Books 2

Wheat

2

Evolution at the Center of Origin

I. Wahl
Y. Anikster
J. Manisterski
A. Segal
Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel

I. Introduction

Rust fungi as obligate parasites have coexisted and coevolved hand in hand with their hosts as components of a system much influenced by ecologic conditions. The concept of host–parasite coevolution first formulated by Dietel (1904) implies that either constituent of this

ISBN 0-12-148401-7

In the hilly steppes of Asia Minor is commonly found the diploid einkorn wheat *T. boeoticum* Boiss. emend. Schiem. (Fig. 3 in Harlan and Zohary, 1966), with two races: a small one-seeded race, often called *T. aegilopoides*, and a large two-seeded race, frequently designed *T. thaoudar* (Harlan and Zohary, 1966). The cultivated relative of this species is *T. monococcum* L. Both *T. aegilopoides* and *T. monococcum* possess resistance to stem rust and leaf rust (Zhukovsky, 1959). Also *T. thaoudar* contains rust resistant plants (Zhukovsky, 1964). Gerechter-Amitai *et al.* (1971) transferred stem rust resistance from *T. aegilopoides* collected in Turkey to susceptible *T. durum* cultivars. The F_3 and F_4 progenies displayed low reaction resistance to a broad array of stem rust races. The resistance was apparently controlled by a single dominant gene, or by a set of linked factors.

Of the tetraploid wheats endemic in the geographic regions concerned, two are of particular interest: *T. timopheevi* Zhuk., a half-weed, half-cultivated wheat of Soviet Georgia and Armenia, which is often used in breeding as a source of disease resistance (Vavilov, 1939), and *T. persicum* Vav. ex Zhuk. (*T. carthlicum* Nevski), a cultivated species from Gruziya, highly resistant to rusts and powdery mildew (Vavilov, 1939; Zhukovsky, 1965; Leppik, 1970).

The hexaploid *T. zhukovskyi* Men. et Er. is a spontaneous hybrid between *T. timopheevi* and *T. monococcum*, combining resistance genes of its parents (Leppik, 1970).

Description of the aforementioned *Triticum* species and information concerning their genomic formulas and geographic distribution are presented by Feldman and Sears (1981), Harlan and Zohary (1966), Peterson (1965), and Zohary (1971, 1973).

C. WHEAT RUSTS IN THE CENTERS OF *Triticum* ORIGIN

Zhukovsky (1961) and Vavilov (1939) ascertained that the epicenters of wheat are also the homeland of the most destructive wheat rust parasites, *Puccinia recondita*, *P. striiformis*, and *P. graminis*. The uredia and telia of *P. graminis* capable of developing on wheat, parasitize many genera of Gramineae (Zhukovsky, 1961). Protracted observations have proved that all wheats of the Caucasus rust to various degrees of severity. Even the ordinarily rust-resistant species *T. timopheevi*, *T. carthlicum*, *T. zhukovskyi*, and *T. monococcum* are protected by field resistance and not by absolute immunity (Zhukovsky, 1959, 1961, 1964). Reactions of *T. persicum* (*T. carthlicum*) to stem rust, leaf rust, and stripe rust range from field resistance to susceptibility (Zhukovsky, 1961).

D. ORIGIN AND EVOLUTION OF *Puccinia graminis*

The problem of origin and evolution of wheat stem rust is of great theoretical and practical importance (Anikster and Wahl, 1979). Klebahn (1904) considered barberry as the primary source of *Puccinia graminis* Pers. Leppik (1961, 1965, 1970) postulated that the stem rust fungus has originated in central Asia and East Africa on its aecial *Berberis* host. Both *Berberis* spp. and grasses belonging mainly to the subfamily Festucoideae that harbor the sporophytic stage of *P. graminis* f. sp. *tritici*, have coexisted with the parasite for a sufficiently long time to enable the evolution to the full heteroecious cycle of the fungus. "It is not a mere coincidence that the assumed aboriginal area of stem rust matches well with the terrain where all gene-centers of cultivated Festucoideae are located" [Figs. 1 and 2 of Leppik (1965). The same figures appear in Leppik (1961), and partly in Leppik (1970).]

Notably, the sporophytic generation of the fungus inhabits 70–80 genera of grasses with several hundred species, whereas the gametophytic generation is limited to the two closely related genera *Berberis* and *Mahonia*. This pattern of uneven biologic specialization suggests that barberry was the source host and grasses the secondary host of *P. graminis* f. sp. *tritici*. From the center the parasitic fungus migrated westward and eastward in association with the alternate host. However, the worldwide distribution of the fungus is a result of the ever-expanding cultivation of wheat (Leppik, 1965; Fig. 3 of Leppik, 1970). In many regions the parasite has become independent of the aecial host and even innocuous on it (Anikster and Wahl, 1979).

1. *Taxonomy of* Puccinia graminis *on Wheat and Related Grasses*

Puccinia graminis is a complex "mammoth" (Gäumann, 1959) species, and numerous attempts have been made to subdivide it into simpler taxa. Urban (1968, 1969, 1980) adopted a "phytocenotic"–phylogenetic approach for taxonomic classification of the fungus. He separated the European stem rust into two subspecies (see also Savile, Chapter 3, this volume), one of them compatible mainly with wild grasses was designated as *P. graminis* Pers. ssp. *graminicola* Urban. This subspecies alternates with *Berberis* and ordinarily does not attack cultivated cereals in nature.

In Czechoslovakia, subspecies *graminicola* has evolved by repeated cycling annually between grasses and *Berberis* (Urban, 1961). The other subspecies that parasitizes cultivated cereals and is independent of *Berberis*, was designated *P. graminis* Pers. ssp. *graminis* (with no

combined authority). The two subspecies are cross-incompatible. These data gained primarily in Czechoslovakia question the importance of *Berberis* and wild grasses in the epidemics of stem rust in cultivated cereals and indicate the need for reinvestigation of this problem (Urban, 1968).

Urban attributed the evolution of the two subspecies to phylogenetic processes interlaced with the progress of wheat cultivation. He accepted Leppik's hypothesis that the stem rust organism and *Berberis* have their common center of origin in central Asia where it coincides with the area of wheat and barley origin. The ancestral stem rust forms have parasitized wild grasses, including *T. boeoticum, T. dicoccoides,* and *T. timopheevi.* About 8000 to 9000 years ago, wheat cultivation commenced including the ancient cultivated wheats that belong to the diploid species *T. monococcum,* the tetraploid *T. dicoccum,* and the hexaploid *T. spelta.* They were compatible with *P. graminis* ssp. *graminicola.* With the immense geographic expansion of grain crops, the plants adopted new morphologic and physiologic traits. Conditions were created for urediospore dissemination over huge areas, and the significance of the *Berberis* as an alternate host has gradually diminished. Hence, *P. graminis* ssp. *graminis* adapted to cereal crops is of secondary origin, and its predominance has been favored by our management of agroecosystems. Azbukina's studies (1971) in the far eastern region of the Soviet Union corroborated Urban's classification of *P. graminis.* Urban (1969) is aware of the possible inappropriateness of such a subdivision of stem rust in Transcaucasia, Asia Minor, the Mediterranean regions, and other centers of wheat evolution where the fungus is virulent on wild wheats and their relatives considered to be resistant in other geographic areas, as well as on cultivated wheat. It obviously possesses parasitic affinity to both subspecies, *graminicola* and *graminis,* and may pose a hazard to wheat crops in other parts of the world resistant to local races, if transported there by long-distance wind dissemination. Therefore, utilization of urediospore inoculum from primary and secondary evolutionary centers for screening of stem rust resistance was recommended (Urban, 1980). A similar conclusion was drawn by the senior author (Wahl, 1958), and experience gained in the ensuing years has fully justified it.

