8   The Role of Parasites in Plant Populations and Communities

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8.1   Introduction

All parasites have the potential to induce marked changes in the dynamics of host populations through the action of the generalized selective forces of increased mortality, reduced fecundity and lowered competitive ability. Agricultural experience has underlined the debilitating effects that parasitic plants, nematodes, fungi, bacteria and viruses may have on host plants, but this provides little guide to their importance in the far more diverse and unpredictable world of natural ecosystems.

There is already a substantial body of data showing the importance of herbivory in shaping the size and structure of individual plant populations (Crawley 1989) and communities (Tansley and Adamson 1924; Jones 1933; Brown 1982, 1990). Are plant parasites similarly important components regulating the basic fabric of plant communities or are they simply irrelevant embellishments on the rich tapestry of nature? In contrast to the relatively broad feeding preferences of many mammalian grazers, does the exclusive nature of many plant-parasite interactions reduce the likelihood of any more than individual population effects? Or, alternatively, is the relative lack of recognition of the community importance of plant parasites simply a reflection of their subtle expression, as greater sophistication and patience are needed on the behalf of the observer to identify a cascade of consequences spreading through the community as a result of an initially highly focussed interaction.

Here an attempt is made to answer these questions by providing an assessment of both the potential and the realized consequences of the action of plant parasites as they affect individual host populations and the diversity and structure of associated communities. Because of the extreme diversity of the biology of organisms falling under the plant parasite umbrella, these effects are likely to be highly variable. Consequently, this paper is divided into three sections. The first considers the ways in which different parasitic organisms affect the health of their hosts, the varying levels of specialization of parasite-host associations and the consequences of differences in the levels of specialization for the interaction. By inducing reductions in the fitness of individual plants, pathogens that are restricted in their attack to specific host genotypes only have the potential to promote hidden changes in

the genetic structure of apparently stable populations. The second section deals with this relatively well-documented phenomenon. Finally, the third section considers both the potential and actual effects of parasites on community structure; the relative importance of different parasite groups in inducing such changes; and the difficulties that arise in obtaining an accurate assessment of the overall role of parasites as factors determining community processes.

8.2 The Diversity and Specialization of Parasites and Their Effects on the Fitness of the Host Plant

This paper focuses attention on parasitic angiosperms and on fungal pathogens (see also Oberwinkler, Chap. 7). The action of bacteria and nematodes are largely excluded from consideration because of the almost total lack of information concerning these organisms in non-agricultural communities. In the case of bacteria, this may not be an unrealistic assessment of their importance. Although bacterial pathogens are damaging in a few agricultural situations (for example, fireblight of apples and pears), their number and importance relative to fungi and viruses are strictly limited. It seems very likely that they fulfil a similarly restricted role in natural communities. In contrast, nematodes are ubiquitous members of the soil microfauna. They are often important in agricultural situations either as parasites in their own right (for example, cereal cyst nematode) or as vectors of viral diseases (Thresh 1976). The failure to consider them here should not be interpreted as a lack of importance. Indeed, as virus vectors, nematodes have been shown to play a major role in the distribution and spread of *Arabis* mosaic virus in wild populations of *Primula vulgaris* (Mackenzie 1985, cited in Harper 1990).

8.2.1   Parasitic Plants

Parasitic plants are a diverse group of approximately 3000 species with representative members in the majority of plant communities throughout the world (Press 1989). For both host and parasite, the complexity of any association is greatly influenced by the extent to which parasitism has been embraced. At one extreme are holoparasitic species like *Orobanche* and *Rafflesia* that lack chlorophyll and are totally dependent on their hosts. At the other end of the parasitic spectrum are many genera of hemiparasites that can develop to the seedling stage before attachment to a host becomes essential. Between these extremes lies an almost continuous array of associations of varying physiological complexity.

