2

DISEASE IN CONCEPT

Synopsis: Plant disease is defined in terms of symbiotic, ecologic, and environmental concepts. The scope of pathogen-suscept interactions in tree pathology is delineated. Fundamental terminology is introduced, and disease classification systems are summarized.

2.1 DISEASE DEFINED

Disease is an abnormality factor in populations of all living things. We have all experienced disease in one way or another, whether it be through the personal discomfort of the common cold or through the disappointment of gardens that do not yield. Disease is not always so obvious, however, and more often than not, its effect on living systems is very subtle. Thus, to cope with all the broad ramifications of distinguishing abnormality from normality in trees, disease must be clearly defined at the onset.

There are nearly as many definitions of plant disease as there are books on the subject. Most of the definitions are valid in their own way and in their own time. One of the earliest, that of Whetzel (1925), perhaps has weathered the passage of time better than others. He defined disease as "injurious physiological activity, caused by the continued irritation by a primary causal factor, exhibited through abnormal cellular activity, and expressed in characteristic pathological conditions called symptoms."

If we look at the key words and phrases in this definition, much in the manner of Horsfall and Dimond (1959), many of the common misconceptions about disease can be clarified. Some of these explanations follow.

1. Disease is injurious, but injury, in the sense of being instantaneous rather than a continuing irritation, is not disease. For example, a wound of any sort in a tree does not constitute disease; wounds are often associated with disease, however, because they provide a major means of access by which disease-causing agents gain entry to trees.

2. Disease is not the primary causal factor alone. Disease is the result of a dynamic interaction between the causal agent and the affected tree. Thus, it is not correct to say that the fungus *Cryphonectria parasitica* is chestnut blight but rather that *C. parasitica* is the cause of chestnut blight.

3. Disease is not solely the symptoms, or in medical parlance, the syndrome. Symptoms are the visible expressions or response of the affected tree to the actions of the causal agent.

4. Disease is not catching or contagious, in the sense that only the infectious cause of disease can be transmitted. Although not stated in the definition, Horsfall and Dimond (1959) give the correct version of this aspect of disease when they emphasize the common misconception. The purity of scientific expression, however, often yields to communicative conveniences. For example, the phrase "introduced disease" is commonly employed (Chapter 1) in the literature, even though precision would dictate that it is the infectious agent that is introduced.

Definition and critique are used here to introduce certain basic features of disease as a prelude to additional concepts that follow. No single definition is sacred; if a definition is good, it will promote understanding without memorization. Accordingly, we each have our own defined versions of disease, which the reader may adopt or reject on the strength of additional facts as they are presented. Plant disease is the detrimental interaction of a living plant with its environment. Disease is a sustained impairment in function, structure, or form of an organism as provoked by biological, chemical, or physical factors of the environment.

2.2 THE SYMBIOSIS CONCEPT OF DISEASE

The term *symbiosis* derives from the Greek *sym.* (with) and *bioun* (to live). Literally, symbiosis means the living together or intimate occupation of a single habitat by dissimilar organisms. Infectious disease (disease caused by living organisms) meets these specifications in the form of antagonistic symbiosis in which one symbiont, the parasite, benefits unilaterally at the expense of another, the host. Because the benefit to one and the loss to the other is primarily in nutrient or energy transfer, antagonistic symbiosis is perhaps better known as parasitism. Some endophytic fungi in leaves that survive surface sterilization may play a role in mediating insect attack. This example may be considered as a form of mutual symbiosis.

Disease, however, is not always the end result of parasitism. Figure 2.1 illustrates some of the varying degrees of parasitism. Certain symbioses involving a parasitic union have evolved a balance or mutualistic symbiosis whereby both symbionts directly benefit from the association. The host yields essential growth materials to the parasite, and the parasite reciprocates with off-setting physiological returns to the host. Disease is not expressed. Important and intriguing associations of this type are

1. the legume–bacterium (*Rhizobium* spp.) interaction, which balances host nourishment of the bacterium in root nodules in return for nitrogen via atmospheric fixation by the bacterium (Nutman 1965);
2. mycorrhizae (Chapter 13), which are formed by certain fungi in the parasitism of rootlets of higher plants, benefit the host in a number of ways, particularly through enhanced nutrient absorption (Marks and Kozlowski 1973); and
3. certain algae and higher fungi, which unite so perfectly that the resultant lichen thallus gives the appearance of a single taxon; through the mutual exchange of

