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THERMOGENIC RESPIRATION IN AROIDS

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CONTENTS

INTRODUCTION

For reasons which will soon become obvious, this review—at first glance polemic and too inclusive—pays more than the customary attention to biological matters. It deals with thermogenicity in plants, a property which, according to the available evidence, is connected with "cyanide-resistant respiration," a type of cellular respiration insensitive to inhibition by terminal inhibitors such as cyanide, azide, and carbon monoxide (CO), and by inhibitors such as antimycin A and HOQNO, which act between *b* and *c*-type cytochromes (18, 62, 63, 73, 80; cf 105, 106). The definition is not absolute, since degrees of cyanide resistance varying from 0 to 100%, and even stimulation by cyanide (100), have been found in plant tissues, pollen grains, and mitochondria (18, 19, 23, 25, 46, 70, 82, 86, 145, 146, 201), often as a function of plant or organ development (131, 200). The insensitivity resides in the mitochondria (19, 64, 65, 150, 188, 205, 206). When isolated from resistant tissues, they turn out to contain a "dual pathway" for respiratory electron transfer: the classical, cyanide-sensitive electron transport system which is coupled to phosphorylation, and a cyanide-insensitive pathway which branches from the classical one on the substrate side of cytochrome *c* and is phosphorylative to a much lesser extent (19, 64, 65, 150, 188, 205, 206).

The alternate pathway is specifically inhibited by iron-complexing agents such as hydroxamic acids, α, α'-dipyridyl, K-thiocyanate, and 8-hydroxyquinoline (19, 25, 46, 170). A ferrosulfoprotein with an apparent K_m for O_2 lower than that of a flavoprotein oxidase is probably (but not certainly) involved (83). Temporary re-

placement of a functioning classical electron transport chain by the alternate one may lead to a lowering of the ATP level. This form of "uncoupling" should be distinguished clearly from what may occur in the classical chain under the influence of uncouplers such as 2,4-dinitrophenol (74, 204) or fatty acids (12). The latter type will be referred to as "endogenous uncoupling." Both may lead to an increase in the rate of heat production (103, 151, 204, 205).

PHOSPHORYLATIVE EVENTS

Experimentally it was found that improved isolation methods for plant mitochondria (47, 48, 79, 81) applied to various plant materials, including arum lilies, can lead to preparations which show respiratory control with tight coupling and ADP:O ratios similar to, but slightly lower than, those found with mammalian mitochondria (37, 49, 54, 133, 199, 203). The three sites of phosphorylation suggested for plant mitochondria agree well with those in mammalian mitochondria (37, 188), with site II between *b* and *c*-type cytochromes and site III between cytochrome *a* and a_3. In mitochondria from aroid appendices, all three sites can be operational (112, 204), resulting in ADP:O ratios as high as 2.7 for malate in *Sauromatum* (204). However, on the day of flowering the *Sauromatum* mitochondria are uncoupled (204), either endogenously or because the alternate pathway becomes operational. The low phosphorylative efficiency (75%) of mung bean mitochondria has been ascribed to the latter factor. Phosphorylative site I is retained (13, 14, 150, 188, 205, 206).

TEMPERATURE RISE IN FLOWERS AND INFLORESCENCES

Thermogenicity is especially obvious in floral organs (56) and has been studied most often in the water lily *Victoria* (45, 59, 95, 189) and in arum lilies such as *Arum italicum* (104, 132, 149), *A. maculatum* (24, 58, 66, 86–88, 104, 111, 112, 152, 167, 168, 172–175), *Sauromatum guttatum* (29–31, 38–40, 75, 76, 90, 135, 138, 140, 141, 147, 176, 192–195), *Symplocarpus foetidus* (13, 35, 53, 61, 97, 98, 186–188, 196), *Typhonium divaricatum* (168, 169), *Alocasia pubera* (190), *Schizocasia portei* (52), and *Philodendron selloum* (143). The temperature difference with the environment may reach a value of 22° C in *Colocasia odora* and *Schizocasia portei,* and at least as much in *Philodendron selloum* and *Symplocarpus foetidus.* In biochemical circles, there has been a remarkable lack of precision in referring to the particular species and organ involved, e.g. "skunk cabbage," supposed to be identical with *Symplocarpus foetidus,* could refer just as well to *Lysichitum americanum* (Western skunk cabbage) which, however, has never been investigated biochemically.

The central column or spadix of *Symplocarpus* is completely covered with small hermaphroditic flowers which warm up, whereas in *Sauromatum* and *Arum* there has been a differentiation leading to separate staminate and pistillate flowers as well as a special, sterile, club or finger-like organ—the appendix or osmophore (198)—which abundantly produces heat (and smell). In *Philodendron selloum,* incomplete staminate flowers are involved. Frequently overlooked also is the fact that the number of temperature maxima within an inflorescence varies from species to species (124), from two in *Arum, Philodendron,* and *Sauromatum* to five in *Colocasia*

odora. In forms possessing an appendix, the first maximum (produced right there, and the only one studied biochemically so far) is by far the highest. Since the heat serves as a "volatilizer" for the odoriferous compounds—often amines (176) or indole (38–40)—that attract the pollinators, and since in these forms obligatory cross-pollination is combined with proterogyny (55, 96, 102, 134, 153, 191, 198), it is no surprise that this maximum precedes the shedding of pollen by many hours (96).

