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JAN ADRIAAN DINGENIS ZEEVAART
1930–2009

A Biographical Memoir by

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Biographical Memoir

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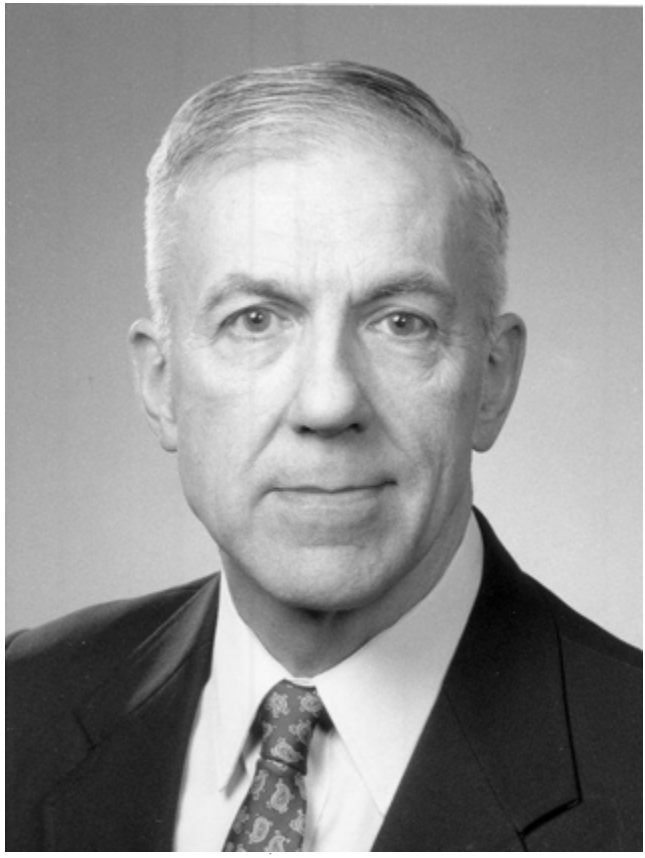

Jan Feevoort

JAN ADRIAAN DINGENIS ZEEVAART

January 5, 1930–November 25, 2009

BY MAARTEN J. CHRISPEELS

DURING HIS LONG CAREER at Michigan State University, Jan A. D. Zeevaart, a Dutchman who emigrated to the United States after obtaining a Ph.D. at the Wageningen *Landbouwhogeschool* (Agricultural University) made fundamental contributions to our understanding of the photoperiodic and hormonal control of flowering. He provided evidence for the existence of florigen, a substance that is transported from the leaves to the apical meristem when flowering is induced by a change in day length. He elucidated the molecular basis of how photoperiod controls stem elongation by modulating gibberellin metabolism. He also described the pathway of abscisic acid biosynthesis from its carotenoid precursor and showed that the gene encoding the rate-limiting enzyme is upregulated during water deficit.

JAN ZEEVAART GROWS UP ON A FARM AND STUDIES HORTICULTURE AT WAGENINGEN AGRICULTURAL UNIVERSITY

Jan Zeevaart was born on January 5, 1930, in the village of Baarland, on the island of Zuid Beveland in Zeeland, the southernmost province of the Netherlands. His parents were farmers, and he was their only son, so it was expected that he would learn to be a farmer and take over the family farm. Baarland is located where the river Scheldt becomes

an arm of the North Sea, and Jan's family name—Zeevaart, meaning *sea voyage*—is quite appropriate. As a boy Jan was fascinated by the ships of all nationalities coming and going on the Scheldt to and from the harbor of Antwerp in Belgium. Undoubtedly he dreamt of going to faraway places. After attending elementary school in Baarland, a school so small it had only two teachers, he enrolled in secondary school in Goes, some 8 miles away. He commuted to school by bicycle regardless of the weather, the same way that thousands of Dutch schoolchildren did then and still do today. Because he lived on a farm he was probably spared the terrible hardships that the Dutch people experienced in the winter of 1945 because of a lack of food. As a farm boy he was imbued with the traditional work ethic: *Idle hands are the devil's playground*. On the farm one worked from morning until night and in fruit-picking season there was no time to go home for lunch. In 1946 while Jan was in secondary school, his father unexpectedly died, and this event changed the course of Jan's life. Clearly a teenager who was still in school could not take over the family farm, so his sister's husband took on that job, leaving Jan free of any obligation to continue the family tradition.

