Trees (1994) 9: 1–5

Structure and Function
Trees

Review

Reconsidering the functions of latex

J. Robert Hunter

Botany Department, University of Wisconsin – Madison, 132 Birge Hall, 430 Lincoln Drive, Madison WI 53706, USA

Received: 9 November 1993/Accepted: 14 February 1994

Abstract. Enormous quantities of latex are found in over 40 plant families on a worldwide basis. Despite the proportions involved, the role of this substance within plants is still a matter of conjecture. Latex is closely associated with isoprene which may be emitted as a gas from both plants (that may or may not contain latex) and animals. The volume of isoprene expelled into the atmosphere each year is approximately equal to that of total methane emissions. The latter (but not the former), a known "greenhouse gas", is the subject of considerable concern. It appears reasonable, therefore, that efforts be made to examine more thoroughly the formation and function of latex and associated compounds in order to obtain a better understanding of a number of critical biological and environmental phenomena known to be associated with these phytochemicals. Possible roles played by these substances in both plants and their surrounding environment are described.

Key words: Antidote to ozone toxicity – Carbon sink – Food and moisture storage – Isoprene – Latex

Introduction

Each year, over 5 million metric tons of rubber (dry weight) are processed commercially from natural latex on a worldwide basis (Greek 1991). This quantity is obtained chiefly from the Para rubber tree *Hevea brasiliensis* (Willd, ex Adr. de Juss.) Muell.-Arg. However, a vastly greater quantity remains not only in these plantation trees, but in millions of other *Hevea* species, which are never tapped. Furthermore, in addition to the Euphorbiaceae, 40 other, mostly tropical, plant families including Apocynaceae, Asclepiadaceae, Asteraceae, Moraceae, Papaveraceae, and Sapotaceae, are reported by Lewinsohn (1991) to contain latex. To this list should be added Aceraceae [*Acer platanoides,* which has petioles with a milky sap (Bailey and Bailey 1976)], and Meliaceae [*Chisocheton,* a genus of "laticiferous trees (Backer and Bakhuizen 1965)]. The quantity retained within this multitude of plants must be enormous, possibly exceeding the amount commercially tapped by at least 2 or 3 orders of magnitude; but exactly what is latex?

It was reported (Fisher 1956) that in 1865 G. Bouchard discovered when he heated natural rubber (caoutchouc) to a high temperature he could obtain the volatile substance isoprene. Three years later W. A. Tilden produced isoprene from turpentine which he converted, following Bouchard's methods, into "a tough substance resembling caoutchouc." At that time, no one had any idea what the principal function might be of either latex in plants or isoprene in plants and animals. A review of the literature demonstrates there has been only a modest addition to our knowledge of the role of these two substances, within living organisms or in the lower elevation atmosphere which surrounds them, over the past 125 years. For example, the process of isoprene formation is still unknown (see Sharkey et al. 1991).

Indeed, it is difficult to find a standard definition for latex. It was recently stated (Metcalfe 1967) that "the term latex is used loosely by plant anatomists for fluids with a milky appearance due to the suspension of many small particles in a liquid dispersion medium with a very different refractive index." Furthermore, he continued, "according to Esau (1965) the dispersed particles are commonly hydrocarbons of the terpene type which include essential oils, balsams, and rubber." The New Encyclopaedia Britannica (1986) defines latex as a "plant product (which) is a complex mixture of substances, including various gum resins, fats, or waxes and, in some instances, poisonous compounds, suspended in a watery medium in which salts, sugars, tannins, alkaloids, enzymes, and other substances are dissolved."

No mention is made of the fact that after water, one of the principal ingredients of latex is isoprene (2-methyl-1,3-butadiene), a colorless, volatile liquid hydrocarbon which may also be obtained by processing petroleum or natural gas for use as a chemical raw material, particularly in the fabrication of rubber. Many plant substances are derivations of this substance. Combinations of two or more (up to many thousands) isoprene units constitute a class of organic compounds known as isoprenoids. Among these are menthol, camphor, vitamin A, and, of course, natural rubber. However, according to Giessman and Crout (1969) "although many terpenes possess structures that can be dissected formally into 5-carbon units with the isoprene skeleton, it is now known that terpenoid compounds are not derived from isoprene." Thus, isoprene should not be considered as a substance solely related to, nor to be found exclusively within, latex. It is produced by many plants during photosynthesis as well as by animals (Cailleux et al. 1992) and may be emitted by both.