HISTORY

Explicit formulation of the dual pathway concept goes back to 1932, when Okunuki (145, 146) discovered the cyanide and CO insensitivity of *Lilium auratum* pollen. Light-reversal of the partial CO inhibition in certain pollens sometimes led to respiration values exceeding those of untreated material—the first indication that the action of cyanide and CO may involve more than a simple replacement of the blocked classical pathway by another (cf 70).

Thermogenesis in *Arum* was discovered by Lamarck in 1778 (104). Garreau (58) demonstrated the close relationship between heat development and oxygen consumption here. van Herk (192) ascribed the cyanide insensitivity of the respiration of the *Sauromatum* appendix to the absence of the cytochrome/cytochrome oxidase system and the presence of an autoxidizable flavoprotein. His ideas were essentially adopted, in the case of *Arum maculatum*, by James & Beevers (85, 86). However, the presence of the classical electron transfer system can be demonstrated easily in both cases, and at present the dual pathway concept seems the most suitable for explaining the cyanide-resistant respiration in *Arum*, *Sauromatum*, and *Symplocarpus* (172, 173, 207, 208). The various alternatives have been discussed ably by Bendall & Bonner (19). In the meantime, cyanide-resistant respiration had been demonstrated in storage tissues of potato, sweet potato, carrot, and Jerusalem artichoke (6–9, 27, 42, 50, 63–65, 68, 69, 101, 115–123, 126, 144, 155, 158, 161–164, 197). It is now known to play a role also in the so-called climacteric respiration of fruit (180, 181), in roots (91–94), in mung bean seedlings (25, 79, 81, 82, 182–185), and in various microorganisms (67, 107–110, 171). Several reviews of cyanide-insensitive respiration in plants and the dual pathway concept are now available (18, 25, 80).

The brilliant contributions made by the workers at the Johnson Foundation (13, 19, 25, 36, 37, 49, 53, 105, 113, 170, 180–188) in "sequencing" the electron carriers in mitochondria have been acknowledged by Ikuma (80), but new evidence requires modification of his scheme (p. 429). In 1974, Storey (personal communication) pulsed anaerobic CO-saturated *Symplocarpus* mitochondria with O_2 and looked at the kinetics of the carriers oxidized mainly by the alternate pathway. Rapid kinetics were observed for ubiquinone (UQ, midpoint potential +70 mV) and a portion of the flavoprotein component, indicating that a nonfluorescent flavoprotein F_{ma}, with a midpoint potential of about 20 mV in *Symplocarpus* and 40 mV in mung bean mitochondria, is the link between the classical and the alternate pathway. The more highly oxidized F_{ma} is, the less well it functions as electron donor to the alternate oxidase. The redox states of UQ and F_{ma} in state 4 and 3 are such that the plant

mitochondrion can shift most of its electron transport through the cytochrome chain in state 3 and through the alternate pathway in state 4.

STRUCTURAL AND DEVELOPMENTAL FEATURES

The importance of cellular organization in fruit ripening has been stressed by Solomos & Laties (179). During the development of the appendix of *Arum* and *Sauromatum,*

ment of individual mitochondria with a corresponding increase in the number of cristae per mitochondrion (22, 175). Microbodies or peroxisomes (21, 149) do not seem to be involved in the metabolic flare-up. Nitrogen metabolism (20, 57) is especially intense on the day of flowering and afterwards. The notion that the amines which attract the pollinators are formed through decarboxylation of amino acids (156, 174) has recently been challenged (71, 72); amino acid/aldehyde transamination may be the preferred pathway for biosynthesis of primary aliphatic amines in flowering plants. In *Sauromatum,* the respiratory CO_2 produced by the appendix shows a marked decrease in ^{13}C on flowering day (204; cf 84). This may reflect a greater metabolic participation of fatty acids, important because these may act as uncouplers (12).

The increased cyanide-insensitive respiration of slices of storage tissue is accompanied by an increase in the number of mitochondria, presumably through fission of preexisting mitochondria (123) without a corresponding increase in cell number (8, 9, 122, 144). The newly formed mitochondria are heavier than the preexisting ones, probably because they contain more NADH dehydrogenase (64) and nonheme iron oxidase and are more resistant to cyanide (144, 164). Their aerobic biogenesis is, understandably, accompanied by the synthesis of new RNA species and proteins (11, 28, 42, 50, 121, 197), while various metabolic activities such as the uptake of phosphate, sulfate, and glucose (6, 64, 69, 100, 117, 126, 158), operation of the pentose phosphate pathway (6), and glycolysis-fed Krebs cycle activities (3–5, 117, 118, 158) are also boosted. In potato slices, certain changes occur in the NAD/NADP ratio (27), important because plant mitochondria have been said to lack NADP (78, 80, 113).