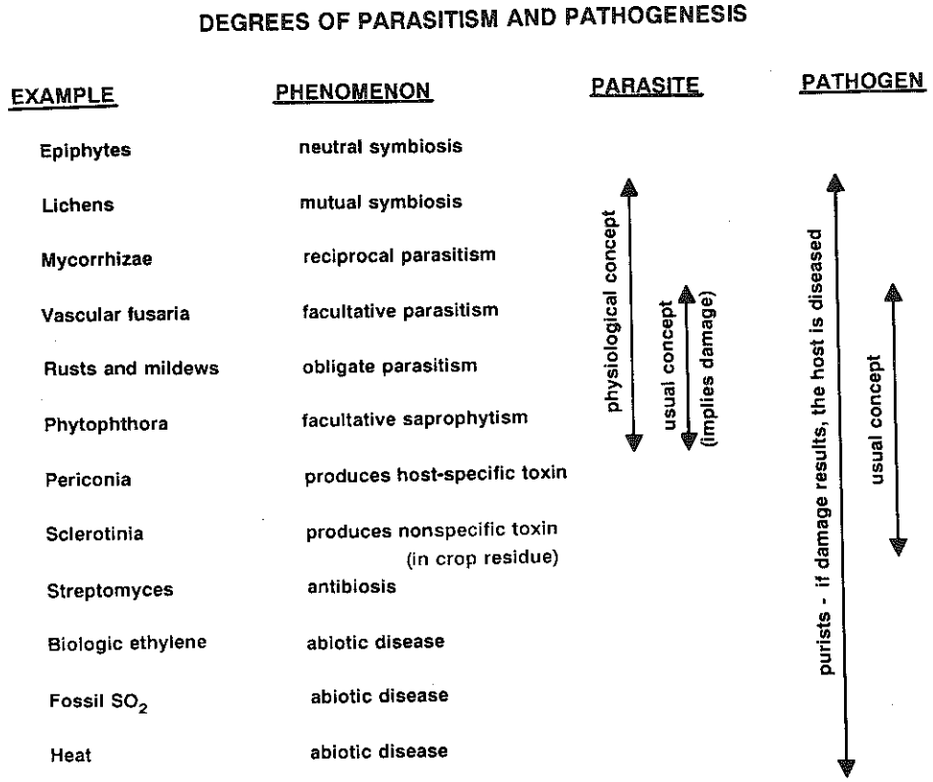

FIGURE 2.1 Degrees of parasitism and pathogenesis.

materials necessary to the nutrition of each, some combinations have even attained synergism whereby both symbionts grow better in the consortium than either does alone (Culberson 1970).

Finally, neutral symbiosis implies that the symbionts have no perceptible effect on each other. Neutral symbionts with trees are important here only from the standpoint that, unless carefully scrutinized, they sometimes produce an appearance that can be misinterpreted as disease. Certain epiphytes such as Spanish moss on the branches of live oak (Fowells 1965) and surface growths of fungi such as *Septobasidium* spp. on tree bark (Couch 1938) are strictly superficial in their growth habit. The latter example is of additional interest in that it also involves a symbiosis with insects.

Organisms growing in close proximity but not in symbiotic contact may exert ecological influences upon the course of disease by way of antibiosis, metabiosis, and synergism, as described in some detail by Stakman and Harrar (1957). Antibiosis between organisms involves the metabolic products (antibiotics) of one having inhibitory or toxic effects upon another. Antibiotic influences upon disease-causing organisms are implied primarily in relation to root diseases (Chapter 12) because *in vitro* antibiosis is so easily demonstrated with almost any sample of soil-microbial popula-

tions. There is evidence (Leben 1965), however, that antibiosis could likewise prevail between the established epiphytic microflora of aerial plant parts and disease-causing agents, if and when they are deposited. Gibbs (1980) showed that if *Ceratocystis piceae* were introduced to a fresh wound on healthy oak prior to its inoculation with *C. fagacearum,* no infection would result. *C. piceae* is very common in oak-wilt trees (Shigo 1958). Could the action of *C. piceae,* then, be considered as an example of antibiosis? In opposite function to the biological system that might serve to block disease development, as just described, metabiosis introduces the possibility that one kind of organism may create an environment that is favorable to another. Drawing just one example, such successions leading to the discoloration and decay of wood in living trees have been demonstrated and reviewed by Shigo (1967). Ecological synergism, as involved in disease causation, means that two, or possibly more, different disease agents produce greater effects conjointly than can one separately. Examples of pathological synergism discussed later include black root decay of tree seedlings (fungus + fungus) (Hodges 1963) and mimosa wilt (nematode + fungus) (Gill 1958).

2.3 THE DISEASE SQUARE

To this point, new terminology has been minimized as much as possible. Because the disease square concept is presented as a unifying view of disease, it is the most appropriate vehicle for introducing and emphasizing the basic vocabulary of plant pathology.

Disease Components

Our concept of disease would not be complete without stressing the constant regulatory role of the environment upon the disease agent (pathogen), the plant (suscept), and their interaction (disease), should it occur. Disease then is really a quadripartite entity; the so-called disease square is illustrated in Figure 2.2. Note, in particular, that abiotic, or physical, factors of the environment are not only conditioners of disease but also primary causes of disease when conditions such as nutrition, temperature, moisture, and air pollutants are deficient or excessive. These diseases caused by abiotic factors are the noninfectious diseases, sensu Smith (1970). The biotic environment includes competitors for a substrate as a multitude of antagonistic interactions.