Latex is not a uniform material. As indicated above, the water and isoprene units contained in latex are mixed with other compounds which vary in quantity, number, and concentration depending upon the species and the environment. Indeed, it is this heterogeneous mixture of substances in natural rubber latex which, when converted into examination gloves and condoms, are believed to form the barrier that inhibits the passage of the HIV virus (Klein et al. 1989). To date, it has not been possible to approximate the composition of this conglomerate artificially.

Finally, considering the current rapid and thorough pace of scientific endeavor, it is curious that there continues to be such a dearth of knowledge about or understanding of the function of the considerable quantities of latex found in a number of different plant species. For example, only 30 years ago, Polhamus (1962) stated that "no one has demonstrated why a plant makes rubber and it does not appear to be a food reserve. Strong evidence indicates that rubber is an end-product that is not reused in the metabolism of the plant." More recently, after reviewing theories concerning the role of latex, Webster and Baulkwill (1989) concluded that "as none of the above hypotheses has been proven, the function of latex and rubber in the plant remains unknown."

As stated by Metcalfe (1967) "the fact that latex is restricted to a small number of plant families between many of which there is no evidence of close taxonomic relationship, suggests that the capacity to produce latex has been evolved more than once." This lack of close cladistic affinity has recently been further substantiated (Chase et al. 1993).

Evolutionary theories all have in common the concept that selection pressure does not favor the wasteful, neutral, or deleterious presence of any particular substance or characteristic within living organisms. In earlier epochs, perhaps both latex and isoprene may have performed different and distinct roles than they do today. However, as they are still to be found in copious quantities in a variety of living matter they must continue to play some significant role in the Earth's overall ecosystem.

Possible roles of latex in plants

Plant defense system

Farrell et al. (1991) states "Ehrlich and Raven's postulate (1964) that rapid diversification follows innovation in plant defense has often been involved *a posteriori* for plant lineages of unusual diversity and chemical distinctiveness" as a basis to question whether latex and resin canals might spur plant diversification. They further claim, as many have for some time (Stahl 1888; Rhoades 1979; Rosenthal and Janzen 1979), that it is quite proper to suggest that latex evolved in response to the obvious plant need of protection from predation.

Carbon sink

Concern over carbon cycles and the possible "greenhouse effect" (Post et al. 1990; Schneider 1989) stress the importance of a balance in cycles of atmospheric gases and argue for increasing the capabilities for storage of carbon to compensate for the growing amounts currently being emitted into the atmosphere.

Dewar (1992) suggests that "the interpretation of northern hemisphere carbon sinks remains unresolved but that it most likely contains both terrestrial and oceanic components." He adds that as much as 2.8 Gigatous of Carbon (Gt C) per year is sequestered in tropical biotic sinks. Uncertainity as to the specificity of the sinks as well as the quantify of carbon involved is due to increasing deforestation in this part of the world. Sundquist (1993) also stresses that "unidentified terrestrial CO_2 sinks are important uncertainties in both deglacial and recent CO_2 budgets."

Food and moisture storage

According to Mahlberg (1993), classical writers and herbalists attributed such practical applications as food and water storage to latex and the system of laticifers as replicating the circulatory system in animals. More recent proposals have also been made that a function of latex is to serve as a food storage system (Maksymowych and Ledbetter 1987) as well as a method of maintaining water balance (Sen and Chawan 1972). However, as previously noted, Polhamus (1962) stated that "there is evidence that rubber is an end-product that is not reused in the metabolism of the plant." This might further imply its possible role as a carbon sink.

