metabolic changes that are associated with decreased carbon fixation could contribute.

We do not imply that early stomatal closure is the only causal factor initiating dieback; the relationship is certainly much more complex. We merely suggest that stomatal sensitivity to drought stress in white ash may be an important factor coupling dieback to drought. Ross (1966) concluded his study of ash dieback by suggesting that Bier's (1964) hypothesis which related relative turgidity of young bark to fungal infection could be relevant to ash dieback. Since bark moisture content would be highly correlated to plant drought stress and resulting stomatal closure, experiments which separate these phenomena should be initiated.

BIER, J. E. 1964. The relation of some bark factors to canker susceptibility. Phytopathology, **54**: 105–107.
HORSFALL, J. G., and A. E. DIMOND. 1957. Interactions of tissue sugar, growth substances, and disease susceptibility. Z. Pflanzenkr. Pflanzenschtuz, **64**: 415–421.
ROSS, E. W. 1964. Cankers associated with ash dieback. Phytopathology, **54**: 272–275.
——— 1966. Ash dieback. State Univ. Coll. For., Syracuse, Univ. Tech. Publ. No. 88.
SILVERBORG, S. B., and E. W. ROSS. 1968. Ash dieback disease development in New York State. Plant Dis. Rep. **52**: 105–107.
TOBIESSEN, P. L., and T. M. KANA. 1974. Drought stress avoidance in three pioneer tree species. Ecology, **55**: 667–670.
UNITED STATES FOREST SERVICE. 1965. Silvics of forest trees of the United States. Agric. Handb. No. 271.

Heat production and pollination in Araceae

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The ecological role of heat production in Araceae has not been extensively investigated. The possibility that carbon dioxide and heat production are components of a carrion, dung, and mammal mimicry syndrome deserves consideration. Warm inflorescences might also serve as significant shelters for pollinators of species flowering during cold seasons.

Several members of the family Araceae as well as a few species in other families have elevated respiratory rates which result in heat production. A brief literature survey revealed the capacity in seven species in seven genera.

Most work on the subject has been of a physiological nature (Buggeln *et al.* 1971; Knutson 1974). The ecological role of this remarkable activity has apparently attracted less attention. The general assumption is that the heat serves to volatilize and thereby helps disperse odors which are themselves produced by the respiration of the plant (Meeuse 1966*a*). While this seems likely, it is interesting that many of the amines released by Aroids (Meeuse 1966*b*) are probably as, or more, volatile than the essential oils produced by other plants which do not require heat for satisfactory odor dispersal. A second advantage is that the rising odor column is particularily attractive to passing insects which commonly pollinate these sapromyophilous plants (Faegri and van der Pilj 1971). In the eastern skunk cabbage, *Symplocarpus foetidus* (L.) Nutt., heat production may enable the species to bloom when several inches of snow covers the ground; the tissues are otherwise not frost resistant (Knutson 1972, 1974).

The purpose of this note is to suggest possible additional benefits of elevated temperatures and associated carbon dioxide release by certain Aroids.

Mimicry of carrion and dung in some of these

plants goes beyond that of odor. Colors are often dark as in dung and carrion and there may be dark spots which are thought to represent previously arrived insects (Proctor and Yeo 1973). Food may also be available in some species (Faegri and van der Pilj 1971).

The production of heat could represent another aspect of what may be a quite detailed form of mimicry serving to deceive pollinators. Mammalian feces are warm on deposition. A large mass of carrion may also give off heat as a result of the respiration of decomposer organisms. In cases (below) where Arums are pollinated by insects which normally feed on warm-blooded mammals, the heat released by the plant may be mimicking the elevated temperatures of mammals. Although Knoll (in Proctor and Yeo 1973) was unable to show that heat was an attractant to the pollinator species he studied, his results do not rule out the possibility of such attraction in other species. Nor do these results exclude the possibility that warmth serves to prevent the premature departure of pollinators.