FUNCTION OF THE ALTERNATE PATHWAY

Upon injury, many plants release HCN from cyanogenic glycosides, but the latter are not in evidence where the alternate pathway is the most obvious (*Arum, Symplocarpus, Lilium auratum* pollen). Free CO, although present in concentrations up to 12% in the internal cavity of the brown alga *Nereocystis* (114, 157), is rare in plants. Confrontation of plant tissues with cyanide or CO thus is largely a laboratory event—hardly something Nature could have selected for. Therefore, no student of evolution can easily accept the idea that the alternate pathway has become fairly common in plants when it will become functional only after exposure of tissues to cyanide or CO (188).

Of course, the situation in isolated mitochondria may not always reflect the situation in intact tissues. When plants produce the heat that will volatilize the

odoriferous principles that attract the pollinators, the survival value of the alternate pathway seems obvious. In *Symplocarpus,* the long-lasting heat production guarantees development of the inflorescence and pollination, even at subfreezing environmental temperatures (97, 98). Associating the alternate pathway with thermogenesis remains legitimate, for although it is true that its operation does not in all cases lead to a drop in the ATP level (which may even rise somewhat), it is obvious that a greatly increased flow of respiratory electrons is needed to maintain such ATP constancy when the number of phosphorylative sites is reduced from three to one (188, 206). Crudely phrased, more "fuel" has to be "burned" to obtain the same amount of ATP as in the classical situation, and this constitutes thermogenicity.

For *Arum* mitochondria, Passam & Palmer (150) recently have supplemented this circumstantial evidence with direct experimental data. The rate of oxidation of ascorbate plus tetramethylphenylene diamine (TMPD), which enters the cytochrome chain at cytochrome *c,* in this case is somewhat lower than that of malate or succinate, in contrast to the situation in mitochondria from rat liver, Jerusalem artichoke, and mung bean, where the effect of ascorbate plus TMPD far surpasses that of the other two electron donors. In the absence of cyanide, cytochrome oxidase therefore may not always act as the major terminal oxidase in *Arum* appendix mitochondria. Since heat development in the appendix of *Arum* and *Sauromatum* is confined to less than 12 hr, meticulous attention to the particular developmental stage of the appendices used is clearly imperative. In 1974, Lance (112) reached a similar conclusion on the basis of ADP:O ratios. As the inflorescence of *Arum* develops, the efficiency of oxidative phosphorylation decreases due to increased participation of the alternate pathway, endogenous uncoupling, and activity of a mitochondrial ATPase (cf 29).

In bean hypocotyl mitochondria, where thermogenicity is not at issue, the alternate pathway comes into play only when the ADP level is low enough to limit the cytochrome pathway rate (13). It may be required either to increase the flux through the citric acid cycle or to increase the oxidation of cytoplasmic NADH (48) in the absence of a phosphate acceptor (81). The alternate pathway probably modulates a balance between the availability of reducing equivalents and that of high energy adenylates (3–5, 63, 80, 100). The latter affect various enzymes allosterically (10, 90, 159), are obligatory for the functioning of succinyl-CoA synthetase in plants (148), and strongly influence the fate of malate (210), which has been receiving increased attention (77, 128–130).

CONTROL OF THE ALTERNATE PATHWAY: RELATIONSHIP WITH CLIMACTERIC FRUIT RESPIRATION AND ETHYLENE

In slices of storage tissues, oxygen plays an important role in the development of cyanide-resistant respiration (64, 115; cf 33). Volatile aldehydes may act as the trigger (115, 116). In the brown adipose tissue of mammals, thermogenicity—probably based on endogenous uncoupling—is under the control of hormones and external temperature (15, 41, 43, 44, 89, 125, 177, 178, 202). The environmental temperature rise in the daytime has also been invoked to help account for the climacteric events in *Arum;* unfortunately, they do not start until late in the after-

noon. In actuality, thermogenicity in arum lilies is controlled primarily by the light/dark regime (135, 136, 139, 167; cf 59), and secondarily by hormonal influences (30, 139, 193, 194). Exposure of *Sauromatum* inflorescences, kept in constant light, to a single 6-hr "dark shot" leads to a metabolic peak 40–45 hr after the beginning of the shot (31). The regime probably leads to production in the staminate flower primordia of a triggering hormone ("calorigen"), which can be shown to be present in the appendix about 22 hr before the heating starts. Injection of the extracted hormone into appendices amputated 2 days before the expected metabolic explosion leads to heating and smell production after a lag time of about a day (30, 193, 194). Chen & Meeuse (38, 40), concentrating on the production of the easily demonstrable compound indole under the influence of the hormone, have designed a bioassay for calorigen and have purified two active principles (calorigen I and II) with its aid. Both are low-molecular compounds which have now been characterized chemically to a considerable extent.