Antidote to ozone toxicity

It has been postulated (Margulis and Lovelock 1974) that the most serious threat to primitive life on Earth was the accumulation of oxygen (O_2) and ozone (O_3) in the atmosphere once primitive plants began to photosynthesize. While oxygen is essential to all aerobic life (continuing to be toxic to anaerobic forms), ozone remains noxious to both (Lefohn 1992; Runeckles and Chevone 1992; Sanders et al. 1992). Since, it has now been demonstrated that isoprene appears to be an effective counteractant to ozone injury (Paulson et al. 1992), could it not follow that a primary, if not the principal, function of this phytochemical today is that of overcoming or combatting the destruction of plant tissues by ozone? This line of reasoning is, of course, another argument that latex and isoprene are produced by plants as mechanisms for their defense, but from a distinct, and heretofore not well recognized source of injury.

Discussion

Role of latex of protection against insect predation

In his discussion of latex, Dussours (1990) may have been referring to such authors as Bonner and Galston (1947), or Polhamus (1962) among those who discounted the notion that latex is simply a defense against enemies. The first two authors wrote "the suggestion that latex might serve to protect the plant against attacks from herbivorous animals ... has been disproved by Tobler." To substantiate this statement, they include references to snails, camels, and insects which consume all or some parts of latex-bearing plants. According to Polhamus, termites, *Atta* (leaf cutting) ants, the giant snail (*Achatina fulica*), and two species of slugs (*Mariaella dussumieri* and *Paramarion martensi*) are attracted to the leaves, roots, and bark of *Hevea* trees to such an extent as to present serious plantation management problems.

In addition to these examples, it has been known for some time (LaFont 1909), that single-celled flagellates live in the laticifers of various species of plants. The use of latex by humans as a substitute for milk or cream is also well known (Allen 1956).

From a pathological standpoint, although there are instances where latex may provide antifungal action (Giordani et al. 1991), there appears to be scant evidence of any extensive inhibition of this nature. In contrast, for example, the number of micro-organisms which utilize *Hevea* as a principal resource base is considerable. These include *Mycrocellus ulei* which causes South American Leaf Blight; *Phytophthora palmivora,* responsible for black thread or black stripe, leaf fall, and die back; and *Ceratocystis fimbriata* which brings on moldy rot. To this list must be added a number of micro-organisms which cause a variety of root diseases (Cook 1981).

That latex serves a certain spectrum of plant species by inhibiting predation while at the same time acting as a resource base for other organisms does not imply that its major function is a specialized plant defense mechanism or one of providing sustenance for animals ranging from protozoa to man. This simply echoes the statement of the philosopher Lucretius (1st Century BC), "Quod ali cibus est aliis is fiat acre venenum" or whats food to one may be fierce poison to another. However, from an evolutionary standpoint, a defense mechanism is beneficial to the plant while providing sustenance to herbivores is not.

As stated above, the latex in a few, but certainly not all, plants does contain poisons. The most obvious case is that of the opium poppy, *Papaver somniferum,* the source of opium, heroin, and morphine. However, taking into account the enormous quantities of latex produced by substantial numbers of different plant species its insecticidal properties do not appear to serve as its major role in global ecology. Furthermore, despite conjectures (Fraenkel 1959) that secondary plant substances arose as a means of protecting plants from insects and now guide insects to food, there are no data to show that either latex or isoprene are attractants.

Role of isoprene and latex as a carbon sink

One of the first to seriously consider the role of isoprene in the atmosphere was Went (1955, 1960) who, during the 1950s and 1960s, sought to determine the cause of what he spoke of as a "blue haze" which emanates from forests such as those in the Blue Ridge mountains of Virginia. Since that time, a number of other investigators (Rasmussen and Khalil 1988; Monson and Fall 1989; Loreto and Sharkey 1990; Sharkey et al. 1991) have demonstrated that considerable amounts of isoprene are generated during the process of photosynthesis from the leaves of a variety of tree species. It is also known that isoprene is a natural by-product of animal physiology (Klein et al. 1989) and emitted in large quantities from many species, including humans. What is not well understood is the origin and function of this compound in either plants or animals.