The terminology of the disease square's components requires definition and clarification. Pathogen, as originally employed (Whetzel 1926), meant any organism capable of inducing disease. Contemporary use of the term (Agrios 1969, Strobel and Mathre 1970), however, has broadened its meaning to an entity or anything that can produce disease. Thus, as used hereafter, pathogen carries the same connotation as causal agent (i.e., any biological, chemical, or physical factor of the environment that is capable of causing disease). The term *suscept* was coined by Whetzel (1926) in an effort to avoid the pitfalls of equating pathogen with parasite–host in relation to disease. The parasite–host combination, by definition, denotes a nutritional relationship that may or may not produce disease as governed by the nature of the symbiosis. Therefore, if we define suscept as any plant that can be or is attacked by a given pathogen, a terminology that accommodates all types of disease is available and war-

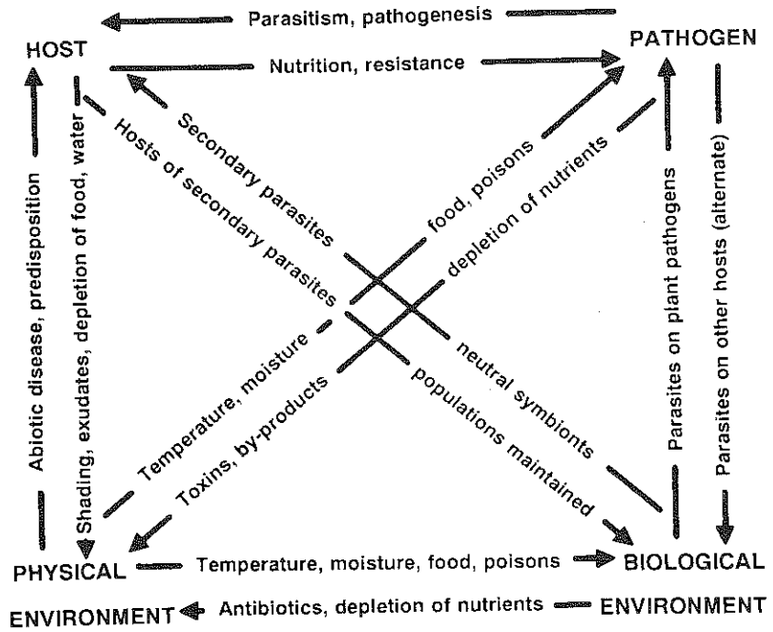

FIGURE 2.2 The disease square, showing the principal possible interactions of the four groups of variables that contribute to the occurrence and intensity of plant disease. This is a qualitative diagram; it does not include any quantitative information such as amount of inoculum, temperature, and moisture.

ranted. The use of the terms *parasite* and *host* is entirely appropriate when parasitism is involved because the majority of plant and tree diseases are caused by parasitic organisms. Be aware, however, that not all parasites are pathogens and vice versa; and that not all hosts are suscepts and vice versa; therefore, choose the proper terms accordingly.

Another version of disease (Walker 1957) would have *incitant* serve as a singular term for pathogen and environment in the sense that an organism incites or causes a disease under the influence of other factors. In our opinion, *incite* and *incitant* tend to project a more restricted view of disease, when, in fact, the basic components of the disease square are often a complex of multiple interactions. The environment in particular is a composite of factors that may differentially influence the suscept, the pathogen, and the suscept–pathogen interaction.

Therefore, disease is a coalition of suscept, pathogen, and physical and biological environments relative to space and time. In a single suscept, the ultimate severity of disease is primarily a function of its inherent susceptibility in relation to the aggressiveness of the pathogen and the modifying effects of the prevailing environment. The real impact of a forest disease, however, is measured in terms of its epidemiology (its generative capacity within a population of suscepts).

A closer look at each component of disease will permit a brief preview of pertinent functions, additional terminology, and scope of the subject matter.

2.4 THE DISEASED TREE—THE SUSCEPT

2.4.1 Suscept Lists

Some 845 species of native trees exist in the United States including Alaska but not Hawaii; 165 are listed as commercially important in forestry (Little 1949). Many of these are also indigenous Canadian trees. Grouped taxonomically and geographically, the American species number 58 conifers or softwoods (23 in the east and 35 in the west) and 107 broadleaf trees or hardwoods, of which 86, the greatest majority, are found in the east. Fowells (1965) documented the silvicultural characteristics of 122 species, furnishing habitat and life history data of considerable value in judging normality of growth relative to the effects of disease. A diagnostic index to the diseases of 214 species of trees and ornamental shrubs by Hepting (1971) provides another primary and comprehensive source of information. This descriptive sourcebook is complemented by a host index (Anonymous 1960), which lists known pathogens and other organisms circumstantially associated with disease on each and all plants in taxonomic order. In combination, these indices of tree and disease information essentially delineate the spectrum of suscepts most likely to be encountered in forest practice.