   Parasitic plants are similarly diverse in the degree of specialization they show with respect to host species. Many root hemiparasites of temperate grass and marshland communities possess very broad host ranges, apparently indiscriminately forming haustorial connections with any adjacent plant (Wilkins 1963). Thus, *Rhinanthus minor* may parasitize at least 50 species from 18 families (Gibson and Watkinson 1989), while in Australia, species of mistletoe (*Amyema* spp.) are found on a range of eucalypts, the occasional *Acacia* and even on introduced species of *Quercus*. Despite the apparently broad nature of this parasitism, there is considerable evidence of variation within parasitic taxa as to the relative suitability of different plant species as hosts. Clay et al. (1985) showed that seeds of the mistletoe, *Phoradendron tomentosum*, grew better on the host species from which they were taken than on other known hosts. In a detailed study of *Orthocarpus purpurascens*, Atsatt and Strong (1970) found that fecundity was markedly affected by the host species. In a trial involving six potential hosts, *Trifolium repens* proved to be the least beneficial, while *Hypochoeris glabra* and *Spergula arvensis* were the most advantageous. Furthermore, there was considerable variation between *O. purpurascens* individuals in their per-formance on individual host plants. A further complication in consideration of the selectivity of parasitic plants has been introduced by the observation that host species preferred by *Rhinanthus minor* in some communities were avoided in others (Gibson 1986).
   The converse side of the beneficial effect obtained by a parasite from its host is the detrimental effect it simultaneously inflicts on that host. This ranges from the barely detectable to major reductions in host fecundity and even death of the host prior to reproduction. The best documented examples of such phenomena come from agriculture, where heavy infesta-tions of sorghum, maize or millet crops by *Striga hermonthica* lead to substantial reductions in yield (Last 1960). In contrast, the direct measure-ment or observation of the effects of parasitic plants in natural communities is very limited, although infestation by dwarf mistletoes (*Arceuthobium* spp.) clearly leads to a rapid decline and death of the parasitized hosts (Kuijt 1969; Baker and French 1991). In more experimental investigations of natural associations, hemiparasitic plants like *Rhinanthus* may substantially reduce the competitive ability of the preferred host (Gibson and Watkinson 1989), while others like *Orthocarpus* may even kill particularly preferred hosts through over-parasitization (Atsatt and Strong 1970).

8.2.2   Fungal and Viral Pathogens

In contrast to parasitic plants that catch the imagination of many by their obvious presence and ecophysiological interest, parasitic fungi and viruses suffer a "secretive and insidious" factor (Price 1980) that leads to a severe underestimation of their occurrence in plant communities. In reality, the

total number of species of fungi and viruses attacking plants is enormous. Pathogens are to be found in all plant communities, and within most, plant species are host to several pathogens. This diversity is particularly apparent in a survey of the North American literature that recorded an average of 15 fungal pathogens per tree species, 7 per shrub and 5 per herbaceous species (Strong and Levin 1979). A similar assessment of the number of fungal parasites attacking trees in Britain also recorded approximately 15 fungal species per host tree taxa (Strong and Levin 1975). Individual values ranged between 4 (*Aesculus hippocastanum*) and 41 (for *Quercus petrea* and *Q. robur* combined). Far less is known about viruses in natural ecosystems, but a literature survey of their incidence in 37 species of forest tree found that the number of different viruses ranged between 1 and 7 per tree species, with an average of 2.3 (Nienhaus and Castello 1989).

As a group, plant pathogens show a wider range of host specificity than do parasitic plants. At one extreme are relatively unspecialized pathogens like some *Pythium* and *Rhizoctonia* species that are responsible for the damping-off diseases which threaten the majority of plants during germination and early seedling establishment phases of growth. Individually, however, the majority of fungal and viral pathogens show a specificity that restricts them to just one or a few host species. Moreover, amongst these pathogens, considerable variation often occurs in the ability of individual isolates to attack different plants from the one host species. Indeed, for very many species of highly specialized basidiomycete and ascomycete fungi (for example, rusts and smuts, mildews and ergots respectively), the association between pathogen and host has been carried to a very high level of specialization. Resistance in the host is conferred by single genes with major phenotypic effects, while pathogenicity in the pathogen is conferred by corresponding single genes for virulence (cf. "gene-for-gene" interaction; Flor 1971).