What is known is that the quantity of carbon contained in a specific volume of isoprene is 5 times that found in either carbon dioxide or methane. In addition to the latex contained therein, it is estimated that approximately 1.0–2.0 Gt of isoprene are stored in thousands of latex-bearing plants found chiefly in tropical regions ranging from very humid to quite xerophytic conditions. This compares with the estimates of between 1.6 and 2.4 Gt of carbon (Dewar 1992) taken up annually by the lakes and oceans of the world. If an increase in atmospheric carbon brought about through additions of growing amounts of methane and carbon dioxide is of present concern (Hogan et al. 1991; Mooney et al. 1987), the carbon sink provided for by plant latex and isoprene is most significant in this balance.

Role in the storage of food and moisture

The idea that a role of latex is to furnish a storage facility for the nonfunctional by-products of cellular metabolism, which may then be reused in some form, has generally been rejected (Polhamus 1962; Rhoades 1979; Fahn 1982). Even in regards to the case of latex starch grains in *Euphorbia esula* L., Nissan and Foley (1986) concluded, after examining the grains during a lengthy light starvation period, that they did not function as utilizable carbohydrate.

Role of isoprene as antidote to ozone toxicity

It has been suggested (Lovelock 1987) that in the regulation of the Earth's atmosphere, methane, of which approximately 1000 megatons are emitted annually, may play a very critical role. The volume of isoprene which enters the atmosphere from all sources probably equals that of methane. Current confusion over, and ignorance of, the relative importance of the many atmospheric gases, may come from inattention to the length of their atmospheric residence. For example, owing to its saturated condition, methane is relatively stable and has an approximate lifetime of 10 years in the atmosphere while isoprene, with its two double bonds, lasts but a few hours before it combines with some other element, compound, or molecule.

In polluted air, often referred to as smog, where oxides of nitrogen (NOx) are present, the atmospheric decomposition of isoprene may produce more ozone than is used in its oxidation (Trainer et al. 1987; Chameides et al. 1988), which may lead to increased damage to vegetation (Sanders et al. 1992), as well as posing a serious health risk to humans. However, in unpolluted air, such as that over tropical forests, trees photosynthesize throughout the year and emit the greatest quantity of isoprene per unit of land area on the Earth's surface, the reverse occurs with a decreased scavenging of OH radicals (Harriss 1987), and greater quantities of ozone are consumed than produced. In this regard it is interesting to speculate as to why oaks, aspens, and other trees (Loreto and Sharkey 1990; Monson and Fall 1989) emit isoprene only during the day and when they are in leaf and thus capable of photosynthesis, while *Hevea*, which actively photosynthesizes throughout the entire year (except for a brief period following leaf fall before new leaves are formed), never emits isoprene in gaseous form (F. Loreto, personal communication) yet manufactures considerable amounts of this substance which it stores in the latex found within its laticifers and latex ducts. Why do no gymnosperms and so few monocotyledonous species contain latex while others [e.g. *Pinus* sp. and *Arundo donax* (Hewitt et al. 1990)] either produce terpenes or isoprene? Is it not possible then to argue that the both latex and isoprene serve as defense mechanisms of an atmospheric nature which could be recognized as being perhaps of greater value to the Earth's ecosystems than serving to deter herbivory?

Furthermore, the ability of insects to mutate (McGaughey and Whalon 1992) and thus overcome or even take advantage of many plant defense mechanisms, as in the case of the utilization of the milkweed's latex by the monarch butterfly (Brower et al. 1967), casts doubt on the theories that latex evolved solely for this end. This is probably a secondary, and constantly changing benefit to plants, in the struggle between herb and herbivore.