2. *Interrelationship between Stem Rust on Wheat and Grasses in Israel*

Studies pursued over many years in Israel have shown that stem rusts on wheat crops and on native wild grasses are closely interrelated in their parasitic traits and epidemic development (Gerechter-Amitai and Wahl, 1966; Gerechter-Amitai, 1973). The same parasitic races predominante on wheat and grasses. For example, race 14 of *P. graminis* f. sp. *tritici,* which ranked first in the frequency of occurrence on wheat at the time of investigation, was also the most common on grasses and had the widest host range during the entire period of studies. It was isolated in nature from 26 grass species of 8 genera. Race 21 rated second in both host groups and was identified on 18 species of 6 genera. Stem rust on native grasses is represented by the following four *formae speciales: P. graminis* f. sp. *avenae, P. graminis* f. sp. *tritici, P. graminis* f. sp. *secalis,* and *P. graminis* f. sp. *lolii.* Nearly all hosts are in the subfamily Festucoideae.

Some grasses carried more than one *forma specialis* of stem rust, and a single plant of *Poa sinaica* Steud. was compatible with all four *formae speciales,* allowing urediospore production of each of them. The broad spectrum of wheat stem rust hosts among native grasses is assumed to be an outcome of prolonged host–parasite coevolution involving the dikaryotic stage of the fungus, in the absence of the alternate host in Israel. Notably, samples of wheat stem rust 3300 years old were found in Israel (Kislev, 1982).

Common hosts for different genetic entities enable somatic hybridization of the fungus and may play an important role in increasing the range of parasitic variation. Wild grasses in Israel are of paramount significance in the development of stem rust epidemics on wheat crops. The occurrence of the same parasitic races in grain fields and in grasses in their neighborhood indicates "a large-scale exchange of inoculum between the two host groups" (Gerechter-Amitai, 1973). The wild grasses can play a very essential role in trapping urediospores, building up of inoculum, and disseminating it to cereal fields. Obviously, races in Israel combine parasitic attributes of both subspecies, *P. graminis* ssp. *graminicola* and *P. graminis* ssp. *graminis.* Their coevolution with the host was much different from that of wheat stem rust in Czechoslovakia.

Savile and Urban (1982) and Savile (see Chapter 3, this volume) discussed the possibility of nuclear exchange between hyphae of the two stem rust subspecies on a common host, and evidence of such hybridization has presumably been found (Savile, Chapter 3, this volume).

3. *Stem Rust Reaction of Indigenous Wild Wheat and* Aegilops *Species*

The tetraploid wild emmer *Triticum dicoccoides* Körn., discovered in Israel by Aaronson in 1906, is one of the ancestors of cultivated wheat (Feldman and Sears, 1981). This species, recognized by Aaronson

cance of these perpetuation foci in the development of stem rust epidemics is not clear.

For decades races 72 (= 6F) and 8 were the most prevalent. In recent years race 7 has become common. These races embrace a broader spectrum of virulence genes. The host range of *P. graminis* f. sp. *avenae* in native grasses is broad. It parasitizes plants of 107 species belonging to 44 genera. Significantly, a single isolate of race 2 produced urediospores on 80 species of native grasses (Gerechter-Amitai, 1973).

In *Avena sterilis* L., indigenous to the Mediterranean region and the putative progenitor of cultivated oats (*Avena sativa* L.), resistance of low-reaction type to stem rust operating over the whole life of the plant is very rare (Sztejnberg and Wahl, 1976). J. Manisterski (unpublished) found that numerous accessions harbored uredia of both susceptible and resistance classes on the same stems, sheaths, or blades of the flag leaf and other leaves. The patterns of their distribution on the host resembled the phenomenon of "regional resistance."

Protection of the slow-rusting type against stem rust was discovered in *A. sterilis* by Murphy (Sztejnberg and Wahl, 1976). It is manifested in reduced infectability of the host and diminished spread of the disease, while uredia denote susceptible reactions. Slow-rusting resistance was proven to be stable and effective against many races. Zillinsky and Murphy (1967) found in *A. sterilis* that plants that "exhibited a resistant reaction to stem rust prior to heading, may be susceptible at later stages of maturity. This type of resistance, however, provides considerable protection among species which remain in the juvenile stage for extended periods of their natural habitat."

Distribution of defense components in *A. sterilis* varies with the region. In locations situated below sea level, plants rusted severely but ripened early, thus avoiding the damaging impact of the disease. In communities originating from the central coastal plain, the protection system is composed of 25% of slow rusters, which had infection severity of less than 40% even at the milk–early dough stage. Notably, slow rusters, late rusters, and some of the moderately fast rusters harbor uredia with necrotic lesions interspersed with uredia of susceptible class. The symptoms of late rusters are those of Luke *et al.* (1975).

The brief coexistence of *A. sterilis* with *P. graminis* f. sp. *avenae* during the season apparently prevents severe disease damage. "The *A. sterilis* stem rust–environmental system in Israel seems to be less balanced and coordinated than the system involving crown rust. The difference is reflected in the evolution of defense mechanisms against the two rust organisms" (Segal *et al.*, 1980). The most salient distinction is manifested in the common occurrence of low reaction in defense systems against crown rust, and its insignificance in stem rust.

E. LEAF RUST OF WHEAT

1. *Pathways of Evolution*

Leaf rust of wheat caused by *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* Eriks. has become an extremely serious disease worldwide and accounts for the greatest loss among cereal rusts over the long term.

Evolution of various lineages of the fungus with alternate hosts in the Ranunculaceae and Boraginaceae was discussed by Anikster and Wahl (1979). One physiologic group completes the life cycle on *Thalictrum*, another group alternates with plants of the Boraginaceae family, and the Siberian group alternates with *Isopyrum fumarioides* L. Congeniality among the lineages was found to exist only when the gametophytic and sporophytic hosts belong to the same center of origin. Marková and Urban (1977) postulated that the recent form of wheat leaf rust represents at least in some countries an autonomous species and has no alternate host. They surmised that the recent form descended from an ancestral progenitor the that has its origin in the evolutionary centers of hexaploid wheats (Near East, the Mediterranean region). "Originally it was heteroecious (species of *Thalictrum* and other genera) and plurivorous," that is, parasitic on a broad variety of hosts. Conceivably, evolution of wheat leaf rust in other geographic regions may have proceeded along different pathways.