The courses in Goes were rigorous, and Jan did very well. So well in fact that he received a full scholarship to go to university. He had always been interested in the orchard on his parents' farm and in 1949 he enrolled at the Wageningen Agricultural University to study horticulture. After the usual introductory courses he enrolled in horticulture classes with Professor S. J. Wellensiek, who taught him all about rootstocks, grafting and incompatibility, vernalization, flowering, and photoperiodism. A whole new world opened up for Jan. He learned that plant physiologists postulated that an as yet unidentified substance called "florigen" appeared when plants were induced to flower and probably moved

inside the plant, causing flower buds to be formed. During the second part of his university studies, he had to do four research projects in areas of his own choosing. He chose horticulture, genetics, plant physiology, and plant pathology. He found research extremely rewarding, and upon graduating in 1955 as an agricultural engineer (more or less equivalent to an American master's degree) he accepted an offer from Professor Wellensiek to become an assistant in his laboratory and work toward a doctoral degree.

THE WINTER OF 1953

Skating is the favorite winter sport of the Dutch and it is more than a sport, it is a culture. The winter of 1953 was severe. The Rhine overflowed its banks and adjacent meadows were under water and frozen. On Friday afternoon January 23 Jan went skating and spotted a girl with a red jacket. Her boss had given her the afternoon off to go skating. They met on the ice, had a chat, and skated. When time came to go home Jan made sure that Riet, his future wife, got home safely on her bike. He planned to come see her again soon, but a week after the encounter on the ice, in the night of January 31, the North Sea visited its fury on the Netherlands and especially on the province of Zeeland, most of which is below sea level. A tidal surge and windswept waves raised the average sea level by more than 5 meters. Zeeland's dikes broke and by morning most of the province was under water. More than 2,000 people and many heads of cattle drowned. Jan heard that his mother, his sister, and a young nephew were trapped on the upper floor of the house. Without hesitating and like a good Dutchman he jumped on his bike and rode the 175 kilometers to Baarland to go help his family. He knew the area well, having cycled there as a child, and flawlessly navigated the system of internal dikes to get to his destination. After he got back two weeks later, he looked Riet

up again. They were married in 1956 and she remained his lifelong companion and cared for him during his terminal illness in 2009.

CHASING AFTER FLORIGEN

The topic chosen for Jan's dissertation resulted from a controversy that arose at the eighth International Botanical Congress in Paris in 1954. One of Wellensiek's assistants (Dick de Zeeuw) had obtained data that supported the hypothesis that flowering is induced when an inhibitory substance disappears and a new balance is reached between assimilates and growth substances. Anton Lang, who was at the University of California in Los Angeles (elected to the National Academy of Sciences in 1967), on the other hand presented data showing that flowering depended on a graft-transmissible stimulus. His work with *Hyoscyamus niger* supported the florigen hypothesis. Wellensiek charged Jan with finding out who was right. Starting in 1955 Jan made thousands of grafts using the short-day plant *Perilla crispa*. He showed that a leaf from an induced plant when grafted to a noninduced plant could cause it to flower and that just a portion of the leaf was sufficient. He also found that detached leaves of *Perilla* could be rooted rather easily and that this would keep them green. When exposed to the correct day length, such leaves could also be induced and then grafted onto noninduced plants, causing them to flower. He also found that once a leaf had been induced it would continue to produce the flowering stimulus for weeks and weeks if one could keep it healthy as by allowing it to root or grafting it on another plant. He confirmed that the floral stimulus (florigen) originates in the leaf and exerts its effect in the bud, but the bud need not be present for the plant to receive the stimulus and react to it.

In retrospect we see that the entire body of work was vintage Zeevaart; it was extremely systematic, detailed, thorough, and meticulous. The conclusions reached were completely justified by a mass of data. This rigorous approach to research characterized Jan Zeevaart's entire career. The excellence of Jan's dissertation research was recognized by his institution. At about that time the Agricultural University instituted a prize that has been given every four years for the best Ph.D. dissertation. In 1959 Jan Zeevaart was the first recipient of this prize. He used the prize money to buy a plane ticket to Montreal to present his scientific results (see below).

Over the next 20 years many scientists, including some in Zeevaart's laboratory, tried to isolate and identify florigen, but success always eluded them. Most eventually believed the hypothesis to be wrong, but Jan kept the faith. Eventually he was proven right but not until molecular genetics with *Arabidopsis thaliana* made it possible to tackle problems that could not be solved with traditional techniques. Florigen turned out to be a small protein and its existence was not confirmed until 2007. No wonder then that standard techniques to fractionate plant extracts to isolate hormones, which are small molecules, never bore fruit with respect to the isolation and identification of florigen.