Such tight gene-for-gene associations have frequently been regarded as the preserve of highly specialized fungal pathogens. This is not necessarily the case. Similar single gene reciprocal effects have been documented in *Phytophthora megasperma* attacking *Glycine max*, in several nematode-plant interactions and in a range of nectrophic fungal-plant associations (for example, scald of barley).

Collectively, pathogens may attack any part of a plant at any stage in the life cycle. Individually, however, they tend to be far more selective, attacking particular stages of the host's life cycle and/or particular plant organs. These effects can be divided broadly into three categories that focus attention on the predominant way in which particular pathogens affect host fitness (Burdon and Jarosz 1988). Some pathogens kill their hosts rapidly, either through destruction of seedlings (for example, damping-off diseases; Fig. 8.1a) or adult plants (for example, vascular wilts). Others partially or completely sterilize their hosts through either local or systemic infection (for example, smuts; Fig. 8.1b), while yet others affect the host's com-
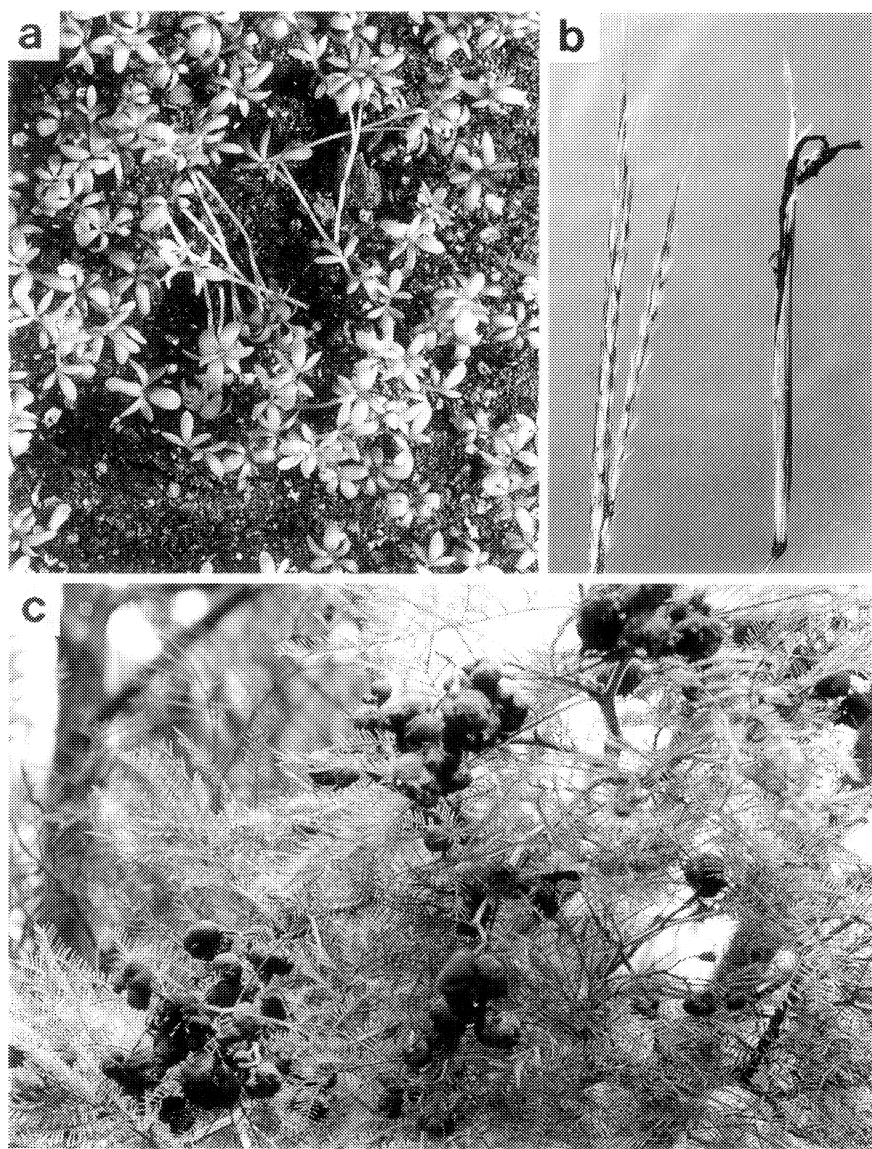
Fig. 8.1a–c. Examples of the three broad categories whereby fungal pathogens affect their hosts: **a** damping-off of *Lepidium sativum* seedlings by *Pythium irregulare*; **b** inflorescences of *Bothrichloa macra* taken from a healthy plant (*left*) and a plant systemically infected with the floral smut *Sporisporium amphilophis* (*right*); **c** discrete galls on *Acacia dealbata* caused by the rust pathogen *Uromycladium* sp.