At the intracellular level, Bahr & Bonner (13) have shown the complete independence in vitro of the alternate path from ATP and ADP. For isolated *Symplocarpus* mitochondria, they have suggested (14) that the distribution of respiratory electrons over the two pathways is regulated by an equilibrium mechanism of two postulated carriers possessing E_0' values of such magnitude that they ensure full reduction of the component connected to the cytochrome oxidase, while the carrier feeding electrons into the alternate path is completely or partially oxidized. It is difficult to see, however, how such a system could lead to the nearly complete suppression of the classical pathway under certain circumstances.

Ethylene, like cyanide, often stimulates respiration (1, 2). In postharvest fruit respiration (160), the exact role of ethylene is hard to evaluate because of the multiplicity of events (32, 103, 142, 209). However, for intact avocados and for potatoes (where ripening is not at issue) Solomos & Laties (180, 181; cf 33, 154) could show that ethylene and HCN (gas) produce identical responses in glycolysis and respiration. The presence of the cyanide-resistant path, and not necessarily "ripening," seems to be the prerequisite for ethylene to stimulate respiration. Indeed, tissues stimulated by ethylene are also stimulated by cyanide (154), while conversely ethylene has no effect on plant materials strongly inhibited by cyanide (180). Both agents are thought to divert electrons actively from the classical respiratory chain to the alternate path, an ability which they probably share with calorigen (137). The mechanism giving rise to the increase in glycolysis which accompanies the respiratory boost is not clear. In some other instances of glycolytic boosts (no matter what the cause), phosphofructokinase (PFK) and/or pyruvate kinase (PK) have been implicated (16, 17, 26, 34, 60, 75, 76, 99, 127, 155). In banana, preclimacteric PFK displays toward its substrate a negative cooperativity (165, 166) which is partially abolished at the start of the climacteric; this amounts to an activation of the rate-limiting enzyme PFK.

EPILOGUE AND PROGNOSIS

In 1973, Dizengremel et al (46) found that cyanide-resistant and cyanide-sensitive mitochondria contain about the same proportion of ferrosulfoproteins with non-

heme iron and labile sulfur. They interpreted this to mean that the alternate pathway is common but is operational in some cases only. They use the observation that cyanide resistance can be induced easily by certain experimental treatments (64, 107) as further evidence that the "switching on" of the alternate pathway does not depend on a de novo large-scale synthesis of ferrosulfoproteins, but rather on a control mechanism that makes enzymatic proteins already present in the mitochondrial membrane more accessible to oxygen (cf 84, 204). The problem is how to reconcile this concept with the proved production of new and heavy mitochondria in storage tissue slices (8, 9, 122, 123, 144). The first order of the day will be to solve this controversy. Identification of the "second oxidase" is essential. It is also imperative to elucidate the chemical nature of calorigen and to compare its triggering action with that exerted by ethylene, CO, and cyanide. Details of respiratory electron transfer mechanisms and phosphorylative sites remain to be worked out in several cases.