2.4.2 Vital Functions

Because symptoms are the ultimate indicators of abnormality in the suscept, comparison with a like but disease-free tree should reveal the internal attributes of the disorder. Consequently, a diagnostician relies heavily upon a basic knowledge of normal tree anatomy and physiology in order to interpret pathological alteration of tissue and function. For now, this complex of cells which compose the roots, stem, and crown of a living tree can be reduced to two basic factors to affect two critical determinants of infection by a given pathogen—its access and nutrition. Once the pathogen has gained entrance and begun to derive sustenance, host physiology is altered in various ways in response to specific pathogens.

At least six vital processes can be affected according to McNew's (1959) scheme of classifying associated symptom and pathogen types. The effects of disease on these critical physiological functions are illustrated in Figure 2.3 and listed as follows:

1. food storage in the form of seed, root, stem, and bud reserves;
2. juvenile growth as either seedling or shoot development;
3. root extension in the procurement of water and included minerals;
4. water transport;
5. food manufacture or photosynthesis;
6. translocation of photosynthate to sites of cell utilization; and
7. structural integrity.

The last function is not a physiological process, but it is exceedingly important in trees because many are weakened to the point of stem and root breakage from internal decay of physiologically inactive heartwood. If any of the first six functions is completely disrupted, the tree dies. Ordinarily, the function is impaired but not destroyed, so that only the efficiency and yield of the tree are reduced. On a tree population or

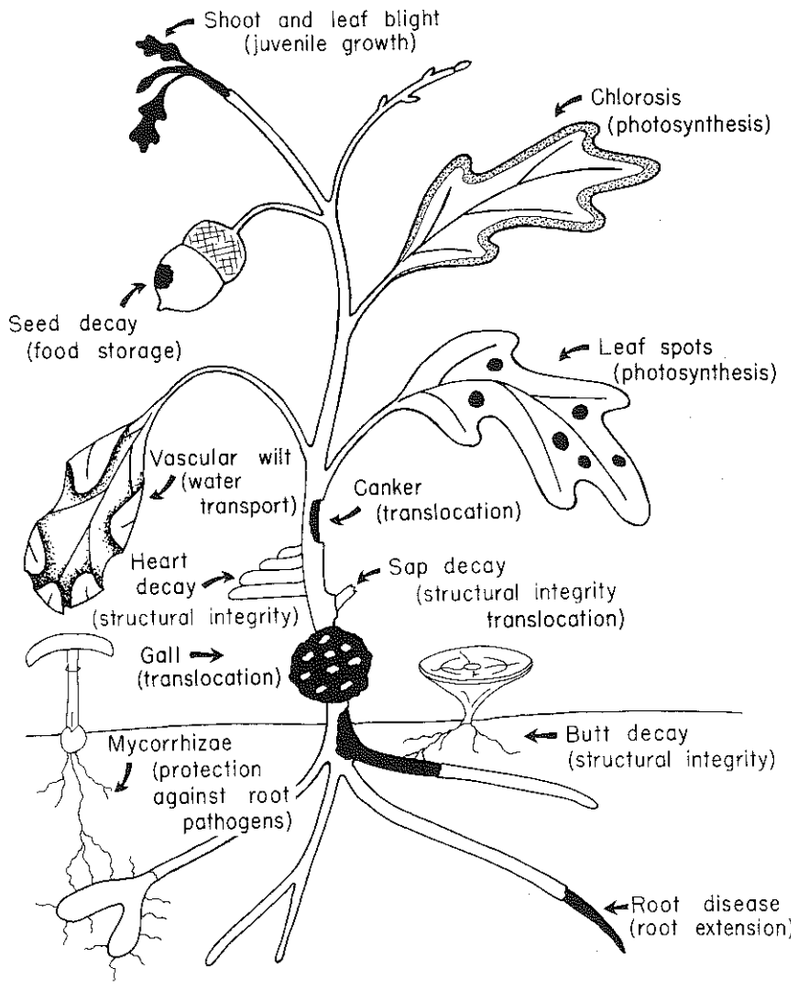

FIGURE 2.3 Schematic representation of the effects of diseases on tree health, showing the vital functions of a tree and their impairment by various types of pathogenic influences.

forest basis, however, growth retardation from disease can be highly significant in limiting the productivity potential of a given forest site.

