continue to do so, attest to the facilities he has constructed, his experimental skills, his potent intellect, his creativity in designing experiments to test questions, his amenable nature and to his positive attitude to collaborative research and sharing knowledge. For a more personal insight into Klaus Winter's career the reader should visit 'Brief reflections on 50 years as a plant ecophysiolgist' (Winter, 2023).

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TABLE 1. Authors with whom, whilst at STRI, Klaus Winter has collaborated most frequently on CAM topics. Exemplar references are provided.

Information summarised from https://stri-sites.si.edu/docs/cvs/CV_Klaus_Winter_Oct_2022.pdf.

Collaborator	Institution	Topics and number of joint publications	Example publication
Joseph Holtum	James Cook U, Australia	CAM discovery, facultative CAM	35 Winter <i>et al.</i> , 1981a
Andrew Smith	U Oxford, UK	CAM cell physiology and evolution	19 Winter and Smith, 2022
John Cushman	U Nevada-Reno, USA	Evolutionary biology of CAM	9 Yang <i>et al.</i> , 2017
Erika Edwards	Yale U, USA	Evolution of CAM, CAM in Carophyllales	8 Winter <i>et al.</i> , 2019
Katja Silvera	STRI/ U California, USA	Evolution of CAM in orchids	8 Silvera <i>et al.</i> , 2014
Darren Crane	STRI/ James Cook U, Australia	CAM within Bromeliaceae	7 Crayn <i>et al.</i> , 2015
Anne Borland	Newcastle U, UK	CAM evolution and water relations	6 Leverett <i>et al.</i> , 2023
Howard Griffiths	U Cambridge, UK	CAM water relations	6 Mejia-Chang <i>et al.</i> , 2021
Hans Gehrige	STRI, Panama	CAM PEPC and evolution of <i>Clusia</i>	4 Gehrige <i>et al.</i> , 2005
John Skillman	California State U, USA	CAM in the understorey	4 Skillman <i>et al.</i> , 1999
Simon Pierce	STRI / U Milan, Italy	Ecophysiology of Bromeliads	3 Pierce <i>et al.</i> , 2002

TABLE 2. Authors with whom, whilst at STRI, Klaus Winter has collaborated on non-CAM topics of tropical plant ecophysiology. Exemplar publications are provided. Information summarised from https://stri-sites.si.edu/docs/cvs/CV_Klaus_Winter_Oct_2022.pdf.

Collaborator	Institution	Topics and number of joint publications	Example publication
Ben Turner	STRI, Panama	Effects of nutrition/climate change on trees	24 Nasto <i>et al.</i> , 2019
Heinrich Krause	U Düsseldorf, FRG	Tropical photosynthesis under high irradiance and temperature stress	23 Krause & Winter, 2021
Martijn Slot	STRI, Panama	Tropical tree functional responses to climate change	19 Slot <i>et al.</i> , 2021a, b, c
Lucas Cernusak	STRI/ James Cook U, Australia	Effects of climate change, nutrients, high [CO ₂] on tropical angiosperms and conifers	15 Cernusak <i>et al.</i> , 2008-13
Gerhard Zotz	STRI/ U Oldenberg, FRG	Tropical tree epiphytes and hemiepiphytes	12 Zotz and Winter, 1996
Cathy Lovelock	STRI / U Queensland, Australia	Effect of elevated CO ₂ on mangroves and mycorrhiza	11 Lovelock <i>et al.</i> , 1997
Jim Dalling	STRI/ U Illinois, USA	Tropical angiosperms and gymnosperm responses to [CO ₂], nutrient levels and water availability	7 Dalling <i>et al.</i> , 2004

Marianne Popp	U Vienna, Austria	Responses on tropical vegetation to elevated CO ₂	6	Lovelock <i>et al.</i> , 1998
Alex Cheesman	STRI/ James Cook U, Australia	Responses to ozone, nutrients and temperature	6	Schneider <i>et al.</i> , 2017
Ruth Reef	STRI/ Monash U, Australia	Effects of CO ₂ and environment on mangroves	2	Reef <i>et al.</i> , 2016

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FIGURE LEGENDS

FIG. 1. Klaus Winter perched upon a *Mesembryanthemum*-growing coastal cliff near Caesarea in Israel, 1977. Photo: K Winter.

FIG. 2. Enjoying Nobby's Nuts and the sunshine in the Fellows' Garden of University House, ANU, 1978. From left to right, Olle Björkman, Otto Lange, Erika Winter, Rosemary Dunn, Joe Holtum, Jennifer Holmgren, Steve Powles, Klaus Winter, Grahame Farquhar. Photo: SC Wong.

FIG. 3. Klaus Winter and epiphytes in an eastern Australian rainforest, 1978 or 1979. Photo: CB Osmond and C Büchen-Osmond.

FIG. 4. The Madison years, at the home of Gerry and Sandy Edwards, 1980. From left to right: Joyce Foster, Joe Holtum, Klaus Winter, Hitoshi Nakamoto. Photo: GE Edwards.

FIG. 5. Klaus Winter in the Papua New Guinea Highlands in the vicinity of Mt Wilhelm during the 1984 Oakham School Expedition to Papua New Guinea. Photo: K Winter.

FIG. 6. Winter's open-air laboratory, "Winterland", the STRI Gamboa Research Station with climate-controlled domes, CO₂-controlled enclosed chambers, open-top chambers, tree-sized pots and the *Clusia* collection. Photo: M Garcia.

FIG. 7. The engine-room of the STRI Winter lab: Dr Aurelio Virgo in the cloud-forest at Cerro Jefa, Panama (a), Milton Garcia the technical whiz (b), and Jorge Aranda processing a leaf of *Tectona grandis* (teak) (c). Photos: K Winter (a and b) and M Guerra (c).

FIG. 8. For his first 20 years at STRI, Klaus produced hundreds of metres of chart paper to record plant gas-exchange results, all of which was patiently transcribed to digital values by hand. Photo: K Winter.

FIG. 9. Attendees of CAM: 2001 held amongst the rainforest of Cape Tribulation in northern Queensland, Australia. From left to right: Front row – Lonnie Guralnik, Rowan Sage, Jennifer Henry; Second tier – Stefan Arndt, Uwe Rascher, Maik Zabrowski, Hideaki Usuda, Jack and Nicholas Christopher, Mark Schöttler, Mandy and Ruby Christopher, James Hartwell, Andrew Smith, Anne Borland, Wolfgang Wanek, Jeremy Barnes, Klaus Winter, Tahar Taybi, Howard Griffiths, Jiri Santrucek; Back tier – Dieter von Willert, Fernanda Reinert, Joe Holtum, Kate Maxwell, Ulrich Lüttge, Hugh Nimmo, Bill Cockburn, Olga Cockburn, Akihira Nose. Photo: J Henry.

FIG. 10. Rehydrating during the 34th New Phytologist Symposium on Systems Biology and Ecology of CAM Plants, Lake Tahoe, 2014. From left to right, Erika Edwards, Joe Holtum, Andrew Smith, Howard Griffiths and Klaus Winter. Photo: RF Sage.

FIG. 11. Klaus Winter, Joe Holtum and Noris Arrocha enjoying the fruits of photosynthesis and contemplating the next 50 years on a rooftop balcony during a balmy tropical evening at San Felipe, Panama City. Photo: JAM Holtum.

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