Upon graduating in 1958 Jan was called up to serve in the Dutch armed forces. After his basic training he received intelligence training and was stationed in Ede, just a half hour by bike from Wageningen. So he came home every night and was able to keep up with his field. Luckily he was given a brief leave of absence in 1959 to present his findings at the ninth International Botanical Congress in Montreal, having been invited by Anton Lang. Before going to Montreal he had obtained a postdoctoral fellowship from a Dutch government research organization (*Zuiver Wetenschapelijk Onderzoek*),

and he had decided to join James Bonner's lab at Caltech. At the botanical congress Jan learned that Anton Lang was moving to Caltech to become the director of the Earhart Plant Research Laboratory (also called the "Phytotron"). Jan realized that Caltech would offer him the opportunity to work not with one but two of the most outstanding plant biologists in the world. In 1960 Jan and Riet sailed on the S. S. *Rijndam* of the Holland-America Line and made their way to Pasadena after arriving in New York.

POSTDOCTORAL RESEARCH ON FLOWERING AT CALTECH AND AN ACADEMIC APPOINTMENT AT MCMASTER UNIVERSITY

James Bonner was interested in the role of nucleic acids in plant development and the use of substituted purines and pyrimidines (e.g., 5-fluorouracil) applied to whole plants made it possible to interfere with RNA synthesis and determine whether RNA synthesis was required for a specific physiological response. Jan's research showed that these inhibitors did not interfere with the generation of the flowering stimulus (florigen) but inhibitors that interfered with DNA synthesis prevented the formation of the flower. Anton Lang was interested in the role of gibberellins (GAs) in flowering and had shown that when long-day plants are grown under short days and treated with GA, this is sufficient to induce flowering. This raised the question: does GA induce the floral stimulus? Jan used the long-short-day plant *Bryophyllum daigremontianum* for his work. This plant can be induced to flower by GA under short days but not in long days. The results showed unequivocally that GA induced the floral stimulus. Furthermore, application of a GA synthesis inhibitor blocked flowering under inductive conditions. Attempts to duplicate the work of another group who had obtained evidence that an extract of an induced plant could induce flowering in another plant grown under noninducing

conditions failed. It was just one of many attempts in different laboratories to demonstrate the existence of florigen directly rather than by grafting.

In the 1950s and 1960s Caltech was one of the premier places for plant biology research in the United States. Standards and expectations were very high. The plant physiologists—as they were then called—met twice a week at 8:00 AM and everyone regardless of rank was expected to be present, attend the lecture, and participate in the discussions. Jan got his first taste of American academic life, and it suited him just fine.

Jan and Riet also got their introduction to other aspects of life in California and America. Trees with oranges and lemons in the backyard. Poinsettias in bloom outdoors in the gardens at Christmas. What an amazing place. They toured the southwestern part of the country and visited many national parks. A postdoc took them to the coliseum in Los Angeles, where they heard John F. Kennedy give his "New Frontier" acceptance speech as the presidential nominee of the Democratic Party. It was certainly an interesting time to be moving to America.

After three years Jan's J-1 visa ran out, and he had to leave the country. (This is a condition of all J-1 exchange scholar visas). From James Bonner he heard that a faculty position was available at McMaster University in Hamilton, Ontario, and he accepted it sight unseen. That position involved a lot of teaching, and the first year that he was at McMaster there were no research facilities. A new building opened the second year, and Jan resumed his work on growth inhibitors. With Janos ("Hans") Kende (elected to the NAS in 1992), who was also a postdoc at Caltech with Anton Lang, he had shown that the inhibitor CCC inhibits GA biosynthesis in fungi, and at McMaster he showed that this also applied to

plants. Thus, these inhibitors became powerful tools for plant physiologists to study processes controlled by GA.