2.4.3 Symptomatology

With the exception of immunity, all other suscept responses are ultimately expressed as microscopic and macroscopic symptoms. Naturally, susceptible responses exhibit a more pronounced symptomatology than do tolerant and resistant reactions. The suscept may and generally does display more than one symptom, so that a progression of symptoms (the symptom complex) usually characterizes a given disease. Identification or diagnosis of disease is based, in part, on visible alterations in plant morphology, the macroscopic symptoms. Some 40 or more specific symptoms (Table 2.1)

TABLE 2.1 Causes of Plant Disease Symptoms

Necrosis—Death of Cells or Tissues

Cankers—death of cambium
- typical target
- diffuse
- with ooze
- cold or heat, mechanical

Leaf spots—death of a few or many leaf cells
- angular or circular—on deciduous hardwoods
- spot bordered by yellow or brown bar—on conifers
- air pollution, toxic chemicals, temperature extremes

Decay—death of parenchyma cells in wood of roots and stems of living trees
- sap, white, and brown decays

Vascular wilts—death of parenchyma cells in wood of roots and stems of living trees
- sap, white, and brown decays

Blight, or dieback—sudden dying of all or part of tree-due to vascular wilt, sudden temperature change, air pollution, or drought

Hypertrophy—Overgrowth of Tissues

Witches' brooms—proliferation of adventitious buds—dwarf mistletoe
- "Cronartium" bushes—fusiform rust/broom rusts
- genetic abnormality
- mycoplasmas
- some insects, mites and aphids

Leaf blister—localized enlargements causing puckering

Galls—on leaves, stems or roots—due to insects, nematodes, or associated with some cankers and rusts

Atrophy—Failure of Development or Growth of Plant or Some Organs

General, marginal, or interveinal chlorosis—due to absence of chlorophyll
- caused by pathogens, toxins, mineral deficiency, air pollution, drought, excess water, or chemical burns

Dwarfing—due to root disease, mineral deficiency, or mycoplasmas

are classified under three major types of tissue alterations, namely necrosis (death), hypertrophy (overdevelopment), and atrophy (underdevelopment). Symptoms are also indicative of the extent of suscept involvement in that some are consistently localized while others are systemic or expressed by the entire tree. For example, stem cankers (Chapter 16) and leaf spots (Chapter 14, and Boyce 1961, pp. 129–134) are localized necroses of respective tree parts while systemic wilts (Chapter 17) are symptomatic of a malfunction of the water-conducting system of a tree. Multiple local symptoms can coalesce, however, to give the illusion of systemic action by the pathogen. For example, a canker or coalescent cankers may completely girdle a stem causing death of stem, branches, and foliage beyond that point. In this and other like instances, the canker is a primary symptom associated with the direct influence of the pathogen while the distal necroses that follow are secondary symptoms, those arising indirectly and apart from the locus of the pathogen. Yellows, or chlorosis, is a very common symptom of plant disease used to describe any physiological disturbance or

disease that results in the destruction or reduced synthesis of chlorophyll. Factors that can cause chlorosis include saline or alkaline soils, deficiencies or excesses of essential mineral elements, toxic concentrations of pesticides, reduction in number of mycorrhizal feeder roots, parasitic flowering plants, excessive or insufficient soil water, high or low soil and air temperatures, feeding by mites or insects, viruses and mycoplasmas, and parasitic fungi, bacteria, and nematodes. The very excellent book by Sinclair et al. (1987) contains many detailed color photographs of signs and symptoms of most North American tree diseases of importance.

2.4.4 Susceptibility

Suscepts that are amenable to the full potential of a pathogen are considered susceptible, or fully liable, to infection. Susceptibility is an absolute condition, just as immunity, the antonym of susceptibility, implies total exclusion from a given pathogen. Suscept responses intermediate to these extremes are qualified by the terms *tolerance* and *resistance*. Tolerance is the ability of a suscept to sustain a pathogen without suffering serious injury or reduction in yield, whereas resistance is the inherent capacity of a suscept to prevent or restrict the entry or subsequent activities of a pathogen under environmental conditions that favor disease development.

2.5 THE PATHOGEN

2.5.1 Types and Diversity

Tree pathogens show the same diversity that characterizes plant pathogens in general. Although *pathogen* is an inclusive term, a natural division requires that we distinguish between animate and inanimate agents of disease. Thus, we qualify pathogens accordingly or use the synonyms biotic and abiotic.

2.5.2 Biotic Pathogens

The living agents of disease encompass the fungi, bacteria, mycoplasmalike organisms, viruses, parasitic flowering plants, nematodes, and even some insects. They are all capable of infection, meaning that they can become established as parasites within a given suscept. The infectious nature of these kinds of pathogens is especially critical because they can spread from diseased to healthy trees by means of dispersal in growth or reproduction. These vegetative and reproductive structures of pathogens (the signs), in association with symptoms, characterize a given disease and facilitate its identification or diagnosis. However, noninfectious diseases, which are caused by abiotic agents, differ notably in lacking signs and, for that reason, are sometimes more difficult to diagnose.

Chemicals in disease causation may derive from either biotic or abiotic origin. Biochemicals, such as toxins, enzymes, and growth regulators, are, respectively, the mechanisms by which pathogens, especially fungi, kill cells of, obtain nourishment from, and modify tissues of the suscept. Some species of trees, such as black walnut and cherrybark oak, must even be regarded as pathogens on the basis that they release phytotoxins (allelopathy) into their local environment (DeBell 1970, 1971).

2.5.3 Substrate Classification of Biotic Pathogens

What follows now is only a brief characterization of each kind of biotic pathogen; they are covered in more detail in Chapter 4.