Production of latex as well as isoprene within a plant is regulated by plant growth hormones. In this connection, it has been reported (Purseglove 1968) that 2,4-D and 2,4,5-T applied in a palm oil carrier to the lightly scraped bark of Para rubber trees 2–3 inches below the tapping panel not only postpones the sealing of the cut ends of laticifers but increases and prolongs the flow of latex. Yields are thus augmented to such a degree that this scheme has become a standard field practice. The stimulants now being used are variations of ethylene which give yields of 100% over control (Anonymous 1986). It is interesting to note in this respect a release of ethylene by poplar clones following fumigation with ozone (Kargiolaki et al. 1991). Could this not imply that the trees produced ethylene to stimulate isoprene formation in order to combat the deleterious effects of ozone?

It has also been suggested (Osmond et al. 1992) that "in some species the production of large amounts of highly reduced secondary plant substances (terpenes etc) under stress conditions might also serve as a sink for photochemical energy under conditions of limiting CO_2." This implies that isoprene with a high demand for energy for its synthesis may be helpful in mitigating the potentially dangerous assimilatory power (ATP + reducing equivalents) under such conditions.

Conclusions

The current dilemma is that we do not now fully understand, or have we yet given sufficient attention to the function of latex. The principal and generally acknowledged fact concerning the truly abundant amounts of this compound is that its very existence in a large number of plants provides storage for a considerable number of chemical compounds, including vast quantities of isoprene. Why would a plant expend energy simply to produce an end product for which it had no further use?

By definition, isoprene is not a "greenhouse" gas. These are only those, such as methane and carbon dioxide, which are capable of absorbing infra-red rays which isoprene does not. However, once emitted, the effect of its combining rate with the principal greenhouse gases themselves, including ozone, methane, the hydroxyl radical, and the nitrate radical (NO_x), must now be taken into consideration. How can thousands of tons of a gas enter the atmosphere each year and simply disappear, unaccounted for, without leaving some mark? Another question to be answered relates to the vast amount of isoprene which remains tied up within plants, especially in the latex, as this probably greatly exceeds the quantity emitted from both plants and animals at any one time. Is this simply a matter of isoprene storage? If so, for what purpose?

Concurrently, it is important that animal physiologists strive for a more thorough understanding of the origins and pathways of isoprene in their subjects. If there is serious concern about the impact of such a relatively stable gas as methane in the overall greenhouse picture (Grubb et al. 1991; Hogan et al. 1991), isoprene should merit at least equal attention.

Finally, the U. S. National Academy of Sciences (Blakeslee 1990) recommended that the National Research Council undertake a 2 year feasibility study on the possibility of "pumping billions of pounds of carbon dioxide into microscopic plant life in Antarctic oceans as a means of storing large quantities (of carbon) in an inert form." Considering the funds required, doubling or tripling the acreage planted with the Para rubber tree throughout the tropics could achieve this same end result less expensively, much more efficiently, and with the added advantage of producing not only a product essential to modern-day society but an economic return on the investment as well.

Acknowledgements. I thank A. Alverson, R. Evert, H. H. Iltis, E. P. Imle, E. Loreto, J. E. Lovelock, H. Newcomb, F. E. Putz, T. D. Sharkey, E. Singsaas, D. Tennessen, A. M. Young and H. Ziegler for helpful suggestions and criticisms.

References

Allen PH (1956) The rainforests of Golfo Dulce. University of Florida Press, Gainesville, p 144

Anonymous (1986) From trees to telephones: a review of the 1985 annual report of the Rubber Research Institute of Malaysia. Rubber Dev 39: 110

Backer CA, Bakhuizen Van Der Brink RC Jr (1965) Flora of Java, vol 2. N. V. P. Noordoff, Groningen, p 124

Bailey LH, Bailey EZ (1976) Hortus Third. Macmillan, New York, p 14

Blakeslee S (1990) New York Times. 20 November, p B9

Bonner J, Galston AW (1947) The physiology and biochemistry of rubber formation in plants. Bot Rev XIII: 543–596

Brower LP, Brower JVZ, Corvino JN (1967) Plant poisons in a terrestrial food chain. Proc Natl Acad Sci USA 57: 892–898