The 10th International Botanical Congress held in 1964 in Edinburgh, Scotland, brought another lucky turn of events. Anton Lang had accepted the directorship of the new Plant Research Laboratory at Michigan State University (MSU) and was actively recruiting faculty members. He invited both Jan Zeevaart and Hans Kende (who had come from Israel to attend the Congress) to dinner and offered them positions as junior faculty members. The laboratory would be funded by the Atomic Energy Commission and there would be no obligation to teach undergraduates. It sounded like heaven to Jan who wanted to spend most of his time doing research. Indeed, the lab had been founded by the AEC specifically to carry out basic research in plant biology and train Ph.D. students and postdoctoral researchers. Jan Zeevaart accepted and after only two years in Hamilton, Jan and Riet moved to MSU in 1965. Hans Kende also accepted; these two outstanding plant hormone researchers became lifelong colleagues and friends and passed away within three years of each other. It is at this time, when I was a postdoc in the lab of Joe Varner, that I met and got to know Jan Zeevaart. The Plant Research Laboratory had a general midmorning coffee break that was well attended during those first few years of its existence. Students, postdocs, and faculty met and discussed scientific and other issues.

RESEARCH AT MICHIGAN STATE UNIVERSITY

The Plant Research Laboratory had an excellent set of greenhouses where Jan could carry on his research on whole plants and he continued his work on flowering. If flowering is caused by a graft-transmissible signal, it should be possible to obtain extracts or phloem exudates from induced plants and apply these to noninduced plants and get them to

flower. Both positive and negative results were reported in the literature. The Zeevaart lab also did such experiments but never obtained reproducible results. While in Jan's lab Rod King showed that much more phloem exudate can be collected from the cut end of a stem when EDTA is added to the solution into which the exudates are being collected. This finding was extremely useful to phloem physiologists, but florigen remained as elusive as ever; in the 1970s physiologists began to doubt its very existence, but Jan never wavered even if he could not find it. His 1976 review summarizing all the evidence in support of the florigen hypothesis and published in the *Annual Review of Plant Physiology* was widely quoted after it was discovered that florigen was a protein. Scientists rediscovered Jan's voice in the wilderness. The Dutch were quick to recognize Jan's remarkable early achievements, and in 1974 he was elected a corresponding member of the Royal Netherlands Academy of Sciences.

At Caltech Jan had worked on gibberellins in collaboration with Anton Lang. In 1957 Lang published a paper in the *PNAS* (vol. 43, p. 709) showing that GA applied to long-day plants at the rosette stage and growing under short-day conditions induced elongation of the stem and eventually flowering. The hypothesis that flowed from this observation was that long days induced GA biosynthesis in the plant and that GA then induced stem elongation and flowering. Jan chose the long-day plants spinach and *Silene armeria* to test this hypothesis. First, using inhibitors of GA biosynthesis Jan was able to separate stem elongation and flower formation and showed that one without the other was possible. Next, he extracted GAs from the plants and used a bioassay to determine GA levels (the *dwarf-5* maize bioassay). The results were disappointing because the amounts of GA present in the induced plants and the controls were rather similar.

Jan, who started his research with simple technologies such as grafting, discovered the power of more sophisticated technologies. His lab acquired the first high-performance liquid chromatography system on the MSU campus. A number of different GAs had been discovered in various laboratories, and Jim Metzger in Jan's lab was able to separate and identify in spinach extracts five of these that formed a biosynthetic sequence: $GA_{53} \rightarrow GA_{44} \rightarrow GA_{19} \rightarrow GA_{20} \rightarrow GA_{29}$. By fractionating spinach extracts by GC-MS they were able to show that GA_{20} dramatically increased under long-day conditions and that its precursor GA_{19} decreased.

Being a university professor, Jan was now seriously into the mentoring business. As he had done his own Ph.D. work pretty much independently, he expected that also of his students. Jim Metzger recalled that when he went to Jan and asked what he should do, Jan's answer was, "Jim, it's not my thesis, it's your thesis." Jim Metzger recalled, "At that point, it really hit home what being a Ph.D. was really about. This is not to say that Jan left students to fend for themselves; indeed, he provided ample feedback, suggestions, and rigorous critiques of their work. I felt that Jan's style of mentoring served me well in my professional career." Toward the end of his career Jan lamented that this approach seemed to be going out of fashion and that he saw more and more that the professor was doing the intellectual work with the Ph.D. student being a highly qualified technician.

The results they were obtaining about the levels of specific GAs immediately suggested new experiments, and Jan Zeevaart started a collaboration with Jan Graebe from the University of Goettingen. Graebe was making radioactive GAs by feeding radioactive mevalonate to the liquid endosperm of pumpkin seeds. Sarah Gilmore in Jan's lab used such radioactive GAs as substrates and showed that a number of enzymes of GA metabolism are under photoperiodic control. GA_{19} oxidase,

which makes GA_{20}, increases under the long-day conditions that induce flowering. Because these enzymes were labile they were difficult to assay and it seemed that traditional biochemical approaches were not going to get them much further.