2. *Studies in Israel*

This research is in preliminary stage and deals mainly with disease incidence on *Triticum dicoccoides*, one of the cultivated wheat progenitors. Populations of the species at some locations are seriously stricken by *P. recondita* f. sp. *tritici*.

a. Parasite Specialization. Fungus isolates sampled from *T. dicoccoides* across the country were inoculated to seedlings of wheat cultivars carrying genes for low reaction, *Lr1, Lr2a, Lr2c, Lr3a, Lr3b, Lr3c, Lr9, Lr10, Lr17, Lr18, Lr19, Lr21, Lr23, Lr24*. The results (unpublished) revealed considerable diversity in parasitic traits. Accessions with genes *Lr24* and *Lr19*, respectively, were highly resistant. This was also true to a lesser degree of seedlings with gene *Lr2a*. Seed-

lings endowed with gene *Lr9* were often moderately susceptible, carrying infection type 3.

b. Types of Protection in Triticum dicoccoides. In wheat breeding, genes for low reaction (Browder, 1980) and slow-rusting resistance (also referred to as "partial resistance"; Parlevliet, 1979a) are utilized. We have intended to identify the defense types evolved in undisturbed stands of *T. dicoccoides*. Therefore, single heads were sampled with the transect method from plants in natural habitats at about 1-m intervals, regardless of their reaction to the disease. Seeds were planted in 1-m rows in field nurseries in the order of the disposition of their parents in nature. Border rows sown to a universally susceptible cultivar were periodically inoculated with leaf rust cultures collected across the country. In these reconstructed stands of *T. dicoccoides*, a small number of accessions showed low reaction with infection ranging from 1 to 2+. Most plants displayed symptoms of slow rusting or later rusting. Severely rusted plants were always present. Presumably some of them have been protected by tolerance.

c. Search for the Alternate Host. So far, alternate hosts of *P. recondita* f. sp. *tritici* have not been found in Israel. Studies by Chabelska (1938) in this country demonstrated that the leaf rust fungus, *Puccinia aegilopis* Maire, which in nature inhabits *Aegilops variabilis* Eig [*Ae. peregrina* (Hack.) Eig], alternates with *Anchusa strigosa* Labill. Y. Anikster (unpublished) inoculated leaf rust teliospores produced, respectively, on cultivated *T. durum* wheat, *T. aestivum* wheat, *T. dicoccoides, Ae. variabilis, Ae. longissima*, and *Ae. sharonensis* to plants of the following Boraginaceae species: *Anchusa azurea* Mill., *A. strigosa*, *A. hybrida* Ten., *Echium angustifolium* Mill., and *E. judaicum* Lacaita. Aeciospores were formed on all listed Boraginaceae species inoculated with teliospores from *Aegilops* plants, but not with teliospores from the *Triticum* plants. These aeciospores inoculated to the *Aegilops* source hosts elicited formation of urediospores. Obviously, leaf rusts of *T. durum* wheat, *T. aestivum* wheat, and *T. dicoccoides* differ from leaf rust on *Aegilops*, even though the genus *Aegilops* is considered to be a part of the genus *Triticum* (Feldman and Sears, 1981).

F. WHEAT STRIPE RUST

1. *Evolution*

The disease is caused by *Puccinia striiformis* West. (see chapter by Stubbs in Vol. II). Its center of origin coincides with that of wheat (Zhukovsky, 1965). In Hassebrauk's opinion (1965, pp. 6–7) wild grasses were ancestral hosts of the fungus, from which it expanded to cereals. This hypothesis is substantiated by observations in countries where the rust only recently became established on cereal crops. For example, the disease appeared in North and South America first on wild grasses and later on wheat, barley, and rye. *P. striiformis* putatively originated from a heteroecious progenitor (Hassebrauk, 1965, p. 8).

2. *Wheat Stripe Rust in Israel*

The disease appears sporadically on wheat cultivars and on wild grasses belonging to *Triticum dicoccoides, Aegilops, Hordeum*, and other genera. Some isolates of the fungus have a host range embracing over 40 species of 17 genera (Z. K. Gerechter-Amitai, unpublished). Most of the isolates studied by Gerechter-Amitai were virulent on seedlings of Lee C.I. 1248 and Compair. Both accessions are resistant to the pathogen in some countries. The cultivar Compair possesses the resistance gene *Yr8* derived from *Aegilops comosa* Sibth. et Sm. Lee is characterized by susceptibility to race group 20A, common in the Mediterranean region (E. Fuchs, personal communication). Zadoks (1965) suggested that the rise of stripe rust importance in the Mediterranean region may be due to a better adaptation of some of the fungus biotypes to higher temperatures than the others. Z. K. Gerechter-Amitai (unpublished) proved that stripe rust inoculum isolated from *Aegilops kotschyi* Boiss. and *H. spontaneum* in the arid southern region with average annual rainfall of below 100 mm was virulent on wheat.

Gerechter-Amitai (1982) found in *T. dicoccoides* diverse types of resistance. Accessions from 44 locations were resistant to stripe rust cultures from India, Pakistan, Kenya, Egypt, Tunisia, Chile, North America, and western Europe.

The susceptibility of *T. dicoccoides* and of diverse *Aegilops* species in Israel supports the hypothesis that wild grasses were ancestral hosts of the fungus (Hassebrauk, 1965). The coevolution of *P. striiformis* and wild grasses in Israel apparently has resulted in the presence of numerous genes for resistance in them, as exemplified by *T. dicoccoides*.

G. CROWN RUST OF OATS

1. *Crown Rust of Oats in Israel*

Israel is located in the center of origin and genetic diversification of several oat species that are annually attacked there by *Puccinia coro-*

nata Cda. f. sp. *avenae* F. et L. The inoculum is present throughout the year. The disease gains momentum in March, culminates in April, and declines sharply in May. Of special interest is the disease incidence on *Avena sterilis*.

2. *Life Cycle*

The fungus is heteroecious and alternates with *Rhamnus* species (see chapter by Simons in Vol. II). In Israel *R. palaestina* Boiss. is indigenous and a common element of the Mediterranean vegetation. It functions as the alternate host of *P. coronata* f. sp. *avenae* in the Galilee, Samaria, Mt. Carmel, and the Judean Mountains. Aecia are formed throughout the winter. Because *Rhamnus* shrubs sprout from December to April, they develop hospitable substrate for the parasite for several months. In natural stands in various parts of the country, teliospore germination proceeds from the onset of the rainy season (late November to early December) until April. Therefore, production of basidiospores takes place over several months and coincides with the development of young tissue in *R. palaestina*.

The prevalence and long-lasting coexistence of the *Avena–P. coronata–Rhamnus* system prompted our studies on the effect of the coevolution of the components in this system on the following biologic traits: (i) parasitic specialization of fungus, (2) evolution of different types and levels of protection against crown rust, and (3) evolution of protection systems against the rust in natural, undisturbed populations of *A. sterilis*.

3. *Parasitic Specialization of* Puccinia coronata *f. sp.* avenae

About 100 parasitic races of the fungus were identified in samples of countrywide origin. Some races were discovered first in Israel, including the very dangerous race 264 that combines a very broad range of virulence genes, race 270, and races virulent on Santa Fe but avirulent on Landhafer. The prediction made by the senior author (I. W.) in 1958 that some of the virulent races found in Israel are likely to appear also in other oat-cultivatine regions, was soon confirmed (Wahl, 1959). Studies by Wahl *et al.* (1960) revealed distinct similarity in the composition of race populations in oat species and *R. palaestina*. For example, the "Landhafer races" group 263-264-276-277, the race group 202-203, and races 286 and 270 have appeared in the same order of prevalence on the main and alternate hosts. At the same time the "Victoria races" group 216-217, which is rare in oats, was absent in the aecial material. *Rhamnus alaternus* L., which serves as alternate host in Israel, also harbors aecia of *P. coronata* f. sp. *avenae* in Portugal and seems to be an important source of crown rust inoculum there (D'Oliveira, 1940). According to Santiago (1968), variation of this fungus in Portugal is most probably associated with the infections occurring in the alternate host, which is widely spread throughout the country.

