Responses of Plants to Viruses: Proposals for the Use of Terms

J. I. Cooper and A. T. Jones

Principal research scientists, Institute of Virology, Mansfield Road, Oxford 0X1 3SR, England; and Virology Section, Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, Scotland, respectively.
Accepted for publication 16 August 1982.

In his commentary on the International Meeting on Plant Virus Epidemiology held at Oxford, Thresh (5) drew attention to the communication difficulties attributable to inconsistent use of terms by virologists and plant breeders. This is a problem of long standing. In 1940, the preamble to a Report on Technical Words of the American Phytopathological Society (1) emphasized that "continued misuse of such words as *immunity, resistance, tolerance,* and *klendusity* (with *resistance* as a catch-all) tends definitely to confuse or mislead readers." Some of the confusion that exists is caused in part by the use of resistance terminology that was established in relation to diseases caused by extracellular pathogens. Although viruses share many of the features of other pathogens, they have some features that are unique. Further confusion arises from the different viewpoints often taken by virologists and plant breeders; whereas the latter are largely concerned with visible changes that are subjectively deemed harmful to individual plants or populations, virologists are usually more concerned with the viruses themselves and with events that occur in cells or tissues. In view of this confusion, the Virology Group Committee of the Federation of British Plant Pathologists (FBPP) asked us to define a short list of words to be discussed by participants at a meeting titled "Breeding for resistance to plant viruses" held at Cambridge 4–6 April 1979. We felt that some long-established words in the plant pathologist's vocabulary needed reappraisal, especially against a background of increasing knowledge and experience, and with the exception that knowledge of cellular events will increase. Accordingly, a brief list of terms and definitions was given in an issue of FBPP News, which appeared before the meeting in Cambridge. We now wish to bring our proposals, which have been modified in response to subsequent comment, to the attention of a wider readership.

RESPONSE OF PLANTS TO THE CHALLENGE OF INOCULATION WITH A VIRUS

When a plant is inoculated with a virus, there are two possible outcomes: either infection occurs or it does not (Fig. 1). Although it is known that nucleoprotein virus particles can enter cells in which they do not replicate, we restrict the term *infection* to the act of virus nucleic acid or nucleoprotein entry into cells in which the nucleic acid subsequently replicates. Many pathologists consider infection to be a continuing process, as it undoubtedly is when one extracellular (fungal) thallus is the agent that infects different cells in a tissue or organism. However, when considering viruses, the primary acts that result in the establishment of a parasite-host relationship with a cell may be different from the subsequent events that lead to *invasion* of other cells and which may or may not lead to visible disease symptoms. Operationally, the processes of *infection* and *invasion* are different (eg, [4]).

Immune and infectible. Following the usage recommended by the British Mycological Society (2), it seems appropriate to restrict the word *immune* to the description of an absolute state of exemption from infection with a specified agent. It is not adequate to equate immunity with freedom from disease. The state of immunity may be difficult to demonstrate experimentally and, in view of the need to minimize the possibility of chance escape from infection, it seems reasonable to use the term *immune* to denote plants in which virus cannot be detected after repeated challenge inoculations. When this challenge has been applied under conditions typical for the crop or natural plant community concerned, plants in which infections do not occur can be described as *field immune.*

Unfortunately, there is no unanimous view about the antonym of immune. *Susceptible* has been used in contrasting senses: as the opposite of immune, as a descriptor of the ease of infection in individual plants, as a descriptor of the prevalence of disease in a plant population, or as an indicator of disease severity in individual plants. Because of these difficulties and to unambiguously distinguish hosts from nonhosts, we suggest the term *infectible* as the antonym of immune. In 1940, the American Phytopathological Society (1) defined an infectible organism/plant as "possessing qualities permitting *invasion* by a pathogenic microorganism or virus"; we use it to describe an organism that can be infected by a given parasite (ie, a virus).

RESISTANT AND SUSCEPTIBLE; TOLERANT AND SENSITIVE

Much confusion has arisen over the indiscriminate and undefined use of the above terms. Many workers fail to distinguish between the behavior of a virus in a plant and the response of the plant to virus infection manifested by the appearance of disease symptoms. Thus, the British Mycological Society (2) describes a resistant organism as "possessing qualities that hinder the development of a given disease"; this is often the way breeders apply the term because they measure the resistance of an organism

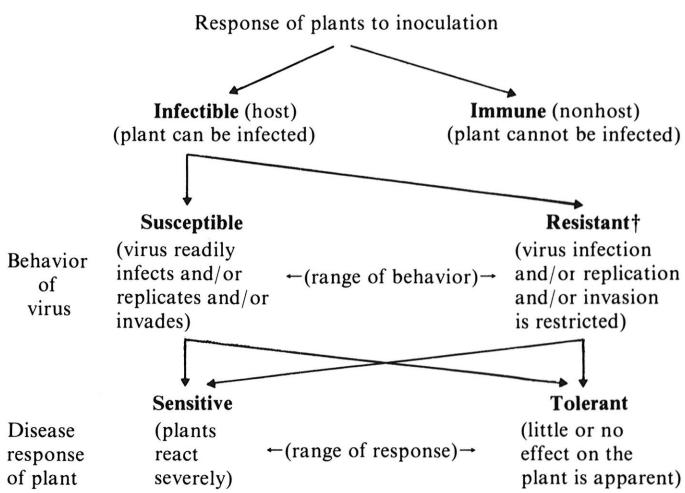

Fig. 1. Diagram to illustrate the distinction of proposed terms to be used for the different kinds of responses of plants to the challenge of virus inoculation and infection.
† Some types of resistance are resistance to virus adsorption, resistance to infection, restricted virus multiplication; and localization of infection.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