ARABIDOPSIS MOLECULAR GENETICS TO THE RESCUE OF UNRAVELING GIBBERELLIN METABOLISM

Jan was an avid reader, and in 1980 he came across an interesting paper by Maarten Koornneef (elected as an NAS foreign associate in 1998) and J. H. van der Veen showing that one could generate mutants of *Arabidopsis thaliana* with phenotypes, that suggested that they had unusually low levels of GA or were insensitive to the hormone. Jan was well aware that the isolation of a GA-deficient mutant in maize had led to major advances in our understanding of GA physiology. *Arabidopsis* is a small plant, much easier to work with than maize, and the group of Maarten Koornneef was exploring its potential. Conveniently they were located in the Department of Genetics at Wageningen Agricultural University. In the summer of 1982 Jan went to visit his wife's family in Wageningen and decided to look in on Koornneef. They had productive discussions (the Dutch group was producing a linkage map) and a collaboration ensued. Koornneef's lab identified the mutant plants and mapped the mutations and Zeevaart's lab characterized the mutants biochemically. This was before the time that *Arabidopsis* had been adopted as *the* model organism for plant biology. Jan applied his analytic technologies to *Arabidopsis* and found that it has 20 different gibberellins that could be organized in three parallel metabolic pathways. Increases or decreases in specific GAs in the mutants made it possible to propose specific steps that were blocked in a pathway. For example, results obtained with the *ga4* mutant suggested that it was likely to be deficient

in a 3β-hydroxylase. The *ga5* mutant had high levels of C_{20} gibberellins and low levels of C_{19} gibberellins suggesting that the GA_5 gene encoded a GA oxidase. An important finding from these experiments was that in *Arabidopsis,* GA_4 was found to be the most active gibberellin and not GA_1 as had been supposed until then.

In 1982 the year that Jan started his collaboration with Maarten Koornneef, Chris Somerville (elected to the NAS in 1996) joined the Plant Research Laboratory at MSU as a faculty member, and he introduced *Arabidopsis* molecular genetics to his colleagues. This facilitated the transatlantic collaboration of Zeevaart and Koornneef. The first gene for a GA metabolic enzyme was cloned in the old-fashioned way. Antibodies to purified 20-oxidase were prepared and used to screen an expression library in *E. coli* made with the RNA extracted from pumpkin liquid endosperm. The cDNA clone they obtained was used to screen a genomic *Arabidopsis* library. Expression in *E. coli* showed this to be a multifunctional enzyme that catalyzed three steps in the GA pathway from GA_{53} to GA_{20}. Subsequent work showed that GA_{53} is an important branch point in spinach. Under short days it is inactivated by conversion to GA_{97}, but under long days increased 20-oxidase converts it to GA_{20} and 3-oxidase then converts it to bioactive GA_1.

THE BIOSYNTHESIS OF ABSCISIC ACID

In the early 1960s two different laboratories identified a new plant hormone called "dormin" by one lab and "abscisin II" by the other. After the structure was elucidated, researchers agreed on the name "abscisic acid" (ABA). It soon transpired that its activity *in planta* is not related to either dormancy or abscission, but the name stuck. ABA was reported to be an inhibitory hormone, and Jan Zeevaart had been interested in inhibitors from his early work on the induction of flowering.

One of the difficult-to-verify hypotheses had always been that flowering is induced when inhibitors disappear. Jan checked the level of ABA in his favorite plants under inductive and noninductive conditions but could find no correlation. He did observe that the level of ABA had shot way up in a batch of plants that had wilted. This observation confirmed one earlier published report and piqued his interest in the role of ABA in the control of water relations. His work profited from spending a sabbatical leave (1973-1974) at the Milstead Laboratory for Chemical Enzymology in Sittingbourne, England, where ABA had first been isolated.