The alternate host contributes to the diversification of the parasitism spectra of race populations in crown rust in Israel. Wahl *et al.* (1960) obtained only one race in eight collections from oats, but one in three from buckthorn and more than one race from a single aecial cup. Oat crown rust races selfed by Dinoor (1967) were heterozygous, entailing more variability of the fungus. Browning and Frey (1969) suggested that in the dikaryotic rust fungi, heterozygosity provides survival advantage to the organism. Eshed (1978) concluded that heterozygosity of pathogenicity is common in the *formae speciales* of *P. coronata*. Despite the continuous production of new races, the composition of race populations has remained stable over nearly three decades of race surveys. For example, the very versatile race 276 has predominated annually throughout Israel for many years. The same is true to a lesser degree also of races 202 and 264. This stability is attributable to the permanence in the composition of wild oats and other compatible native grasses, undisturbed by human interference, because oat cultivation is very limited. *Avena sterilis* and *A. barbata* Pott., which are very congenial hosts for *P. coronata* f. sp. *avenae*, represent most important constituents of the country's herbaceous vegetation. Additionally, prevalent races possess preferential survivability as expressed in their adaptation to a broad spectrum of ecologic conditions and prolific sporulation in such environments (Brodny, 1980).

4. *Defense against Crown Rust*

Vavilov (1939) reported good resistance to crown rust in Mediterranean oats. Studies in Israel, the United States, Puerto Rico, Canada, and elsewhere (Wahl, 1970) have proved that *A. sterilis* populations are abundant, diversified reservoirs of new and readily usable genes for low reaction resistance to *P. coronata* f. sp. *avenae*. Murphy *et al.* (1967) postulated that "a natural balance . . . appears to have been established between *A. sterilis*, crown rust, and *R. palaestina*, in which *A. sterilis*, although infected, produces seed of good quality." Various types and levels of resistance and tolerance "have apparently resulted from natural selection under conditions of regular and heavy crown rust infection and a relatively high level of outcrossing in *A. sterilis*" (Murphy *et al.*, 1967).

The following components of defense have been identified in *A.* sterilis: (*a*) conventional resistance associated with low reaction, (*b*) slow rusting, (*c*) tolerance, and (*d*) escape (avoidance).

a. Low Reaction Resistance. Numerous accessions of *A. sterilis* are endowed with resistance of this type to at least 14 races of *P. coronata* f. sp. *avenae* embracing a broad spectrum of virulence (Brodny *et al.*, 1976). Simons *et al.* (1978) provided a list of 25 genes for resistance to oat crown rust derived from *A. sterilis,* mainly of Israel origin. Zillinsky and Murphy (1967) found crown rust resistance in *A. sterilis* sampled in Italy, Morocco, Algeria, Tunisia, and Tripolitania. Harder (1980) reported in Canada that genes extracted from *A. sterilis* "generally proved a high level of resistance to *P. coronata*. . . . Further studies on wild *A. sterilis* accessions are expected to reveal additional resistance genes for use in breeding programs." Studies in Israel (Wahl, 1970) have ascertained that distribution of sources for low reaction to crown rust is countrywide and falls in natural populations in distinct geographic patterns that have remained unchanged over many years. The accumulation of resistance is conditioned by ecologic conditions favoring intense selection pressure on *A. sterilis*. Segal's investigations (1981) brought out that the evolution of resistance is much influenced by the prevailing races of the parasite. "Intermediate" resistance associated with infection types 2–3 is rather common but sometimes more sensitive to rise of temperature than resistance expressed by infection types 0;–1. Plant accessions vary in the spectrum of resistance, some of them being effective to several races, whereas others offer protection to a single race only. Segal (1981) also reported that in some entries, resistance operates throughout the whole life of the plant, whereas in others it is limited to certain growth stages of the host.

b. Slow-Rusting Resistance. This type of protection is featured by low receptivity, retarded disease progress, and reduced sporulation, whereas uredia are mostly of infection type 3, denoting susceptible reactions. Slow rusting is of overriding importance across the country. Ordinarily, it is more common than the low-reaction type of resistance, being less influenced than the latter one by race composition but more sensitive to fluctuations of climatic factors. In slow-rusting accessions, infection severity in field trials was within the range of 5 to 20%, whereas in fast rusters it amounted to 70 to 80%.

c. Tolerance. In identifying the tolerance form of protection, we adopted Simons' definition (1969): "A tolerant variety shows signs and

symptoms similar to those on a susceptible variety, but it is damaged less by infection than is the susceptible variety." Wahl (1958) reported that in Israel, "despite severe rust infection the wild oats do not seem to suffer from the disease, they show excellent tolerance to both rusts." On the examined plants, infection severity ranged from 50 to 80%, and reactions to the disease belonged to the susceptible and very susceptible class. Simons (1972) found that some progenies of crosses between *A. sativa* cultivars susceptible to crown rust and tolerant *A. sterilis* accessions "were as much as 15% higher than the cultivated parent in kernel weight response and 20% higher in yield response."

d. Escape. Disease escape is the ability of an otherwise susceptible plant to avoid damaging disease stress because it grows in places and times unsuitable for the parasite. This form of protection is particularly useful in natural ecosystems (Nelson, 1973). In arid regions, *A. sterilis* is either completely free of crown rust, because adverse climatic conditions avert the disease, or the plant escapes infection for long periods thanks to early ripening.

Littlefield (1981) has stressed the importance of the search for genes for crown rust resistance in Israel as follows: ". . . the great genetic diversity in oats in Israel has provided sustained resistance to crown rust. The magnitude and diversity of rust resistance genes, both of race-specific and race-non-specific nature, in that center of origin of oats, have provided an invaluable contribution to plant pathologists and breeders alike [p. 94]."

5. *Integration of Defense Components against Crown Rust in* A. sterilis

Studies on natural defense systems were pursued by inoculating parasite cultures of countrywide origin to plant populations reconstructed in test plots (Segal *et al.*, 1982). The reconstruction was achieved by sampling single panicles from plants at 1-m intervals, regardless of the disease performance on the parental plant. In the ensuing season seeds were sown in the nursery in the order of disposition of their parents in natural habitats. The nursery was periodically inoculated with crown rust cultures isolated countrywide. Infection type and infection severity were recorded several times during the season. The composition of defense systems against crown rust in *A. sterilis* vary distinctly with the locations. They comprise the aforementioned four types of protection in different proportions. The profiles of their interaction at a given site are stable (Segal *et al.*, 1980). For instance, in the Plateau Menashe, prevalence of low-reaction resistance has remained unchanged during

17 years of study. Details concerning the most common protection systems were reported by Segal *et al.* (1980) and are shown in Fig. 1. They are characterized by the high percentage of plants with infection type 3 and low to moderate infection severity, whereas in about 30% of the plants infection type 2 is associated with infection severity of 5 to 30%.