Elevated plant temperatures could also probably benefit pollinating insects in cool climates and seasons. Conditions for insect activity must be marginal in places where *S. foetidus* flowers while snow covers the ground. The warmth of the inflorescence could provide a shelter wherein insects could remain active. The usefulness of flowers as insect shelters is unclear: Faegri and van der Pilj (1971, p. 79) doubt their general importance; however, elsewhere (Faegri and van der Pilj 1971, p. 97) they do not dispute the suggestion by Hocking and Sharplin (1965) that insects might benefit by basking in sun-heated Arctic flowers. That Arctic insects indeed gain heat when resting in heliotropic flowers has been demonstrated by Kevan (1975). He states the extra warmth must be valuable in increasing their metabolism, hastening the maturation of ova, and giving them greater mobility by preheating them for flight. Interestingly, one of the flowers studied by Kevan, *Dryas integrifolia* M. Vahl., relies in part, on the services of the basking insects for pollination (Kevan 1975).

A concomitant of heat release is the production of carbon dioxide, sometimes in large amounts (Buggeln *et al.* 1971). Adaptive benefits of this byproduct are also conceivable. Like odor, color, color pattern, provision of food, and perhaps heat, release of carbon dioxide mimics a characteristic of carrion and dung inhabited by populations of respiring decomposer organisms. The narcotic effect of carbon dioxide on insects (Hoar and Hickman 1967) may also be significant and comparable to the 'narcotic' substances produced by some Araceae to attract bees (Faegri and van der Pilj 1971). Stupification, like provision of food, may serve to delay the pollinator's departure.

Supportive evidence for these hypotheses is unfortunately not readily available. However, it is known that all insects are sensitive to high temperatures (Wigglesworth 1965). Some species which feed on mammals use heat to help locate their prey (Wigglesworth 1965). *Arum conophalloides* is pollinated by flies of the families Ceratopogonidae and Simuliidae (Proctor and Yeo 1973) which normally feed on mammals. It would be most interesting to know whether any of the dung and carrion insects which pollinate many of the foul-smelling, heat-producing Aroids use temperature or carbon dioxide gradients as cues to locate food or egg-laying sites, use the warm spadix region as a shelter, or are narcotized by the prevailing carbon dioxide levels. Fruitful experiments might be executed in areas where these plants are native.

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BUGGELN, R. G., B. J. D. MEEUSE, and J. R. KLIMA. 1971. The control of blooming in *Sauromatum guttatum* (Araceae) by darkness. Can. J. Bot. **49**: 1025–1031.

FAEGRI, K., and L. VAN DER PILJ. 1971. The principles of pollination ecology. 2nd ed. Pergamon Press, Oxford.

HOAR, W. S., and C. P. HICKMAN, JR. 1967. A laboratory companion for general and comparative physiology. Prentice-Hall Inc., Englewood Cliffs, N.J.

HOCKING, B., and C. D. SHARPLIN. 1965. Flower basking by arctic insects. Nature (London), **206**: 215.

KEVAN, P. G. 1975. Sun-tracking solar furnaces in high arctic flowers: significance for pollination and insects. Science, **189**: 723–726.

KNUTSON, R. M. 1972. Temperature measurements of the spadix of *Symplocarpus foetidus* (L.) Nutt. Am. Midl. Nat. **88**: 251–254.

——— 1974. Heat production and temperature regulation in eastern skunk cabbage. Science, **186**: 746–747.

MEEUSE, B. J. D. 1966*a*. The voodoo lily. Sci. Am. **215**: 80–88.

——— 1966*b*. Production of volatile amines and skatoles at anthesis in some arum lily species. Plant Physiol. **41**: 343–347.

PROCTOR, M., and P. YEO. 1973. The pollination of flowers. Collins, London.

WIGGLESWORTH, V. B. 1965. The principles of insect physiology. Methuen, London.