petitive vigour, fecundity and longevity through the cumulative consequences of many discrete lesions (for examples, many rusts and mildews; Fig. 8.1c).

The consequences of these effects have been documented time and again in agriculture; many of the significant famines of human history can be traced back to a pathogen-induced failure of staple food production (for example, the Irish Potato Blight Famine of 1847–1851). Equally, in natural communities an increasing number of studies have quantified the significant effects of fungal pathogens on seedling (Augspurger 1983), juvenile (Alexander and Burdon 1984) and adult plant mortality (Wennström and Ericson 1990; Jarosz and Burdon 1991) and on fecundity (Parker 1986; Paul and Ayres 1986; de Noiij and van der Aa 1987).

8.3   The Hidden Effects of Parasite Attack –
Changes in the Genetic Structure of Plant Populations

The diversity of plant communities can be viewed at two distinct levels, that of the genetic diversity of individual populations and species and that of the demographic and structural diversity of entire plant communities. In this context, what are the effects of parasites on their hosts? Depending on the nature of the association, its degree of specificity, the magnitude of the damage inflicted and the frequency of episodes of parasitism, parasites may have no effect or may induce profound changes in the structure and diversity of individual populations, of species as a whole or of the communities of which they are a part. While a change in the numbers of individuals of a species in a community is the most obvious way in which diversity may be affected, changes in the genetic structure of populations should not be ignored.

The possibility of, and way in which, parasites may affect the genetic diversity of host populations is dependent on the level of specificity of parasite attack. Regional differences in the overall resistance of host species to particular parasites may arise in any association in which substantial differences in the likelihood of attack occur across the distribution of the species in question. In forestry provenance trials such differences are often apparent as relatively small but significant differences in the levels of parasite infestation of hosts in a common environment. For example, populations of *Pinus sylvestris* growing in northern Scandinavia are less susceptible to attack by the snow blight pathogen (*Phacidium infestans*) than provenances from further south, even though northern populations may still suffer substantial losses (Roll-Hansen 1989).

More complex patterns of distribution of resistance in host plants are typically associated with parasitic relationships involving highly specialized, isolate-specific interactions. These, too, may show distinct regional differences in the frequency of particular resistances (Dinoor 1970). In addition,

however, host-parasite associations of this type are frequently characterized by differences in the incidence of resistance between populations in a local area (Parker 1986; Jarosz and Burdon 1991) and considerable within-population diversity in the number and frequency of resistances against particular fungal pathogens (Burdon 1987; Burdon and Jarosz 1991).

While such general trends in resistance are usually associated with corresponding changes in the physical environment that affect the growth and reproduction of the pathogen, in some instances other members of the plant community have a direct influence on disease levels. This is particularly the case for heteroecious fungi that undergo an obligate alternation of hosts. Thus, the geographic distribution of resistance to *Cronartium comptoniae* in *Pinus banksiana* and *P. contorta* is strongly correlated with the distribution of the alternate species *Comptonia peregrina* and *Myrica gale*, respectively (Hunt and Van Sickle 1984). A wide range of other rust fungi show similar obligate host alternation (Wilson and Henderson 1966). It seems most likely that as these associations are examined in detail, other examples of correlations between the distribution of resistance in one host species and the geographic range of alternate hosts will be detected.