The fungi (Eumycetes) and bacteria (Schizomycetes) are lower, achlorophyllous plants, which reproduce by spores and simple cell division, respectively.

Mycoplasmas, discovered only recently in 1967 (Doi et al. 1967), are the smallest of living organisms, which apparently bridge the taxonomic gap between bacteria and viruses. The few mycoplasmas identified to date were previously regarded as viruses associated with phloem disorders in yellows-type diseases (Davis and Whitcomb 1971).

Viruses are included in the biotic group despite the fact that they do not possess all attributes of life; nevertheless, in common with the other kinds of biotic agents of disease, they reproduce their own kind and hence are transmissible from tree to tree. Viruses are submicroscopic particles composed of protein and nucleic acid. They reproduce only in living cells of animal vectors and suscepts and at the expense of the latter in eliciting disease by diversion of protein synthesis.

The parasitic flowering plants include the mistletoes (Loranthaceae), dodders (Convolvulaceae), broomrapes (Orobanchaceae), and figworts (Scrophulariaceae). In common, these plants establish rootlike haustorial connections with the vascular elements of suscept stems or roots in the withdrawal of water and nutrients.

Nematodes (Nematoda), or eelworms, are the only members of the animal kingdom that have received major attention as recognized plant pathogens. The plant parasitic types are small, wormlike creatures that feed primarily on plant roots by puncturing them with a hollow, retractable stylet.

2.5.4 Abiotic Pathogens

Noninfectious disease agents or abiotic pathogens are physical and chemical factors of the environment that are unfavorable for normal growth and development of a given suscept at extremes of deficiency or excess. In addition, trees in a stressed or weakened condition from abiotic causes are often more susceptible to biotic pathogens. Abiotic factors function concurrently as agents of predisposition.

The physical extremes of particular note are temperature and moisture. We will find, for example, that a prolonged moisture deficit is largely responsible for dieback and decline epiphytotics of a number of forest tree species (Chapter 3). Chemical effects from abiotic sources range from extremes in mineral nutrition of trees to direct toxicity in the form of air pollution impacts.

2.6 NUMERICAL SPECTRUM OF BIOTIC PATHOGENS

In documenting the fact that parasitism of plants is a common phenomenon, Agrios (1969) estimates that, in North America alone, some 8,000 species of fungi cause approximately 80,000 diseases; in addition, at least 180 species of bacteria, more than 500 different viruses, and over 500 species of nematodes also attack crops. No enumeration has been made for the tree component of this crop total; however, refer-

ence to the current and most comprehensive lists should provide a reasonable numerical estimate of pathogen affinities for native trees.

The fungi are by far the largest group as evidenced by the approximately 1,300 species indexed by Hepting (1971) in this disease compendium of 214 species of woody plants. In comparison, and from the same source, only 21 species of bacteria are listed.

To date, only one mycoplasma seems to be a definite cause of disease; elm yellows, formerly attributed to a virus, recently has been reassessed and reclassified (Wilson et al. 1972). Even at that, there are only 19 different viruses recorded from just nine species of native trees, all hardwoods (Thornberry 1966), and none is considered potent as a forest pathogen. They do, however, represent a considerable potential threat for vegetatively propagated trees. On a worldwide scale, conifers essentially appear immune to viruses. Only one disease, a virosis of spruce, in Czechoslovakia, has been substantiated to date (Cech et al. 1961); however, virus infection of red spruce has recently been reported (Jacobi and Castello 1991).

Nematode associations with forest trees, as compiled by Ruehle (1967), reveal that 94 plant-parasitic species have been found in the root zones of 73 species of timber trees in the United States. Only 30 of these tree species, however, are known to suffer appreciable root damage as caused primarily by species of *Meloidogyne, Pratylenchus,* and *Xiphinema,* the root knot, lesion, and dagger nematodes, respectively.

Of the more than 2,500 species of parasitic flowering plants estimated by Agrios (1969) and reviewed by Kuijt (1969), only the dwarf mistletoes (*Arceuthobium* spp.) are of major concern in forestry. Hawksworth and Wiens (1972) recognized 17 taxa of dwarf mistletoes in the United States, which collectively are principal pathogens of 30 species of conifers, primarily of the western forest types. Other kinds of tree pathogens in the category of parasitic flowering plants, such as dodder in forest nurseries (Latham et al. 1938), true mistletoes on ornamental trees, and, more recently, *Senna seymeria* on planted southern pines (Grelen and Mann 1973), are noteworthy because they may occasionally cause severe damage on a local scale.

Thus, the array of potential tree pathogens, both biotic and abiotic, is rather impressive in scope and may seem quite overwhelming at the moment. Fortunately, the establishment of principles (Part One) permits a systematic cataloging of facts that should dispel such concerns as we prepare the foundation for studying specific diseases in Part Two.