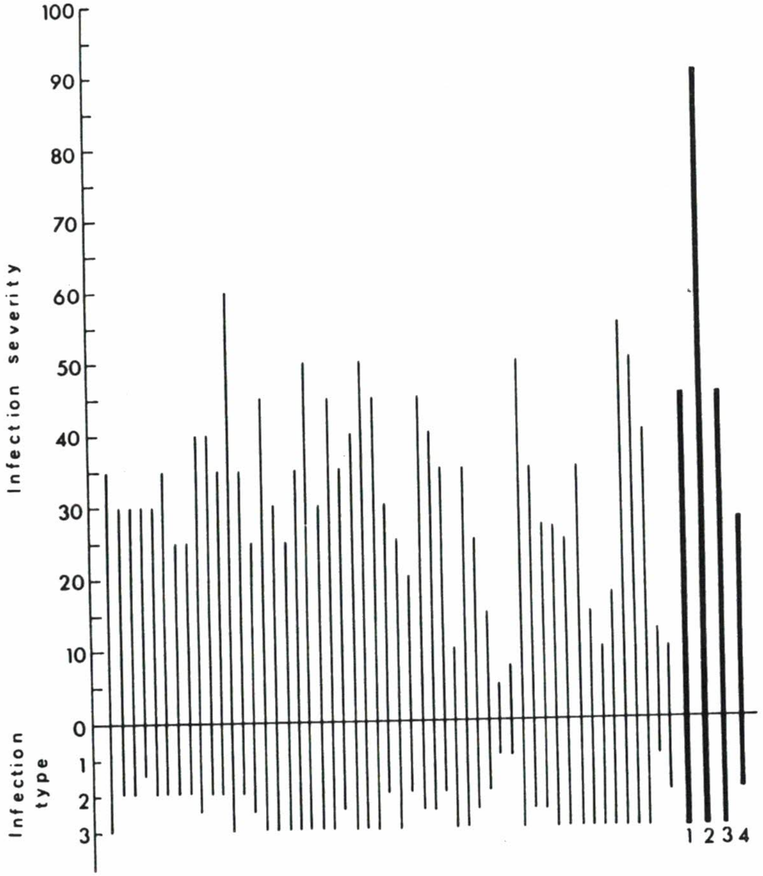

Fig. 1. Representative defense system against *Puccinia coronata* f. sp. *avenae* in transect samples of *Avena sterilis,* as compared with crown rust performance of slow-rusting cultivars Red Rustproof (**1**) and New Nortex (**3**), fast-rusting cultivar Markton (**2**), and cultivar Lodi (**4**), which is moderately resistant—moderately susceptible to crown rust at the adult stage. All accessions at the flowering–early milk age. [From Segal *et al.* (1980), reproduced with permission from "Plant Disease: An Advanced Treatise" (J. G. Horsfall and E. B. Cowling, eds.), Vol. 5, pp. 75–102. Academic Press].

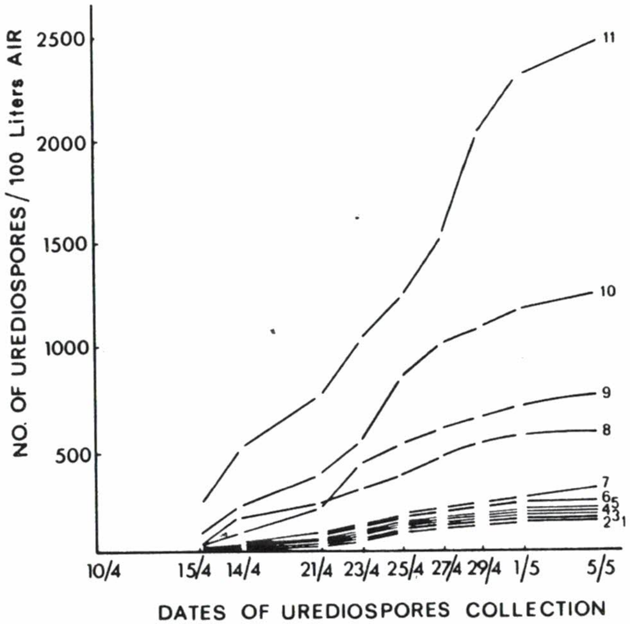

Fig. 2. Cumulative urediospore production of *Puccinia coronata* f. sp. *avenae* on the "standard" susceptible cultivar Markton (**11**); two recurrent hosts of the Iowa Multilines, Clintford + C649 (**9**) and C237-IV-89 (**10**); three Iowa Multiline cultivars (**1, 3, 5**); and five transect-reconstructed populations of *Avena sterilis* (**2, 4, 6, 7, 8**). Field tests, Bet Dagan, 1980. [From Segal *et al.*, (1982), reproduced with permission from "Resistance to Diseases and Pests in Forest Trees" (M. H. Heybroek, B. R. Stephan, and K. von Weissenberg, eds.), pp. 361–370. PUDOC Centre Agric. Publishing & Documentation, Wageningen].

In extensive field trials, the composition of crown rust populations and their urediospore production was studied on (1) natural populations of *A. sterilis,* (2) reconstructed *A. sterilis* populations, (3) Iowa Oat Multilines and their recurrent parents, and (4) the standard susceptible cultivar Markton (Segal *et al.*, 1982). The results have ascertained that although the ubiquitous race group 276-264 prevailed in all populations, its concentration was diluted on *A. sterilis* stands and the multilines. The seasonal urediospore production was lower in both the reconstructed *A. sterilis* populations and Iowa Multilines than on the recurrent hosts and Markton (Fig. 2). Notably, protection against crown rust in *A. sterilis* is conditioned by both slow rusting and low reaction, whereas in the Iowa Multilines defense is based mainly on low-reaction resistance (A. Segal, J. Manisterski, J. A. Browining, G. Fischbeck, and I. Wahl, unpublished). "*A. sterilis* populations con-

stitute to some extent 'natural multilines'" (Segal *et al.*, 1982) in indigenous ecosystems.

6. *Host Range*

The host range of *P. coronata* f. sp. *avenae* in Israel is very broad (Eshed and Dinoor, 1981). Eshed (1978) demonstrated that some plants serve as common hosts to two to seven *formae speciales* of *P. coronata*. Such hosts are conceivably suitable substrates for somatic hybridization between varieties. The performance of *formae speciales* and their hybrids seems to be "a reflection of the evolution of the host–parasite relationships started way back in the past and still going on at present in natural ecosystems" (Eshed, 1978).

7. *Evolution Tendencies*

Rhamnus is the putative primary host of *Puccinia coronata* (Klebahn, 1904, p. 180 and Table VI: Leppik, 1967, Fig. 1). The fungus "radiated" from this source to the secondary Festucoideae hosts. The wide range of alternative graminicolous hosts of *P. coronata* f. sp. *avenae* in Israel attests to the antiquity of the fungus in the region (Wahl and Anikster, 1982). Another piece of evidence supporting this hypothesis is the countrywide prevalence of the microcyclic *Puccinia mesnieriana* Thüm. on *Rhamnus*. This microform most probably descended from *P. coronata* in a process of protracted regressive evolution. Observations of many years have revealed that *P. mesnieriana* is distinctly more common in Israel than aecia of *P. coronata* f. sp. *avenae*. Apparently the evolutionary process has reached a phase marked by decline of the gametophytic stage of the progenitor and upsurge of its short-cycled progeny. The semiarid environment favors evolution of short-cycled rusts that are adapted for survival under adverse conditions (Anikster and Wahl, 1979). Aecia of *P. coronata* f. sp. *avenae* and telia of *P. mesnieriana* are occasionally found even on the same leaf.