Katrina Cornish in the Zeevaart lab studied the rapid accumulation of ABA in dehydrating leaves and found that it was rapidly catabolized to phaseic acid upon rehydration. ABA is a sesquiterpenoid, and mevalonic acid could be reasonably expected to be its precursor (That the prokaryotic pathway for terpenoid biosynthesis is present in chloroplasts had not yet been demonstrated.) Yet when they fed radioactive mevalonate to dehydrating leaves, ABA was not labeled. Ingenuity and technology came to the rescue. Newly synthesized ABA has four oxygen atoms, and Bob Creelman, a graduate student, suggested the use of $^{18}O_2$ to determine which of these four would be labeled. Jan did not immediately endorse this approach enthusiastically, and Bob waited until Jan had gone to Germany to visit Jan Graebe's lab to actually do the experiment. The results were as surprising as they were unequivocal: a single ^{18}O atom was present in the carboxyl group of ABA, indicating that ABA was a breakdown product of a xanthophyll molecule. This idea had been suggested in 1972 by H. S. Taylor and R. F. Burden, two British scientists, but their suggestion had not been given much credence.

Zeevaart was enjoying occasional trips to his homeland and alma mater to collaborate with Maarten Koornneef, who

had discovered a "wilty" *Arabidopsis* mutant (*aba1*) that was deficient in ABA. Chris Rock in the Zeevaart lab showed it to be deficient in the conversion of zeaxanthin to violaxanthin. Clearly they were traveling down the right path. But what was the first enzyme in the pathway? The answer to this question came in a collaboration with Don McCarty at the University of Florida. Don had isolated a viviparous maize mutant. (Vivipary occurs when seeds have low levels of ABA; as a result they germinate on the plant even before they dry). When McCarty's lab cloned the gene, they found it to be homologous to a bacterial lignostilbene dioxygenase. This led to a collaboration between Zeevaart and McCarty and the cloning of the gene that encodes the enzyme 9-*cis*-epoxycarotenoid dioxygenase (NCED) from *Arabidopsis* by Steven Schwartz in Jan's lab. Once the cDNA was available, they could demonstrate that water deficit upregulates this gene at the RNA and protein levels. NCED is a member of a larger class of enzymes called "carotenoid cleavage enzymes," or CCDs, that are present in all organisms, including humans. In humans a CCD enzyme is responsible for the synthesis of retinal from β-carotene. It is a useful reminder that discoveries made in plant physiology sometimes lead to major advances in understanding of human physiology.

A RIGOROUS APPROACH TO SCIENCE UNDERSCORED BY AN OLD-FASHIONED DUTCH WORK ETHIC

No doubt that Jan had that old-fashioned work ethic. He was a regular guy. Came to work every day at 8:00 AM and went home at 6.00 PM to have dinner with Riet and their son Scott. He might take home a paper or grant proposal to review, but work was work and home was home. He also maintained that European tradition of *going on vacation*, and many a summer he went on a camping trip. It was his custom to spend Saturday mornings together with Hans Kende in

the library of the Plant Research Laboratory, making sure that nothing of any importance would escape their notice. Reading was not a chore for him, rather he enjoyed keeping up with everything. Jan had very high standards for his own research, and he continued to work at the bench or in the greenhouse until well after his official retirement. He had equally high standards for his students and postdocs, sometimes to their frustration. He always scrutinized the data of his associates with the utmost care and every paper from his lab that bore his name met his unusually high standards.

For 40 years Jan with his colleague Hans Kende taught a graduate course on plant growth and development with a focus on the physiology and biochemistry of plant hormones. He was fond of asking questions that probed the students' understanding of the subject. His reading lists were legendary and through his rigorous approach he influenced generations of young scientists at the Plant Research Laboratory. Because he was known to be a demanding taskmaster, only four Ph.D. students joined his laboratory. Jan was a much sought after reviewer of scientific papers because of his rigorous approach to science and his incredible grasp of the literature. For several decades he served on the editorial board of *Plant Physiology,* and when I was editor in chief of the journal I was delighted to have him on board. Jan's contributions were recognized by his election to the National Academy of Sciences in 1998; in 2000 the American Society of Plant Physiologists awarded him its highest honor, the Stephen Hales Prize.

THE WRITING OF THIS MEMOIR was greatly facilitated by Jan Zeevaart's 2009 article in the *Annual Review of Plant Biology* and by my own 40-year friendship with him. I am grateful for Riet Zeevaart's help in filling in the details of their early days together and to Jim Metzger, Maarten Koornneef, and Robert Creelman for corrections and inspiration.

SELECTED BIBLIOGRAPHY

1958

Flower formation as studied by grafting. *Meded. Landbouwhogeschool Wageningen* 58(3):1-88.

1962

With J. Bonner. Ribonucleic acid synthesis in the bud, an essential component of floral induction in *Xanthium*. *Plant Physiol.* 37:43-49.