2.7 PARASITISM AND PATHOGENICITY

Because *parasitism* and *pathogenicity* are not necessarily synonymous, a scheme of classifying pathogens based upon substrate and nutritional relationships is appropriate by way of explanation. Like all living things, biotic agents of disease are differentiated nutritionally as either autotrophs or heterotrophs. Autotrophic, or independent, organisms synthesize food from inorganic sources, while heterotrophic, or dependent, organisms require organic materials for nutrient elaboration.

Because the majority of recognized plant pathogens, exclusive of viruses, nematodes, and abiotic factors, are members of the plant kingdom, the distinction between autophytes and heterophytes, respectively, is that of chlorophyllous and achlorophyllous, or higher flowering plants and lower plants, or phanerogams and cryptogams

from older botanical classification. Except for the major group of parasitic flowering plants (Chapter 4), of which the dwarf mistletoes (Chapter 19) are the most important, additional autotrophic pathogens are relatively few in number, and, unlike the mistletoes and their kind, they typify pathogenicity without parasitism. This is evidenced by the allelopathy example (DeBell 1970, 1971) given previously and by the strangulation and shading effects of lianas or climbing vines such as poison oak, honeysuckle, and kudzu.

Heterophytic organisms, which are incapable of synthesizing carbohydrates out of carbon dioxide and water, are linked nutritionally to suscepts either as saprophytes on dead tissue, as parasites in living tissue, or most commonly as both in the course of their life cycles. When a heterophyte can function as both, its parasitic and saprophytic phases are qualified further by the modifying term *facultative,* meaning occasional. Hence, a facultative saprophyte is an organism that usually exists as a parasite but, on occasion, can live or survive as a saprophyte, whereas a facultative parasite usually functions as a saprophyte but, on occasion, can derive its nutrition from living tissue as a parasite. Some heterophytes are restricted to one life system or the other and therefore are identified by the adjective *obligate*. Hence an obligate saprophyte or saprobe exists solely on dead organic matter, while an obligate parasite is strictly dependent upon living tissue of the suscept for sustenance and survival. Although this terminology is most frequently applied to the fungi because of their preponderance in disease causation, other agents of disease are typically, and without exception, obligate parasites, namely, parasitic flowering plants, mycoplasmas, and viruses.

Obviously, pathogen does not always equate as parasite and vice versa. Notable examples of parasites that are not pathogens, as mentioned previously, are the legume nodule bacteria and the mycorrhizal fungi. Pathogens that are not parasites include epiphytes, as previously cited; sooty mold fungi, of questionable pathogenicity; heartwood decay fungi in living trees; and, quite definitely, abiotic causal agents.

Further elaboration of two of the examples of pathogens that are not parasites may clarify these rather perplexing disease relationships. Sooty mold is a sign that is not accompanied by visible symptoms. It is composed of any one or more of a number of species of obligately saprobic fungi that grow superficially and dependently on the sugary secretions or "honey dew" of aphids, which feed on the foliage of many tree species. The growth has the appearance of soot. When it occurs on Christmas tree crops in particular, its unsightliness causes considerable alarm. In fact, uninformed growers have destroyed whole blocks of affected trees thinking they were severely diseased and beyond recovery. Actually, such trees are merchantable because the fungus growth or sooty mold will dissipate with rain wash, or it can be removed from cut trees by spraying them with a directed stream of water. The question remains, is sooty mold a disease? Although most references to the subject, as cited in Hepting (1971), allude negatively to the question, there is the distinct possibility that the mass and opacity of the fungus may, by shielding, reduce the photosynthesis of affected leaves. In addition, the fungus growth may plug stomates and thus affect gas and water exchange. Therefore, it seems quite plausible that sooty mold is a disease, even though tree symptomatology may be evidenced only in slightly reduced growth.

The second example, heartwood decay fungi in living trees, accounts for 73% of the total disease loss in American forests (Hepting and Jemison 1958). Wood decay fungi, which number in the hundreds of species, run the gamut between parasitic and saprophytic types in living trees, dead trees and their debris, and wood in use. Heart

decay, because it involves the central cylinder of physiologically dead wood in living trees, is a saprophytic activity if we consider only the site of action; it could be regarded as parasitism if we take the viewpoint of whole tree involvement. However, the latter interpretation fails to recognize that parasitism is really the yield of nutrients from living host cells and tissues to the demands of a parasite. Consequently, heart-decaying fungi are not parasites, but are they pathogens? They are not, at least according to most definitions of disease, including that of Whetzel (1925) used at the beginning of this chapter. With heart decay, there is no injurious physiological activity or continued irritation; there is only the activity of the fungus in its breakdown of inert, nonreactive heartwood. Yet, even with this in mind, it seems inconceivable that we would not consider heart decay as a disease when it ranks as an important agent of forest degradation. In our opinion, disease alters more than function in the suscept; it also alters structure and form, as defined earlier. By this concept, then, heart decay qualifies as a disease.

In concluding this section, only those attributes of pathogens pertinent to the conception of disease have been employed. Other characteristics, such as variability and infection biology, are more appropriate to later elucidation of specific pathogen types.