H. LEAF RUST OF BARLEY

1. *Life Cycle of* Puccinia hordei *Otth.*

The taxonomy, biology, cytology, and evolutionary trends of *Uromyces* species causing leaf rust of barley were discussed elsewhere (Anikster and Wahl, 1979). Here we deal mainly with leaf rust caused by *P. hordei*. For a general treatment of this disease, see Clifford (Vol. II). *P. hordei* alternates in nature with *Ornithogalum* species (Fig. 3). Tranzschel (1939) reported that the presence of the alternate host in Crimea intensifies the disease on cultivated barley. Telia on the main host are profusely formed where *Ornithogalum* plants are present, and scarce in the central Soviet Union, where the alternate host was not found (Tranzschel, 1939). Similar preferential selection pressure of alternate hosts favoring the evolution of fungus strains developing abundant telia has also been observed in other heteroecious rust organisms (de Bary, 1879, p. 784; Klebahn, 1904, pp. 47–48; Wahl and Anikster, 1982).

The coevolution of the *Hordeum–P. hordei–Ornithogalum* system (Fig. 3) was one of the important topics of D'Oliveira's fundamental studies (1960a,b) on the evolution of rust fungi in the geographic regions where the centers of origin an genetic diversification of the main and alternate hosts overlap. He demonstrated that *P. hordei* from *H. spontaneum* is incompatible with *Ornithogalum* species in the primary centers of their diversification in Africa, south of the Sahara, where no native species of *Hordeum* are known to occur. In contrast, of all 33 species tested that belong to the secondary center of *Ornithogalum* diversification—the Mediterranean, Irano-Turanian, and Saharo-Sindian regions—only one, *Ornithogalum arabicum*, was not compatible with the rust. These regions cover either part of the center of origin and distribution of *H. spontaneum*, or they correspond to regions where barley is cultivated since prehistoric times (D'Oliveira, 1960b).

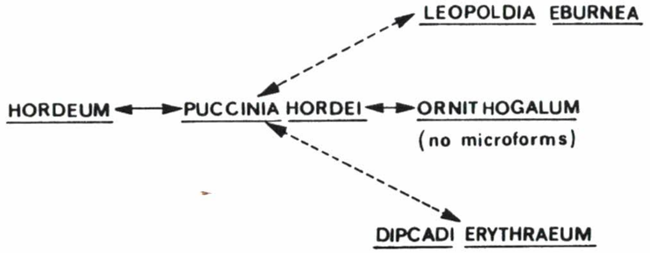

Fig. 3. Life cycle of *Puccinia hordei* in Israel. The fungus cycles in nature between the main *Hordeum* host and alternate *Ornithogalum* host (solid lines). The heteroecious process integrates parallel coevolution of the double complex: (1) *Hordeum*—rust fungus (sporophytic stage), and (2) *Ornithogalum*—rust fungus (gametophytic stage). This coevolution has taken place in geographic regions where the centers of origin and genetic diversification of the main and alternate hosts coincide (Oliveira, 1960b). *P. hordei* also cycles between *Hordeum* and *Dipcadi erythraeum*, or *Hordeum* and *Leopoldia eburnea*, artificially inoculated in the greenhouse or naturally inoculated on transplanting these alternate hosts to humid locations (dashed lines). Microforms correlated with *P. hordei* have never been found.

D'Oliveira postulated, "It seems as if, in that common ground, the rust and the hosts for its sporophytic and gametophytic stages have gone through a parallel process of evolution and adaptation" (1960b). He envisioned "the possible existence of aecidial hosts belonging to genera other than *Ornithogalum* and *Dipcadi,* in different genocenters of . . . *Hordeum* congenial to this rust and to nearly related species, in particular *Uromyces iranesis* Vienn.-Bourg." Studies in Israel have fully substantiated D'Oliveira's hypothesis. Anikster (1982) proved that *Dipcadi erythraeum* Webb et Bert. and *Leopoldia eburnea* Eig et Feinbr. are also potential alternate hosts of *P. hordei.*

2. *Life Cycle in Israel*

Israel is located in the center of origin and genetic diversification of *Hordeum spontaneum* C. Koch. Populations of this species are of countrywide distribution and represent a wide range of morphologic and physiologic variation. In addition, the following species belong to the native *Hordeum* flora, *H. bulbosum* L. (tetraploid type, $2n = 28$), and *H. murinum* L. The *Hordeum* center of diversification coincides with that of the genus *Ornithogalum,* consisting of *O. narbonense* L., *O. brachystachys* C. Koch, *O. divergens* Bor., *O. eigii* Feinbr., *O. lanceolatum* Lab., *O. montanum* Cyr., and *O. trichophyllum* Boiss. et Heldr. The *Ornithogalum* flora coexists in many areas with *Hordeum* plants, and particularly with *H. spontaneum* and *H. bulbosum.*

The listed *Hordeum* species are annually attacked by *P. hordei.* Parasitically the fungus is confined to the source host species, except that reciprocal inoculations with leaf rust of *H. spontaneum* and *H. vulgare* L. were successful. For these reasons, *P. hordei* was subdivided into three *formae speciales* (Y. Anikster, unpublished), namely, *P. hordei* Otth f. sp. *spontanei* Anikst. (also virulent on cultivated barley); *P. hordei* Otth f. sp. *bulbosi* Anikst., and *P. hordei* Otth f. sp. *murini* Anikst. The latter *forma specialis* supersedes *P. hordei* f. sp. *murini* Buchw., which should not be considered as an autonomous species (Anikster and Wahl, 1979). Notably, according to D'Oliveira (1960a), "amongst hundreds of seedlings of *H. bulbosum* tested in Portugal, and belonging to several accessions from different regions, only one plant proved to be congenial to some of our physiologic races of this rust." These results and data obtained from Iran prompted D'Oliveira to suggest that *H. bulbosum* harbors a different *forma specialis* of leaf rust. Studies in Israel are in accord with this supposition. In contrast, Tranzschel (1939) maintained that *P. hordei* hibernates in many parts of the Soviet Union in the uredial stage on wild *H. bulbosum,* and the

alternate host was of little significance for the dissemination of the fungus.