Literature Cited

1. Abeles, F. B. 1972. *Ann. Rev. Plant Physiol.* 23:259–92
2. Abeles, F. B. 1973. *Ethylene in Plant Biology.* New York: Academic. 302 pp.
3. Adams, P. B. 1970. *Plant Physiol.* 45:495–99
4. Ibid, 500–3
5. Adams, P. B., Rowan, K. S. 1970. *Plant Physiol.* 45:490–94
6. ap Rees, T., Beevers, H. 1960. *Plant Physiol.* 35:839–47
7. ap Rees, T., Bryant, J. A. 1971. *Phytochemistry* 10:1183–90
8. Asahi, T., Honda, Y., Uritani, I. 1966. *Arch. Biochem. Biophys.* 113:498–99
9. Asahi, T., Majima, R. 1969. *Plant Cell Physiol.* 10:317–23
10. Atkinson, D. E. 1966. *Ann. Rev. Biochem.* 35:85–124
11. Bacon, J. S. D., MacDonald, I. R., Knight, A. H. 1965. *Biochem. J.* 94:175–82
12. Baddeley, M. S., Hanson, J. B. 1967. *Plant Physiol.* 42:1702–10
13. Bahr, J. T., Bonner, W. D. Jr. 1973. *J. Biol. Chem.* 248:3441–45
14. Ibid, 3446–50
15. Ball, E. C., Jungas, R. L. 1961. *Proc. Nat. Acad. Sci. USA* 47:932–41
16. Barker, J., Khan, M. A. A., Solomos, T. 1967. *New Phytol.* 66:577–96
17. Barker, J., Solomos, T. 1962. *Nature* 169:189–91
18. Beevers, H. 1961. *Respiratory Metabolism in Plants.* Evanston, Ill. & White Plains, N.Y.: Row-Peterson. 232 pp.
19. Bendall, D. S., Bonner, W. D. Jr. 1971. *Plant Physiol.* 47:236–45
20. Berger, C. 1970. *Z. Pflanzenphysiol.* 62:259–69
21. Berger, C., Gerhardt, B. 1971. *Planta* 96:326–38
22. Berger, C. Schnepf, E. 1970. *Protoplasma* 69:237–51
23. Bonner, W. D. Jr. 1965. *Plant Biochemistry,* ed. J. Bonner, J. E. Varner, 89–123. New York/London: Academic. 1054 pp.
24. Bonner, W. D. Jr., Bendall, D. S. 1968. *Biochem. J.* 109:47P
25. Bonner, W. D. Jr., Christensen, E. L., Bahr, J. T. 1972. *Biochemistry and Biophysics of Mitochondrial Membranes,* ed. G. F. Azzone, 113–19. New York/London: Academic
26. Bourne, D. T., Ranson, S. L. 1965. *Plant Physiol.* 40:1178–90
27. Brinkman, F. G., van der Plas, L. H. W., Verleur, J. D. 1973. *Z. Pflanzenphysiol.* 68:364–72
28. Bryant, J. A., ap Rees, T. 1971. *Phytochemistry* 10:1191–97
29. Buggeln, R. G., Meeuse, B. J. D. 1967. *Proc. Kon. Ned. Akad. Wetensch. Ser. C.* 70:515–25
30. Buggeln, R. G., Meeuse, B. J. D. 1971. *Can. J. Bot.* 49:1373–77
31. Buggeln, R. G., Meeuse, B. J. D., Klima, J. R. 1971. *Can. J. Bot.* 49:1025–31
32. Burg, S. P., Burg, E. A. 1967. *Plant Physiol.* 42:144–52
33. Burton, W. G. 1950. *New Phytol.* 49:121–34
34. Chalmers, D. J., Rowan, K. S. 1971. *Plant Physiol.* 48:235–40