8.4   Parasite Attack as a Determinant of Ecosystem Structure

The structural complexity and diversity of plant communities may be increased, decreased or left unaltered by the depredations of parasites. While the ultimate outcomes of parasitic attack at the community level are restricted, there are a multiplicity of pathways by which such changes may be achieved. These are likely to vary according to the attributes of both host and parasite. Parasites limited by their specificity to single host species may have quite different effects to those capable of parasitizing many species within a single community. Equally, parasites that kill hosts rapidly may set in train a different set of events to parasites whose effects are restricted to reductions is fecundity and competitive vigour.

Not all plant species in a community occupy the same functional niche (Solbrig, Chap. 5; Körner, Chap. 6), and these differences may also have a profound effect on the consequences of parasite attack. Loss or severe damage to keystone species that play crucial roles in determining the structure of communities (for example, dominant tree species that affect light and microclimatic regimes on the forest floor; nitrogen-fixing legumes that contribute significantly to the soil nutrient status; or simply highly aggressive species that dominate competition for resources) may be expected to have greater effects than similar damage to more minor component species. Furthermore, the interaction of such parasite and host attributes may produce yet other, unexpected twists in the community consequences of such host-parasite interactions.

What empirical evidence exists to support the concept of parasites shaping ecosystem structure and diversity?

8.4.1   Lessons from Exotic Pathogens and Severely Disturbed Natural Systems

8.4.1.1   Effects on Ecosystem Structure

By far the best-known examples of ecosystem level parasite-host plant interactions involve the epidemic spread of exotic parasites through previously unexposed host populations. Man-initiated epidemics of this kind are extremely valuable in providing a broad picture of the potential ramifications of parasite attack. Not surprisingly, in instances involving parasites with wide host ranges, the structure and diversity of the pre-existing community has been severely disrupted. In both Western Australia and Victoria (Australia) the depredations of *Phytophthora cinnamomi* has led to the replacement of complex heath and eucalypt forest assemblages by floristically poor communities dominated by resistant sedges (Weste 1981; Shearer and Tippett 1989). In many places, these changes are so profound that it seems highly unlikely that the original community will return naturally even if the pathogen were to be eradicated.

In contrast, the consequences of the loss or near loss of single species through the action of exotic host-specific pathogens are more subtle and appear to depend on the status of the host species in the preinvasion community. Thus, in many situations the effects of the loss of *Castanea dentata* due to the invasion of *Cryphonectria parasitica* have been limited to a simple replacement by codominant species (Woods and Shanks 1959). In habitats where *C. dentata* was particularly abundant, however, the diversity of the tree and shrub layer has increased as the number, density and relative importance of species has changed (Stephenson 1986). In mesic sites this may be accompanied by an acceleration of successional changes already in progress, while in many dry ridge habitats the newly developing community is more xeric than previously (Woods and Shanks 1959). Nothing is known about the consequences of such changes for the forb and herb component of these communities, although it is difficult to believe that they have remained unaltered. Studies of other well-known exotic parasite-host interactions (for example, *Nectria coccinea* and *Fagus grandifolia*) have also detected changes in compositional structure ranging from the substantial to the insignificant (Twery and Patterson 1984).

In many ways biological control programs that deliberately release fungal parasites to affect reductions in the density of target weed species are analogous to exotic parasite-host interactions. The control agents released in these situations are always highly specialized and the target weed species a dominant component of the flora in the release area. Without exception,

where these processes have successfully affected the numbers of the target species, community diversity has risen as the aggressiveness of the dominant species is severely curtailed by parasite activity. In Australia, the effect of rust infection on one form of *Chondrilla juncea* apparently allowed two other resistant forms of the weed to spread more rapidly (Burdon et al. 1981). In Hawaii, the successful release of a species of *Cercosporella* to control the introduced weed *Ageratina riparia* has been followed by the collapse of monotypic thickets of the weed and the re-establishment of more floristically diverse communities (Trujillo 1985).