The aforementioned three *formae speciales* of *P. hordei* are compatible with *Ornithogalum* plants being less specialized on the alternate host than on the main one (Anikster, 1982). For example, they all are capable of completing the life cycle on *O. brachystachys, O. eigii,* and *O. trichophyllum.* However, aeciospores from naturally inoculated *O. lanceolatum* and *O. montanum* studied thus far were infectious only on *H. bulbosum.*

The alternate *Ornithogalum* hosts are important in Israel in the perpetuation of *P. hordei* over the year. Barley plants desiccate at the beginning of the rainless season at the end of May and beginning of June. Dormant teliospores in barley stubble retain viability during the summer and start to germinate at the onset of the ensuing season in November, liberating basidiospores that infect the foliage of *Ornithogalum* plants that emerge at the same time. Aeciospores thus formed infect seedlings of the native wild and cultivated barley cultivars. Presumably the coordinated sequence of development of different stages of the life cycle of the fungus and its hosts, and the adaptability to diverse environmental conditions are an outcome of a prolonged host–parasite coevolution (Anikster and Wahl, 1979).

Germinating teliospores of *P. hordei* from *H. spontaneum, H. bulbosum,* and *H. murinum* induce aeciospore formation on *Dipcadi erythraeum* and *Leopoldia eburnea* (Fig. 3). Both species are restricted in distribution to the desert areas of Israel, which are practically free of *P. hordei.* However, accessions of these two species emerging from bulbs planted by us in relatively humid regions became infected by the parasite as a result of natural inoculation (Anikster, 1982).

3. *Evolution of Parasitism*

In some cereal rusts, such as wheat stem rust and oat crown rust, the alternate host plays an important role in evolution of parasitism (Anikster and Wahl, 1979). In view of the significance of *Ornithogalum* plants in the life cycle of *P. hordei* in Israel, the parasitic specializations of cultures of aecial origin and uredial origin were compared. The cultures involved were sampled in nature countrywide over 4 years in five regions from *Ornithogalum brachystachys, O. eigii,* and *O. narbonense,* and from *H. spontaneum.* The experiments led to the following results:

1. Rust populations on the main and alternate host were similar in their parasitic features. For instance, 592 of 615 uredial cultures iso-

lated from *H. spontaneum*, and 348 of 447 cultures of aecial origin, had 17 virulence patterns in common. The term *virulence pattern* denotes a combination of resistant and susceptible reactions induced by a specific rust culture on components of a set of differential cultivars at the seedling stage (Simons *et al.*, 1979).

2. The sexual stage contributes to the diversification of the spectrum of parasitism of *P. hordei*. This conclusion is adduced from the following data: (1) Rust populations on the alternate host included five virulence patterns that were not identified in the inoculum from the main host, whereas only a single pattern was confined to uredial populations derived from *H. spontaneum*; (2) uredial populations isolated from *H. spontaneum* adjacent to a functional alternate host were parasitically more diverse than those originated from the main host distant from *Ornithogalum* plants (Y. Anikster, unpublished); (3) cultures virulent on barley cultivars endowed with the genes of resistance Pa_7 were obtained first from an alternate host and only thereafter from *H. spontaneum* (Golan *et al.*, 1978).

3. Some virulence patterns have predominated in Israel annually on both the alternate and main hosts during the 4 years of studies in all five regions implicated in the research. In contrast, Simons *et al.* (1979) could not find virulence patterns common to 1975 and 1976 aecial isolates of *Puccinia coronata* that were collected in Minnesota buckthorn-oat nursery that had been perpetuated since 1958. The difference is most likely attributable to the fact that in Israel the *H. spontaneum–P. hordei–Ornithogalum* association has evolved for millennia as a part of a natural ecosystem and reached a stage of balance. This does not seem to be the case in the human-managed oats–*P. coronata*–buckthorn association in Minnesota, which is of recent origin.

4. Rust populations on *H. spontaneum* and *Ornithogalum* have comprised cultures rendering ineffective all known genes for leaf rust resistance, including genes Pa_3, Pa_7, and Pa_9.

4. *Evolution of Defense against* Puccinia hordei

Over 10,000 accessions of *Hordeum spontaneum* were screened for low-reaction seedling resistance, by inoculating them with composite cultures of *P. hordei*. About 10% of the accessions showed low-reaction resistance except to the strain(s) virulent on Cebada Capa. The geographic distribution of resistance sources shows a distinct pattern, the sources being concentrated in areas where climatic conditions favor severe disease incidence and strong selection pressure (i.e., the Upper Galilee, Esdraelon Valley, and Judean Foothills) (Fig. 4). Practically no resistance of low-reaction type was detected in arid regions (Fig. 4). Resistance appears to be especially common in the vicinity of rusting *Ornithogalum* plants. G. Fischbeck (unpublished) found that *H. spontaneum* selections that are resistant to powdery mildew in Israel display resistance to this disease, leaf rust, and stripe rust in Europe as well. Moseman *et al.* (1980) reported high resistance to *P.*

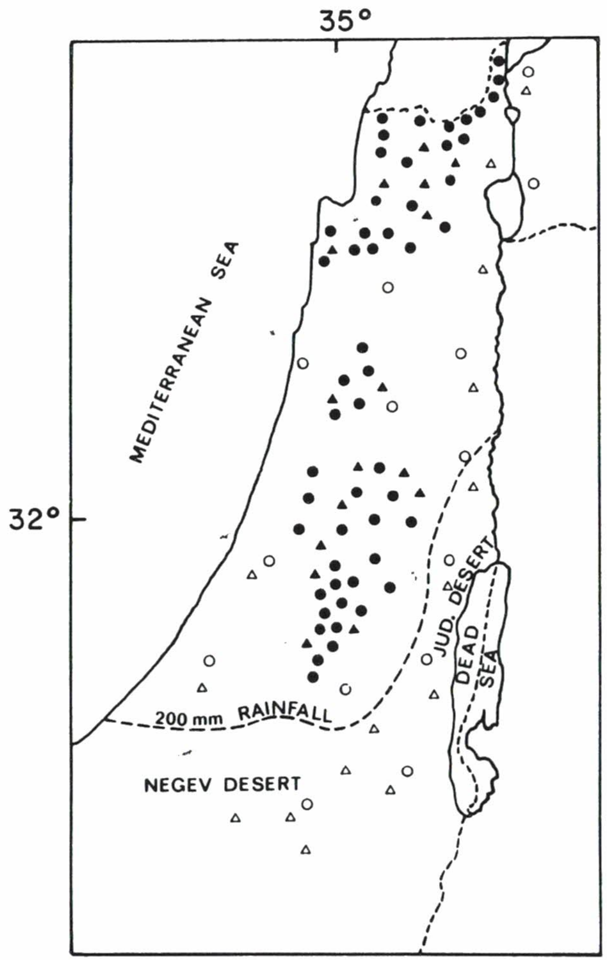

Fig. 4. Effect of *Puccinia hordei* incidence on evolution of low-reaction type resistance in populations of *Hordeum spontaneum*. Resistant barley accessions (▲) were found in geographic regions favorable for disease development, and particularly near rusted *Ornithogalum plants (●). Susceptible accessions of H. spontaneum* (△) were prevalent in the Negev desert and the Judean desert with annual rainfall less than 200 mm, where *Ornithogalum* plants (○) do not rust. Aridity prevents *P. hordei* development and selection for rust resistance in *H. spontaneum* (Y. Anikster, J. G. Moseman, and I. Wahl, unpublished).

hordei in *H. spontaneum* selections from Israel, which was frequently combined with resistance to other diseases in the United States. The minimum number of genes conferring resistance in the five *H. spontaneum* accessions to culture 57.19 of *P. hordei* was one, two, or three, depending on the accession.