by the amount and severity of visible symptoms. Thus, susceptibility and resistance are considered as opposite ends of a seesaw; the more susceptible a plant is, the lower its resistance. However, the redefinition of resistance suggested by the Terminology Sub-committee of the Federation of British Plant Pathologists (3) substitutes the word "pathogen" for "disease." We believe it would be helpful to reserve the terms *resistant* and *susceptible* to denote the opposite ends of a scale covering the effects of an infectible individual on virus infection, multiplication, and invasion, and the terms *tolerant* and *sensitive* to denote the opposite ends of a scale covering the *disease reaction* of the plant to virus infection and establishment (Fig. 1).

Resistant and susceptible. Several distinguishable components of resistance have now been identified and it is appropriate, where possible, to qualify resistance in recognition of this knowledge. Thus, *passive resistance* to virus infection can occur if an infectible individual does not very readily become infected, but once infected, virus replication can occur. For example, the incompatibility of surface properties possessed by virus nucleoprotein for surfaces of potentially infectible cells may hinder infection—*resistance to adsorption or attachment.* Another, though less direct component of passive resistance, might be *resistance to a vector.* Once virus nucleic acid has entered a cell, the availability of enzymes facilitating translation/replication may impose constraints, either on the occurrence or rate of virus multiplication. Thus, resistance may have this additional component—*resistance to virus multiplication.* However, because the occurrence and activity of such enzymes are responsive to environmental conditions such as temperature, cells that are not infectible in some circumstances may be infectible in others.

When invasion of other plant cells occurs, plants may respond in a variety of ways that minimize the rate and extent of invasion. Thus, *hypersensitivity* is a type of severe pathological response that usually takes the form of localized necrosis; it is often, but not necessarily, associated with restricted virus invasion. Indeed, virus infection may be localized within a plant that does not develop necrosis and may show no overt symptoms. The presence of these and other components of resistance, either separately or in combination, may endow a population of infectible individuals with *field resistance* whereby the incidence of infection in the crop is minimized.

Tolerant and sensitive. Because many workers use resistance in an unqualified way, it is not surprising that tolerance has been considered by them as a type of resistance to virus. As indicated earlier, we feel that this attitude should be discouraged. In accord with the views expressed by the American Phytopathological Society (1), the British Mycological Society (2) and the Federation of British Plant Pathologists (3), it is important to recognize that *tolerance* is a subjective description of disease severity in an infectible individual that is assessed in two ways: the absence of symptoms or the occurrence of only mild symptoms, and little or no loss in vigor or yield. In these circumstances, *tolerant* is a term used to describe a HOST that a specific virus can infect and in which it can replicate and invade without causing severe symptoms or greatly diminishing the rate or amount of plant growth or marketable yield. VIRUSES that invade organisms without causing disease are described as *latent.* Tolerance is not necessarily, but in some instances is, correlated with virus concentration. The decrease in concentration may be caused by resistance to virus multiplication and/or invasion and, in such instances, plants are both resistant to virus and tolerant to disease.

It is equally possible for a plant to be resistant to virus but sensitive (for example, in an extreme form of hypersensitivity). Because the word intolerant implies a lack of sympathy with beliefs or concepts, we propose that the antonym of tolerant should be *sensitive.* Like tolerance, sensitivity is a subjective description of disease severity that will often be associated with conspicuous symptoms in an infectible organism and may indicate that infection with a specific virus diminishes the rate or amount of plant growth or marketable yield.

In distinguishing the behavior of viruses in plants from the extent and severity of disease that develops (Fig. 1), we are aware that viruses have some features not shared with other pathogens. We acknowledge that the meaning of a word is affected to some extent by the whole context in which it is used, and that the writer and the reader may have different conceptual backgrounds and prejudices. These proposals are offered with the aim of facilitating the exchange of information unambiguously between scientists, and we welcome comments and suggestions leading to future improvements in usage of terms in this area of science.

LITERATURE CITED

1. American Phytopathological Society. 1940. Report of the Committee on Technical Words. Phytopathology 30:361-368.
2. British Mycological Society. 1950. Definitions of some terms used in plant pathology. Trans. Mycol. Soc. 33:154-160.
3. Federation of British Plant Pathologists. 1973. A guide to the use of terms in plant pathology. Phytopathological Paper 17, Commonw. Mycol. Inst., Kew, Surrey, England.
4. Kuhn, C. W., Wyatt, S. D., and Brantley, B. B. 1981. Genetic control of symptoms, movement, and virus accumulation in cowpea plants infected with cowpea chlorotic mottle virus. Phytopathology 71:1310-1315.
5. Thresh, M. J. 1981. Plant virus disease epidemiology. Rev. Plant Pathol. 60:571-575.