8.4.1.2 Changes in Host Distribution

The association that exists between the regional distribution of resistance in plant populations and physical environmental factors was detailed earlier. There, genetic changes in the host were presumably sufficient to counter the selective pressures imposed by parasite attack, and host and parasite continued to co-exist even within areas most favourable to the parasite. In other parasite-host interactions such interspecific genetic responses may be weak or non-existent. This gives rise to the possibility that some host species may be excluded from parts of their potential range or from particular local habitats by the action of parasites.

Evidence to support this hypothesis in plant-parasite interactions is again circumstantial and relies heavily on forestry experience, where the manipulation of natural communities has been an important management approach. There are several anecdotal reports of marked increases in the incidence of diseases accompanying attempts to extend preferred timber species into habitats in which they do not occur naturally. In parts of northern Scandinavia, attempts to plant *Pinus sylvestris* on mesic sites normally dominated by *Picea abies* have met with an increasing incidence of destructive pathogens like *Phacidium infestans*. Similarly, Large (1940) reported the abandonment of plantations of *Larix decidua* grown in lowland Europe due to the devastation brought about by a pathogen (*Trichoscyphella willkommii*) which is of little consequence in natural stands of *L. decidua* in more montane regions.

A somewhat more complex example is that afforded by the association between *Cronartium quercuum* and its three primary hosts (*Pinus elliotti*, *P. palustris*, *P. taeda*) in the southern United States. These species originally formed a complex mosaic of discrete communities, with each pine species being restricted to specific sites (Dinus 1971). In these forests, fusiform rust was present but relatively rare (Czabator 1971). Since that time, a range of forestry practices has led to an increase in the incidence of alternate hosts (*Quercus* species) and to the expansion of the more susceptible species into habitats from which they were previously absent. Major increases in disease have accompanied these changes (Dinus 1971; Powers 1984), with many of these new areas being particularly heavily diseased.
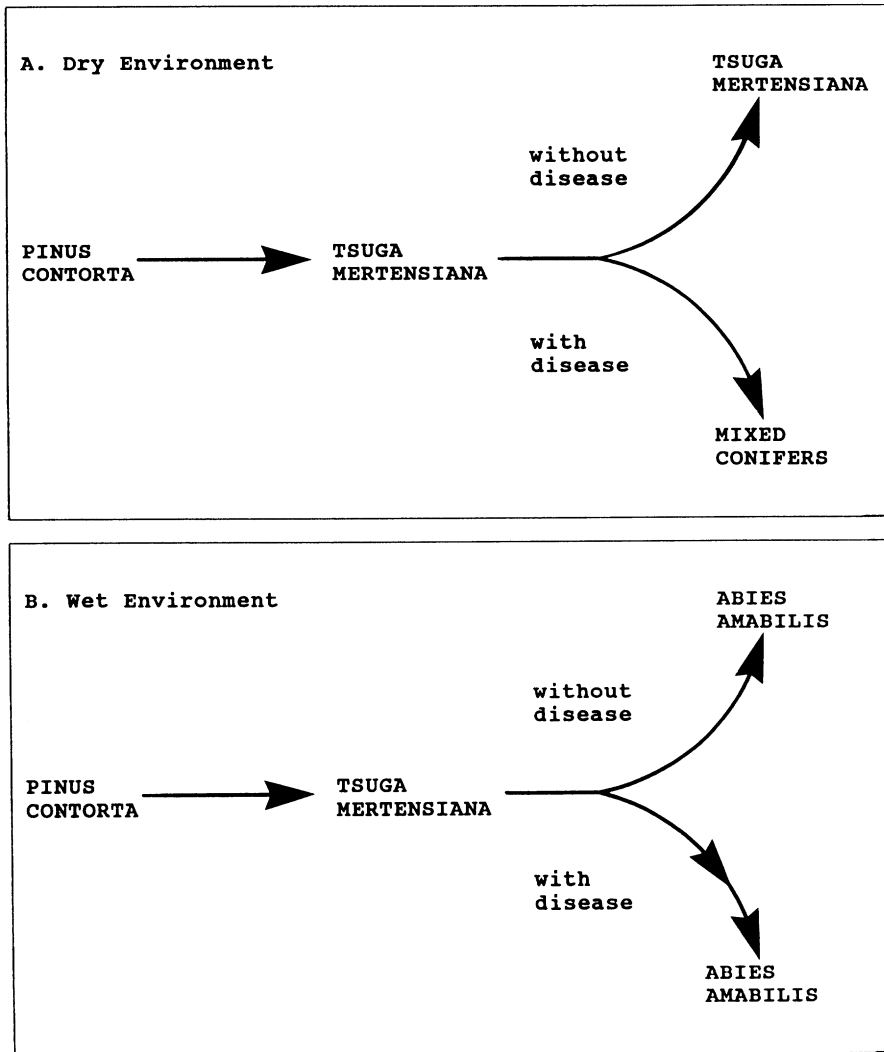
A. Dry Environment