Cailleux A, Cogny M, Allain P (1992) Blood isoprene concentrations in humans and in some animal species. Biochem Med 47: 157–160

Chameides WL, Lindsay RW, Richardson J, Kiang CS (1988) The role of biogenic hydrocarbon in urban photochemical smog: Atlanta as a case study. Science 241: 1473–1474

Chase MW, Soltis DE, Olmstead RG, Morgan D, Les DH, Mishler BD, Duvall MR, Price RA, Hills HG, Qiu YL, Kron KA, Rettig JH, Conti E, Palmer JD, Manhart JR, Sytsma KJ, Michaels HJ, Kress WJ, Karol KG, Clark WD, Hedren M, Gaut BS, Jansen RK, Kim KJ, Wimpee CF, Smith JF, Furnier GR, Strauss SH, Xiang QY, Plunkett GM, Soltis PS, Swensen S, Williams SE, Gadek PA, Quinn CJ, Eguiaret LE, Golenberg E, Learn GH Jr, Graham SW, Barrett SCH, Dayanandan S, Albert VA (1993) Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *reb*L[1]. Ann M Bot Gard 80: 526–580

Cook AA (1981) Diseases of tropical and subtropical field, fiber, and oil plants. Macmillan, New York, pp 253–273

Dewar RC (1992) Inverse modelling and the global carbon-cycle. Trends Ecol Evol 7: 105–107

Dussourd DE (1990) The vein drain: or, how insects outsmart plants. Nat Hist 99: 44–49

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. Evolution 18: 586–608

Esau K (1965) Plant anatomy, 2nd Edn. Wiley, New York

Fahn A (1982) Plant anatomy, 4th edn. Oxford, p 142

Farrell BD, Dussourd DE, Mitter C (1991) Escalation of plant defense: do latex and resin canals spur plant diversification? Am Nat 138: 881–900

Fisher HL (1956) Rubber. Sci Am 195: 74–98

Fraenkel G (1959) The raison d'être of secondary plant substances. Science 129: 1466–1470

Giessman TA, Crout DGH (1969) Organic chemistry of secondary plant metabolites. Freeman Cooper, San Francisco, p 234

Giordani R, Siepaio M, Moulintraffori J, Regli P (1991) Antifungal action of Carica-Papaya latex: isolation of fungal cell-wall hydrolyzing enzymes. Mycoses 34: 469–477

Greek BF (1991) Rubber demand is expected to grow after 1991. C & E News 69: 37–54

Grubb MJ, Victor DG, Hope CW (1991) Pragmatics in the greenhouse. Nature 354: 348–350

Harriss RC (1987) Influence of a tropical forest on air chemistry. In: Dickenson RE (ed) The geophysiology of Amazonian vegetation and climate interactions. Wiley, New York, pp 163–173

Hewitt CN, Monson RK, Falk R (1990) Isoprene emissions from the grass *Arundo donax* L. are not linked to phototranspiration. Plant Sci 66: 139–144

Hogan KB, Hoffman JS, Thompson AM (1991) Methane in the greenhouse agenda. Nature 354: 181–182

Kargiolaki H, Osborne OJ, Thompson FB (1991) Leaf abscission and stem leasions (influmescences) on popular clones after sulfur dioxide and ozone fumigation: a link with ethylene release? J Exp Bot 42: 1189–1198

Klein RC, Party E, Gershey EL (1989) Safety in the laboratory. Nature 341: 288

LaFont A (1909) Sur la présence d'un parasite de la classe des Flagellés dans le latex de *Euphorbia pilulifera*. Compt R Searces Soc Biol Paris. 66: 1011–1013

Lefohn AS (1992) Ozone standards and their relevance for protecting vegetation. In: Lefohn AS (ed) Surface level ozone exposures and their effects on vegetation. Lewis, Chelsea, Minnesota, pp 325–359

Lewinsohn TM (1991) The geographical distribution of plant latex. Chemoecology 2: 64–68

Loreto F, Sharkey TD (1990) Isoprene emissions and photosynthesis in *Quercus*. Planta 182: 523–531