35. Chance, B., Bonner, W. D. Jr. 1965. *Plant Physiol.* 40:1198–1204
36. Chance, B., Bonner, W. D. Jr., Storey, B. T. 1968. *Ann. Rev. Plant Physiol.* 19:295–320
37. Chance, B., Williams, G. R. 1956. *Advan. Enzymol.* 17:65
38. Chen, J., Meeuse, B. J. D. 1971. *Am. J. Bot.* 58:478
39. Chen, J., Meeuse, B. J. D. 1971. *Acta Bot. Neer.* 20:627–35
40. Chen, J., Meeuse, B. J. D. 1972. *Plant Cell Physiol.* 13:831–41
41. Christiansen, E. N., Pedersen, J. I., Grav, H. J. 1969. *Nature* 222:857–60
42. Click, R. E., Hackett, D. P. 1963. *Proc. Nat. Acad. Sci. USA* 50:243–50
43. Dawkins, M. J. R., Hull, D. 1964. *J. Physiol.* 172:216–38
44. Dawkins, M. J. R., Hull, D. 1965. *Sci. Am.* 213:62–67
45. Decker, J. S. 1936. See Ref. 189, pp. 479, 496
46. Dizengremel, P., Chauveau, M., Lance, C. 1973. *C. R. Acad. Sci. Paris Ser. D* 277:239–242
47. Douce, R., Christensen, E. L., Bonner, W. D. Jr. 1972. *Biochim. Biophys. Acta* 275:148–60
48. Douce, R., Mannella, C. A., Bonner, W. D. Jr. 1973. *Biochim. Biophys. Acta* 292:105–16
49. Dutton, P. L., Storey, B. T. 1971. *Plant Physiol.* 47:282–88
50. Edelman, J., Hall, M. A. 1965. *Biochem. J.* 95:403–10
51. Eilam, Y. 1965. *J. Exp. Bot.* 16:614–27
52. El-Din, S. M. 1968. *Naturwissenschaften* 12:658–59
53. Erecinska, M., Storey, B. T. 1970. *Plant Physiol.* 46:618–24
54. Estabrook, R. W. 1961. *J. Biol. Chem.* 236:3051–57
55. Faegri, K., van der Pijl, L. 1971. *The Principles of Pollination Ecology.* Oxford: Pergamon. 291 pp. 2nd rev. ed.
56. Fischer, H. 1960. *Encycl. Plant Physiol.* 2:520–35
57. Fischer, H., Specht-Jürgensen, I., Fleck-Gerndt, G. 1972. *Beitr. Biol. Pflanz.* 48:243–53
58. Garreau, M. 1851. *Ann. Sci. Nat. Bot. (Paris) 3e Ser.* 16:250–56
59. Gessner, F. 1960. *Planta* 54:453–65
60. Ghosh, A., Chance, B. 1964. *Biochem. Biophys. Res. Commun.* 16:174–81
61. Hackett, D. P. 1956. *Plant Physiol.* 31: suppl. XL
62. Hackett, D. P. 1959. *Ann. Rev. Plant Physiol.* 10:113–46
63. Hackett, D. P. 1963. *Control Mechanisms in Respiration and Fermentation,* ed. B. Wright, 105–27. New York: Ronald
64. Hackett, D. P., Haas, D. W., Griffiths, S. K., Niederpruem, D. J. 1960. *Plant Physiol.* 35:8–19
65. Hackett, D. P., Rice, B., Schmid, C. 1960. *J. Biol. Chem.* 235:2140–44
66. Hackett, D. P., Simon, E. W. 1954. *Nature* 173:162–63
67. Hall, D. O., Greenawalt, J. W. 1964. *Biochem. Biophys. Res. Commun.* 17:565–69
68. Hanebuth, W. F., Chasson, R. M. 1972. *Plant Physiol.* 49:857–59
69. Hanebuth, W. F., Chasson, R. M., Pittman, D. 1974. *Physiol. Plant.* 30: 273–78
70. Hanes, C. S., Barker, J. 1931. *Proc. Roy. Soc. B* 108:95–118
71. Hartmann, T., Dönges, D., Steiner, M. 1972. *Z. Pflanzenphysiol.* 67:404–17
72. Hartmann, T., Ilert, H.-I., Steiner, M. 1972. *Z. Pflanzenphysiol.* 68:11–18
73. Hartree, E. F. 1957. *Advan. Enzymol.* 18:1–64
74. Hess, C. M., Meeuse, B. J. D. 1967. *Acta Bot. Neer.* 16:188–96
75. Hess, C. M., Meeuse, B. J. D. 1968. *Proc. Kon. Ned. Akad. Wetensch. Ser. C* 71:443–55
76. Ibid, 456–71
77. Hobson, G. E. 1970. *Phytochemistry* 9:2257–63
78. Ikuma, H. 1967. *Science* 158:529
79. Ikuma, H. 1970. *Plant Physiol.* 45:773–81
80. Ikuma, H. 1972. *Ann. Rev. Plant Physiol.* 23:419–36
81. Ikuma, H., Bonner, W. D. Jr. 1967. *Plant Physiol.* 42:67–75
82. Ibid, 1535–44
83. Ikuma, H., Schindler, F. D., Bonner, W. D. Jr. 1964. *Plant Physiol.* 39: suppl. LX
84. Jacobson, B. S., Laties, G. G., Smith, B. N., Epstein, S., Laties, B. 1970. *Biochim. Biophys. Acta* 216:295–304
85. James, W. O. 1953. *Plant Respiration.* Oxford: University Press. 282 pp.
86. James, W. O., Beevers, H. 1950. *New Phytol.* 49:353–74
87. James, W. O., Elliott, D. C. 1955. *Nature* 175:89
88. James, W. O., Elliott, D. C. 1955. *New Phytol.* 57:230–34
89. Joel, C. D. 1965. *Adipose Tissue (Handb. Physiol. Sect. 5),* ed. A. E. Renold, G. F. Cahill Jr., 59–86. Washington, D.C.: Am. Physiol. Soc.