PINUS
CONTORTA $\longrightarrow$ TSUGA
MERTENSIANA

without
disease

TSUGA
MERTENSIANA

with
disease

MIXED
CONIFERS

B. Wet Environment

PINUS
CONTORTA $\longrightarrow$ TSUGA
MERTENSIANA

without
disease

ABIES
AMABILIS

with
disease

ABIES
AMABILIS

Fig. 8.2. Changing patterns in community succession in the coniferous forests of the Pacific Northwest of the USA in the absence and presence of disease caused by *Phellinus weirii* (data from Cook et al. 1989): **A** dry environment; **B** mesic environment. *Multiple arrowheads* indicate increasing speed of succession

Deliberate perturbation experiments are a respected part of an ecologist's experimental armory. Although the sorts of observations considered above lack proper controls, they do serve to indicate how difficult it may be to recognise the *past* role of parasites in shaping and maintaining *current* host distribution patterns. Once the immediate visual evidence of the damage

wrought by a parasite has disappeared, it is very easy to look to explanations other than disease to account for the structure of the current community.

8.4.2   Evidence from Natural Parasite-Host Associations

8.4.2.1   Correlative Studies

Documentation of the effects of parasites in natural communities is likely to be a protracted process. Epidemics of fungal and viral diseases are frequently relatively short-term episodes that are restricted in space. For much of the time, although parasites may be present, their numbers are low, and their influence on the fitness of their hosts is minimal. In a 6-year study of the interaction between the rust fungus *Melampsora lini* and its host *Linum marginale*, disease was present in all years but only affected host fitness in 2 (Jarosz and Burdon 1991; and unpublished data). Given this unpredictability, it is hardly surprising that there are few studies that have addressed the question of the role pathogens have in shaping community structure. The best example is undoubtedly that provided by the natural spread of the root-rot fungus *Phellinus weirii* in conifer forests in Oregon and British Columbia (see also Vitousek and Hoopel, Chap. 1). These forests are dominated by *Tsuga mertensiana* but harbour a range of other species including *Abies amabilis*, *Pinus contorta* and *P. monticola* (Cook et al. 1989). In the absence of disease, vegetation develops along two alternative successional pathways determined by the availability of moisture on particular sites. In moist situations, an *Abies*-dominated climax forest is reached by way of a *Pinus – Tsuga* succession. In drier situations, *Abies* is unable to establish in large numbers, and *T. mertensiana* dominates the climax community.

The presence of disease caused by *P. weirii* may produce marked changes in these patterns. *P. weirii* infestations are typically characterized by discrete patches of disease expanding radially outwards by mycelial growth into adjoining unaffected forest. As a result, it is possible to compare closely disease-induced changes in the structure of the forest over distances of less than 100 m. As the disease front passes, the majority of trees die and are replaced by seedling recruits of various species. None of the conifers in the area are immune to attack by *P. weirii*, but *T. mertensiana* is particularly susceptible. It is this differential susceptibility of *Tsuga* and *Abies* coupled with their environmental requirements and tolerances that is responsible for marked shifts in the structure of the *P. weirii* aftermath forest (Fig. 8.2). On moist sites, the diversity of the forest is unaffected by the pathogen, but the successional sequence is accelerated as *Abies* is able to establish preferentially. In drier situations, on the other hand, *Abies* is unable to take advantage of the destruction of *Tsuga*. Instead, a renewed cycle of pine establishment occurs, and species diversity increases (Cook et al. 1989).