2.8 THE ENVIRONMENT

Environmental components of the disease square, in the broadest sense, include all biotic, physical, and chemical factors that influence the pathogen–suscept interaction, which by themselves are part of and influenced by their habitat, be it primarily edaphic, atmospheric, or both. Having already addressed the biotic and chemical factors of the environment, we will examine briefly the physical aspects of the atmospheric environment as viewed on three scales—climate, weather, and microclimate.

Weather and climate affect the biotic components of disease through the individual or interacting effects of precipitation, temperature, humidity, fog and dew, wind, and radiation, differing primarily in the time span of influence (Pirone 1959). In this regard, Hepting (1963) points out that annual crops reflect weather changes, whereas trees and other perennial flora will reflect, in addition, climate changes. The latter, as reviewed by Hepting (1963), is especially accountable for a number of regionally important diebacks and declines of forest trees in the United States during the 1930s through the 1950s.

Neither weather nor climate are static, but weather, being more changeable with the seasons, is a more localized determinant of whether a pathogen–suscept combination will develop into disease. Some of the more devastating crop diseases are conspicuously associated with periods of aberrant weather. Normally, disease is such a synchronization of so many biological factors subject to weather regulation that the probability of infection is relatively low. For example, weather influences a pathogen at its source, in terms of its reproduction and liberation, and in reaching the suscept, in terms of transport, deposition, and infection. If any one of several weather factors is unfavorable to the pathogen at any one of these stages in its transmission from source to suscept, disease does not occur. Waggoner (1962) expressed this observation in a different yet interesting way—"A severe outbreak is a rare removal by the weather of obstacles that ordinarily restrain the pathogen."

TABLE 2.2 Plant Disease Classification Systems with Examples and References to Each

Classification Type and Examples	Context	
	Major Emphasis	Chapter Topic
1. Crop Divisions Seedlings, saplings Forest trees	Baxter (1952), Boyce (1961), Smith (1970)	Baxter (1952)
2. Specific Suscepts Oaks, pines, etc.	Hepting (1971)	Pirone (1959)
3. Suscept Culture and Use Nurseries, plantations Shade trees Wood products	Baxter (1952, 1967), Cartwright and Findlay (1950)	Baxter (1952), Boyce (1961)
4. Suscept Age Class Seedlings, saplings	Baxter (1952)	Boyce (1961)
5. Suscept Part Affected Roots, stem, foliage	Boyce (1961)	
6. Symptom Types Decays, cankers, wilts	Boyce (1961)	
7. Suscept Function Affected Photosynthesis, etc.	Horsfall and Dimond (1959)	Agrios (1969)
8. Regional Suscepts Native Exotic	Matuszewski (1973), Spaulding (1958)	Boyce (1961)
9. Pathogen Types Fungi, bacteria, etc.	Agrios (1969), Smith (1970), Strobel and Mathre (1970), Walker (1957)	

Another effect of weather is on the suscept itself. Favorable weather may produce increased growth rates for a time, but, when unfavorable weather is once again prevalent, dieback of roots and reduced photosynthesis may open a "window of susceptibility" to a given pest. Changing weather may also affect the subsequent development of the pathogen in the new host, thus altering the disease. Major environmental stresses, of which changing weather may be one component, may induce "cohort senescence," a concept developed during the study of dieback and decline of ohia forests in Hawaii (Mueller-Dumbois et al. 1983). A group of trees on a poor-quality site and exposed to frequent or prolonged stress may become senescent at an earlier age than the same tree on a good-quality site. This is discussed in more detail in Chapter 18.

The study of microclimate in relation to disease focuses attention upon the environment immediately surrounding the plant and draws upon the biological and physical sciences in the biometeorological measurement and interpretation of physical parameters that govern plant infection processes (Brooks 1963, Lowry 1963, Platt 1963). By means of sophisticated instrumentation and methodology, the importance

of applying micrometeorological precision to the evaluation of plant disease epidemiology has been convincingly demonstrated (Van Arsdel 1965). Correlation of these kinds of data with synoptic weather patterns has permitted sufficient accuracy to recommend the use of synoptic weather charts in appraising at least one tree disease hazard, the important fusiform rust of the Gulf Coast area (Davis and Snow 1968).

The edaphic environment of pathogen and suscept is sufficiently complex and so oriented to root diseases that the topic is deferred to Chapters 10, 11, and 13, where fundamentals of root pathology will be developed.

2.9 CLASSIFICATION OF PLANT AND TREE DISEASES

As a final consideration in this chapter, we call attention to the various ways of classifying plant diseases. The orderly indexing of causes, suscepts and parts affected, symptoms, and the like is essential to the communication and retrieval of information pertinent to the diagnosis and control of disease. Most plant pathology texts use more than one type of classification, as shown by the cross references in Table 2.2.

Part Two of this text, which deals with the biology of specific forest diseases, is organized according to tree parts affected and their symptoms.

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