90. Johnson, T. F., Meeuse, B. J. D. 1972. *Proc. Kon. Ned. Akad. Wetensch. Ser C* 74:1–19
91. Kano, H., Kumazawa, K. 1972. *Plant Cell Physiol.* 13:237–44
92. Ibid 1973. 14:673–80
93. Kano, H., Kumazawa, K., Mitsui, S. 1969. *J. Sci. Soil Animal Fertilizers Jap.* 40:473–78
94. Ibid 1970. 41:213–17
95. Knoch, E. 1899. *Bibliog. Bot.* 9, 47:1–60
96. Knoll, F. 1926. *Abh. Zool.-Bot. Ges. Wien* 12:379–482
97. Knutson, R. M. 1972. *Am. Midl. Natur.* 88:251–54
98. Knutson, R. M. 1974. *Science* 186: 746–47
99. Kohr, M. J., Beevers, H. 1971. *Plant Physiol.* 47:48–52
100. Kolattukudy, P. E., Reed, D. J. 1966. *Plant Physiol.* 41:661–69
101. Kozuka, Y., Uritani, I. 1973. *Plant Cell Physiol.* 14:193–96
102. Kugler, H. 1970. *Einführung in die Blütenökologie.* Stuttgart: G. Fischer. 345 pp. 2nd ed.
103. Lacher, J. R., Amador, A., Snow, K. 1966. *Plant Physiol.* 41:1435–38
104. Lamarck, J. B. de 1778. *Flore Française* 3:538
105. Lambowitz, A. M., Bonner, W. D. Jr. 1973. *Biochem. Biophys. Res. Commun.* 52:703–11
106. Lambowitz, A. M., Bonner, W. D. Jr. 1973. *Plant Physiol.* 51: suppl. 10
107. Lambowitz, A. M., Slayman, C. W. 1971. *J. Bacteriol.* 108:1087–96
108. Lambowitz, A. M., Slayman, C. W., Slayman, C. L. 1972. *J. Biol. Chem.* 247:1536–45
109. Lambowitz, A. M., Smith, E. W., Slayman, C. W. 1972. *J. Biol. Chem.* 247:4850–58
110. Ibid, 4859–65
111. Lance, C. 1972. *Ann. Sci. Nat. Bot. 12e Ser.* 13:477–95
112. Lance, C. 1974. *Plant Sci. Lett.* 2:165–71
113. Lance, C., Bonner, W. D. Jr. 1968. *Plant Physiol.* 43:756–66
114. Langdon, S. 1916. *Publ. Puget Sound Biol. Sta.* 1:237–46
115. Laties, G. G. 1962. *Plant Physiol.* 37:679–90
116. Laties, G. G. 1963. See Ref. 63, 129–55
117. Laties, G. G. 1964. *Plant Physiol.* 39:391–97
118. Ibid, 654–63
119. Laties, G. G. 1967. *Aust. J. Sci.* 30:193–203
120. Laties, G. G., Hoelle, C. 1965. *Plant Physiol.* 40:757–64
121. Leaver, C. J., Key, J. L. 1967. *Proc. Nat. Acad. Sci. USA* 57:1338–44
122. Lee, S. G., Chasson, R. M. 1966. *Physiol. Plant.* 19:194–98
123. Ibid, 199–206
124. Leick, E. 1915. *Ber. Deut. Bot. Ges.* 33:518–536
125. Lindberg, O., Ed. 1970. *Brown Adipose Tissue.* New York: Elsevier
126. Loughman, B. C. 1960. *Plant Physiol.* 35:418–24
127. Lynen, F. 1963. See Ref. 63, 289–306
128. Macrae, A. R. 1971. *Phytochemistry* 10:1453–58
129. Ibid, 2343–47
130. Macrae, A. R., Moorhouse, R. 1970. *Eur. J. Biochem.* 16:96–102
131. Marsh, P. B., Goddard, D. R. 1939. *Am. J. Bot.* 26:724–28
132. Matile, P. 1958. *Ber. Schweiz. Bot. Ges.* 68:295–306
133. Matlib, M. A., Kirkwood, R. C., Smith, J. E. 1971. *J. Exp. Bot.* 22:291–303
134. Meeuse, B. J. D. 1961. *The Story of Pollination.* New York: Ronald. 243 pp.
135. Meeuse, B. J. D. 1966. *Sci. Am.* 215: 80–88
136. Meeuse, B. J. D. 1968. *Atomes* 256: 428–36
137. Meeuse, B. J. D. 1972. *What's New in Plant Physiology,* ed. G. J. Fritz, 4(2): 1–4
138. Meeuse, B. J. D., Amundson, R. G. 1973. *Plant Physiol.* 51: suppl. 48
139. Meeuse, B. J. D., Buggeln, R. G. 1969. *Acta Bot. Neer.* 18:159–72
140. Meeuse, B. J. D., Buggeln, R. G., Summers, S. N. 1969. *Abstr. 11th Int. Bot. Congr. Seattle,* 144
141. Meeuse, B. J. D., Chen, J., Johnson, T. F. 1971. *Plant Physiol.* 47: suppl. 27
142. Millerd, A., Bonner, J., Biale, J. B. 1953. *Plant Physiol.* 28:521–31
143. Nagy, K. A., Odell, D. K., Seymour, R. S. 1972. *Science* 178:1195–97
144. Nakano, M., Asahi, T. 1970. *Plant Cell Physiol.* 11:499–502
145. Okunuki, K. 1932. *Bot. Mag. (Tokyo)* 47:45–62
146. Okunuki, K. 1939. *Acta Phytochim.* 11:27–64
147. Olason, D. M. 1967. *Changes in cofactor levels in the flowering sequence of some arum lilies.* MSc. thesis. Univ. Washington, Seattle
148. Palmer, J. M., Wedding, R. T. 1966. *Biochim. Biophys. Acta* 113:167–74
149. Parish, R. W. 1972. *Z. Pflanzenphysiol.* 67:430–42