1966

Reduction of the gibberellin content of *Pharbitis* seeds by CCC and after-effects in the progeny. *Plant Physiol.* 41:856-862.

1971

Effects of photoperiod on growth rate and endogenous gibberellins in the long-day rosette plant spinach. *Plant Physiol.* 47:821-827.

1974

With R. W. King. Enhancement of phloem exudation from cut petioles by chelating agents. *Plant Physiol.* 53:96-103.

1976

Physiology of flower formation. *Annu. Rev. Plant Physiol.* 27:321-348.

1980

With J. D. Metzger. The effect of photoperiod on the levels of endogenous gibberellins in spinach as measured by combined gas chromatography—selected ion current monitoring. *Plant Physiol.* 66:844-846.

1982

With J. D. Metzger. Photoperiodic control of gibberellin metabolism in spinach. *Plant Physiol.* 69:287-291.

1984

With R. A. Creelman. Incorporation of oxygen into abscisic acid and phaseic acid from molecular oxygen. *Plant Physiol.* 75:166-169.

With K. Cornish. Abscisic metabolism in relation to water stress and leaf age in *Xanthium strumarium*. *Plant Physiol.* 76:1029-1035.

1986

With S. J. Gilmour, L. Schwenen, and J. E. Graebe. Gibberellin metabolism in cell-free extracts from spinach leaves in relation to photoperiod. *Plant Physiol.* 82:190-195.

1988

With R. A. Creelman. Metabolism and physiology of abscisic acid. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 39:439-473.

1990

With M. Talon and M. Koornneef. Endogenous gibberellins in *Arabidopsis thaliana* and possible steps blocked in the biosynthetic pathways of the semidwarf *ga4* and *ga5* mutants. *Proc. Natl. Acad. Sci. U. S. A.* 87:7983-7987.

1991

With C. D. Rock. The *aba* mutant of *Arabidopsis thaliana* is impaired in epoxy-carotenoid biosynthesis. *Proc. Natl. Acad. Sci. U. S. A.* 88:7496-7499.

1993

With D. A. Gage and M. Talon. Gibberellin A_1 is required for stem elongation in spinach. *Proc. Natl. Acad. Sci. U. S. A.* 90:7401-7405.

1995

With Y.-L. Xu, L. Li, K. Wu, A. J. M. Peters, and D. A. Gage. The *GA5* locus of *Arabidopsis thaliana* encodes a multifunctional gibberellin 20-oxidase: Molecular cloning and functional expression. *Proc. Natl. Acad. Sci. U. S. A.* 92:6640-6644.

1996

With K. Wu, L. Li, and D. A. Gage. Molecular cloning and photoperiod-regulated expression of gibberellin 20-oxidase from the long-day plant spinach. *Plant Physiol.* 110:547-554.

1997

With S. H. Schwartz, B. C. Tan, D. A. Gage, and D. R. McCarty. Specific oxidative cleavage of carotenoids by VP14 of maize. *Science* 276:1872-1874.

With Y.-L. Xu and D. A. Gage. Gibberellins and stem growth in *Arabidopsis thaliana*: Effects of photoperiod on expression of the *GA4* and *GA5* loci. *Plant Physiol.* 114:1471-1476.

1999

With X. Qin. The 9-*cis*-epoxycarotenoid cleavage reaction is the key regulatory step of abscisic acid biosynthesis in water-stressed bean. *Proc. Natl. Acad. Sci. U. S. A.* 96:15354-15361.

2002

With X. Qin. Overexpression of a 9-*cis*-epoxycarotenoid dioxygenase gene in *Nicotiana plumbaginifolia* increases abscisic acid and phaseic acid levels and enhances drought tolerance. *Plant Physiol.* 128:544-551.

With D. J. Lee. Differential regulation of RNA levels of gibberellin dioxygenases by photoperiod in spinach. *Plant Physiol.* 130:2085-2094.

2006

Florigen coming of age after 70 years. *Plant Cell* 18:1783-1789.

2008

With S.-F. Lo, S.-Y. Yang, K.-T. Chen, Y.-I. Hsing, L.-J. Chen, and S.-M. Yub. A novel class of gibberellin 2-oxidases control semidwarfism, tillering, and root development in rice. *Plant Cell* 20:2603-2618.

2009

My journey from horticulture to plant biology. *Annu. Rev. Plant Biol.* 60:1-19.