Lovelock JE (1987) Gaia: a new look at life on earth. Oxford University Press, Oxford

Lucretius (1st Century BC) *De Rerum Natura* VI: 637

Mahlberg PG (1993) Laticifers: an historic perspective. Bot Rev 59: 1–23

Maksymowych R, Ledbetter MC (1987) Fine-structure of epithelial canal cells in petioles of *Xanthium pensylvanicum*. Am J Bot 74: 65–73

Margulis L, Lovelock JE (1974) Biological modification of the Earth's atmosphere. Icarus 21: 471

McGaughey WH, Whalon ME (1992) Managing insect resistance to *Bacillus thuringiensis* toxins. Science 258: 1451–1455

Metcalfe CR (1967) Distribution of latex in the plant kingdom. Econ Bot 21: 115–127

Monson RK, Fall R (1989) Isoprene emission from aspen leaves. The influence of environment and relation to photosynthesis and photorespiration. Plant Physiol 90: 267–274

Mooney HA, Vitousek PM, Matson PA (1987) Exchange of materials between terrestrial ecosystems and the atmosphere. Science 238: 926–932

New Encyclopaedia Britannica (1986) University of Chicago, Chicago

Nissan SJ, Foley ME (1986) No latex starch utilization in *Euphorbia esula*. Plant Physiol 81: 696–698

Osmond CB, Winter K, Ziegler H (1992) Functional significance of different pathways of CO_2 fixation in photosynthesis. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology. II. Water relations and carbon assimilation. Encyclopedia of plant physiology, vol 12B. Springer, Berlin Heidelberg New York, p 485

Paulson SE, Flagan RC, Seinfeld JH (1992) Atmospheric photooxidation of isoprene. II. The ozone-isoprene reaction. Int J Chem Kinet 24: 103–125

Polhamus LG (1962) Rubber: botany, production, and utilization. Interscience, New York, p 191

Post WM, Peng TH, Emanuel WR, King AW, Dale VH, DeAngelis DL (1990) The global carbon cycle. Am Sci 78: 310–326

Purseglove JW (1968) Tropical crops: dicotyledons. Wiley, New York, p 163

Rasmussen RA, Khalil MAK (1988) Isoprene over the Amazon basin. J Geophys Res 93: 1417–1421

Rhoades DH (1979) Evolution of plant chemical defense against herbivores. Academic Press, New York

Rosenthal GA, Janzen DH (1979) Herbivores: their interaction with secondary plant metabolites. Academic Press, New York

Runeckles VC, Chevone BI (1992) Crop responses to ozone. In: Lefohn AS (ed) Surface level ozone exposures and their effects on vegetation. Lewis, Chelsea, Minnesota, pp 189–270

Sanders GE, Volls JJ, Clark AG (1992) Physiological changes in *Phaseolus vulgaris* in response to long-term ozone exposure. Ann Bot (London) 69: 123–133

Schneider SH (1989) The greenhouse effect: science and policy. Science 243: 771–780

Sen DN, Chawan DD (1972) Leafless *Euphorbia* on Rajasthan (India) rocks. Vegetatio 24: 193–214

Sharkey TD, Holland EA, Mooney HA (1991) Trace gas emissions by plants. Academic Press, New York

Stahl E (1888) Pflanzen und Schnecken. Eine biologische Studie über die Schutzmittel der Pflanzen gegen Schneckenfraß. Jena Z Naturwiss 22: 557–681

Sundquist ET (1993) The global carbon dioxide balance. Science 259: 934–941

Trainer M, Williams EJ, Parrish DD, Buhr MP, Allwine EJ, Westberg HH, Fesenfeld FC, Liu SC (1987) Models and observations of the impact of natural hydrocarbons on rural ozone. Nature 329: 705–707

Webster CC, Baulkwill WJ (1989) Rubber. Longman, New York, p 84

Went F (1955) Air pollution. Sci Am 192: 62–72

Went F (1960) Blue haze in the atmosphere. Nature 187: 641