150. Passam, H. C., Palmer, J. M. 1972. *J. Exp. Bot.* 23:366–74
151. Poe, M., Estabrook, R. W. 1968. *Arch. Biochem. Biophys.* 126:320–30
152. Prime, C. T. 1960. *Lords and Ladies.* London: Collins. 241 pp.
153. Proctor, M., Yeo, P. 1973. *The Pollination of Flowers.* London: Collins. 418 pp.
154. Reid, M. S., Pratt, H. K. 1972. *Plant Physiol.* 49:252–55
155. Ricardo, C. P. P., ap Rees, T. 1972. *Phytochemistry* 11:623–26
156. Richardson, M. 1966. *Phytochemistry* 5:23–30
157. Rigg, G. B., Swain, L. A. 1941. *Plant Physiol.* 16:361–71
158. Romberger, J. A., Norton, G. 1961. *Plant Physiol.* 44:311–12
159. Rowan, K. S. 1966. *Int. Rev. Cytol.* 19:301–91
160. Sacher, J. A. 1973. *Ann. Rev. Plant Physiol.* 24:197–224
161. Sakano, K., Asahi, T. 1969. *Agr. Biol. Chem.* 33:1433–39
162. Sakano, K., Asahi, T. 1971. *Plant Cell Physiol.* 12:417–26
163. Ibid, 427–36
164. Sakano, K., Asahi, T., Uritani, I. 1968. *Plant Cell Physiol.* 9:49–60
165. Salminen, S. O., Young, R. E. 1974. *Nature* 247:389–91
166. Salminen, S. O., Young, R. E. 1974. *Plant Physiol.* In press
167. Schmucker, T. 1925. *Flora* 118:460–75
168. Schnepf, E. 1965. *Planta* 66:374–76
169. Schnepf, E., Czygan, F. C. 1966. *Z. Pflanzenphysiol.* 54:345–55
170. Schonbaum, G. R., Bonner, W. D. Jr., Storey, B. T., Bahr, J. T. 1971. *Plant Physiol.* 47:124–28
171. Sharpless, T. K., Butow, R. A. 1970. *J. Biol. Chem.* 245:58–70
172. Simon, E. W. 1957. *J. Exp. Bot.* 8:20–35
173. Ibid 1959. 10:125–33
174. Ibid 1962. 13:1–4
175. Simon, E. W., Chapman, J. A. 1961. *J. Exp. Bot.* 12:414–20
176. Smith, B. N., Meeuse, B. J. D. 1966. *Plant Physiol.* 41:343–47
177. Smith, R. E., Horwitz, B. A. 1969. *Physiol. Rev.* 49:330–425
178. Smith, R. E., Roberts, J. C. 1964. *Am. J. Physiol.* 206:143–48
179. Solomos, T., Laties, G. G. 1973. *Nature* 245:390–92
180. Solomos, T., Laties, G. G. 1974. *Science* 54:506–11
181. Solomos, T., Laties, G. G. 1974. *Plant Physiol.* In press
182. Storey, B. T. 1970. *Plant Physiol.* 45:447–54
183. Ibid, 46:13–20
184. Ibid, 625–30
185. Storey, B. T. 1971. *Fed. Proc.* 30:1189
186. Storey, B. T. 1971. *Plant Physiol.* 48:493–97
187. Storey, B. T., Bahr, J. T. 1969. *Plant Physiol.* 44:115–25
188. Ibid, 126–34
189. Valla, J. J., Cirino, D. R. 1972. *Darwiniana* 17:477–98
190. van der Pijl, L. 1933. *Trop. Natuur* 22:210–214
191. van der Pijl, L. 1937. *Rec. Trav. Bot. Neer.* 34:157–67
192. van Herk, A. W. H. 1937. *Rec. Trav. Bot. Neer.* 34:69–156
193. van Herk, A. W. H. 1937. *Proc. Kon. Ned. Akad. Wetensch.* 40:607–14
194. Ibid, 709–19
195. van Herk, A. W. H., Badenhuizen, N. P. 1934. *Proc. Kon. Ned. Akad. Wetensch.* 37:99–105
196. Van Norman, R. W. 1955. *Plant Physiol.* 30: suppl. 29
197. Vaughan, D., MacDonald, I. R. 1967. *Plant Physiol.* 42:456–58
198. Vogel, S. 1963. *Akad. Wiss. Lit. Mainz, Abh. Math.-Naturwiss. Kl.* 1962:605–763
199. Wakiyama, S., Ogura, Y. 1970. *Plant Cell Physiol.* 11:835–48
200. Wedding, R. T., McCready, C. C., Harley, J. L. 1973. *New Phytol.* 72:1–13
201. Ibid, 15–26
202. Whittow, C. G., Ed. 1973. *Comparative-Physiology of Thermoregulation, Vol. 3: Special Aspects of Thermoregulation.* New York: Academic. 278 pp.
203. Wilson, R. H., Hanson, J. B. 1969. *Plant Physiol.* 44:1335–41
204. Wilson, R. H., Smith, B. N. 1971. *Z. Pflanzenphysiol.* 65:124–29
205. Wilson, S. B. 1970. *Biochem. J.* 116: 20
206. Wilson, S. B. 1970. *Biochim. Biophys. Acta* 223:383–87
207. Yocum, C. S., Hackett, D. P. 1955. *Plant Physiol.* 30: suppl. 30
208. Ibid 1957. 32:186–91
209. Young, R. E., Biale, J. B. 1967. *Plant Physiol.* 42:1357–62
210. Zimmerman, E. J., Ikuma, H. 1970. *Plant Physiol.* 46: suppl. 37