8.4.2.2 Direct Assessment Through Parasite Exclusion

Ultimately, a definitive assessment of the role parasites play in shaping
community structure and composition can only be obtained through a com-
parison of the development of communities in the presence and absence of
parasites. With one notable exception (parasitic plants, see below), the only
practical way this can be achieved is through the application of pesticides.
Unfortunately, the utilization of pesticides in this way is fraught with poten-
tial difficulties. Pesticides themselves may have phytotoxic effects, depressing
the growth of sensitive species directly (Paul et al. 1989). Alternatively, they
may affect the health and nutrient status of plants through the suppression
of mycorrhizal fungi (Gange et al. 1990).

Despite these potential problems, the judicious use of pesticides to
provide local near extinction of parasites is likely to be the only practical
way to mount community-level investigations of the ramifying effects of
parasites. Provided care is taken in the experimental design and the selection
and application of suitable pesticides, results obtained by these means will
provide valuable insights into the role of parasites. To date, few attempts
have been made to utilize fungicides in this way. Furthermore, those
community-level examples that do exist are agriculturally based. Latch and
Lancashire (1970) investigated the short-term effects of crown rust (caused
by *Puccinia coronata*) on simple *Lolium perenne – Trifolium repens* swards.
In plots where epidemics of rust were allowed to develop, the productivity
of the *Lolium* host fell more than 80% while that of *T. repens* increased by a
similar amount. This trial was not continued for a sufficiently long time to
determine the longer-term consequences of these effects. However, in a
brief report on a comparison of the performance of fungicide-treated and
untreated pure stands of *L. perenne*, Price (1987) mentioned the propensity
of weeds to invade disease-affected stands.

Parasitic plants also have the potential to affect the structure of the
communities in which their hosts occur. Infestations of dwarf mistletoes
rapidly kill host trees and create distinct gaps in parasitized forests. How-
ever, little is known about subsequent changes to the community. Areas of
grassland infested with *Rhinanthus minor* generally have a lower number of
species present and a lower species diversity than do adjacent parasite-free
areas (Gibson and Watkinson 1989). The causal relationship linking these
observations was confirmed by comparisons of untreated areas with ones in
which all *Rhinanthus* individuals were removed. The species diversity of
three out of four sites rose as a result of parasite exclusion, while at a fourth
it fell. It appears that at the latter site, *R. minor* restricted the competitive
vigour of a dominant species.

The approach of hand removal of individual parasites would appear to
have considerable promise for further studies of the role of hemiparasitic
plants in grassland communities. In several environments (for example,
alpine meadows), annual and perennial hemiparasitic plants are particularly

common, and studies of the type described above should be able to clarify their functional role in the community.

8.5   Conclusions

We still have only a skeletal understanding of the role parasites play in natural plant communities. The range of potential parasites is enormous, and the function of many of these has yet to be considered at all. However, a compelling body of circumstantial evidence implicates fungal parasites as major selective forces contributing to ecosystem diversity at two levels.

At a genetic level, pathogens affect:

1. Intraspecific diversity within individual plant populations
2. Geographic patterns of distribution of resistance across the range of entire species

At a structural level there are fewer clear examples. However, evidence from a diverse range of sources including (a) studies of undisturbed natural systems, (b) the invasion of exotic pathogens into previously unexposed communities and (c) the consequences of massive disturbance in existing parasite-host associations all indicate that pathogens can play a major role in:

1. The fragmentation of populations
2. The diversity of whole communities

What we particularly lack at this stage is an objective measure of the importance and pervasiveness of such effects. Are the few documented cases available the tip of an as yet unexplored iceberg or are they outstanding simply because of their uniqueness? Currently, there is no answer to this question, and every encouragement should be given to a concerted effort to provide one. One way in which this will be achieved is through the careful use of parasite exclusion approaches (using pesticides) in a range of early and mid-successional communities.

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