Y. Anikster's recent studies (unpublished) revealed that *H. spontaneum* in Israel is a rich pool of resistance to leaf rust of the slow-rusting and late-rusting type.

5. *Reaction of* Ornithogalum *Plants*

About 8000 accessions of the native *Ornithogalum* species were inoculated with 300 different cultures of *P. hordei*, and about 18,650 successful infections were obtained. Only very few hypersensitive reactions were elicited. They were limited to the foliage of *O. nar-* actions were elicited. They were limited to the foliage of *O. narbonense.* No hypersensitive reactions were found on artificially inocu- *bonense.* No hypersensitive reactions were found on artificially inoculated foliage or bulbs or other *Ornithoealum* species. Presumably, other types of defense protect *Ornithogalum* plants from the rust organism. Cross sections through the fungus-bearing scale tissue stained in cotton blue solution reveal formation of intracellular hyphae invading the host cells by filamentous proliferations (Lumbroso *et al.*, 1977). Such haustoria-like structures, described by Harder and Chong (Chap- ter 14, this volume), differ distinctly in structure and shape from haustoria produced in the cereal host, and occur in a number of alternate hosts of heteroecious rusts.

6. Puccinia hordei–Uromyces *Relationship*

Taxonomic, physiologic, and cytologic problems in *Uromyces* species on barley in Israel were elaborated by Anikster and Wahl (1979). They postulated that all local barley *Uromyces* species and their short- cycled derivatives on Liliaceae are phylogenetically correlated with *P.* *hordei* in the sense of Arthur *et al.* (1929, pp. 100–101) or Cummins (1959, p. 9). Notably, although barley *Uromyces* species are correlated with a number of microcyclic species formed on their Liliaceae alter- nate hosts (Viennot-Bourgin, 1969), microforms associated with *P.* *hordei* were never found. Figure 5 shows the correlation of macrocylic *Uromyces* organisms with their microcyclic derivatives. All impli- cated macrocylic and microcylic taxa of *Uromyces* and *Puccinia* are compatible with *Leopoldia eburnea*. The development of short-cycled descendants attests to the more ancient origin of barley *Uromyces* rusts. *P. hordei* evidently has not yet reached the stage of simplifica- tion in the retrogressive process of evolution, and is presumably younger than its *Uromyces* counterparts.

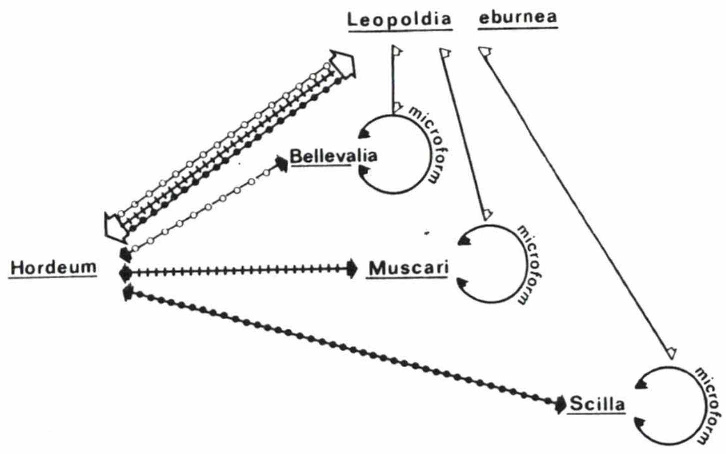

Fig. 5. Heteroecious *Uromyces* species cycling in nature between the *Hordeum* main hosts and alternate hosts belonging, respectively, to the genera *Bellevalia* (-o-o-o-o-o-), *Muscari* (++++++++++), or *Scilla* (•••••••••). Each rust species is compatible only with one of the alternate hosts, but all rusts alternate with *Leopoldia eburnea* in artificial inoculation trials. *Bellevalia, Muscari*, and *Scilla* alternate hosts harbor in nature microforms ↻ confined to the source host and phylogenetically correlated with the respective heteroecious rust species. Each of the microforms is compatible in artificial inoculation trials with *L. eburnea* (▹—▹). The latter species is a common host for all heteroecious *Uromyces* rusts on *Hordeum*, their microforms, and for *Puccinia hordei*. Each rust preserves on *L. eburnea* its parasitic specificity with respect to the source hosts (Y. Anikster, unpublished).

I. DEFENSE OF MAIZE AGAINST RUSTS

The problems of maize protection against the two rust fungi, *Puccinia polysora* Underw. and *P. sorghi* Schw., in the center of evolution of the crop were admirably analyzed by Borlaug (1972). Herein are condensed some of his findings and ideas.

Maize apparently originated in the highlands of Mexico, Guatemala, and perhaps Peru, long before the beginning of recorded history. Its wild forms were used for food about 7000 years ago, whereas cultivation was extensive in some areas about 5000 years ago.

Originally, maize was cultivated as an open-pollinated crop throughout Mexico, Central America, and the highlands of northern South America. Open-pollinated cultivars remain the basis of maize cultivation in most of Latin America, Africa, and Asia.

Two rust species attack maize in Latin America: *P. sorghi*, which is common at higher elevations and lower temperatures, and *P. polysora*, which predominates at higher temperatures. "Although one or the other of these rusts is commonly found infecting nearly every plant of

maize throughout its natural range in Mexico, Central America, and northern South America, infection seldom occurs in sufficient intensity to cause appreciable damage, except rarely and locally," where the equilibrium existing between hosts and pathogens is upset. Borlaug concluded that a host–parasite balance conditioned by general resistance "*is established on the basis of both latitude and elevational environments, resulting in harmonious survival of host and pathogen with little damage being done to either*" (Borlaug's italics).

Kim and Brewbaker (1977) reported the effectiveness of general resistance in maize to *P. sorghi* in Hawaii. According to Hooker (1973), general (nonspecific) resistance to *P. sorghi* is common in American maize and "is believed to be the major reason why *P. sorghi* fails to develop in destructive proportions in the U.S.A." Van der Plank (1968) maintained that resistance to *P. polysora* is general ("horizontal") or at least mostly general. Resistance to both rusts in maize can also be accounted for by the genetic heterogeneity of an open-pollinated crop.

III. Concluding Remarks

A. CENTERS OF COEVOLUTION

Nelson (1979) described host–pathogenic fungi coevolution as "a unique and spectacular biological saga." The saga envelops a multiplicity of fundamental problems, and some of them were elaborated elsewhere (Anikster and Wahl, 1979). This chapter deals mainly with the plant pathological aspects.

There seems to be a general consensus that protection against disease and parasite virulence should be sought and studied in the centers of host–obligate parasite origin. In the case of heteroecious rusts, the studies should be pursued in the common centers of origin of the main and alternate hosts. In such centers, genes of plant defense and fungus virulence are stockpiled. There, the host and parasite have reached a state of balanced polymorphism as a result of reciprocal natural selection, associated with their prolonged coexistence. Recognition of mechanisms regulating the equilibrium provides information that is most useful for managing disease and its control in agroecosystems. Theoretical aspects of such equilibria are discussed by Growth (Chapter 8, this volume).

In the foregoing sections, summaries have been made of the basic attributes of host–parasite coevolution and balance, in three different

regions: (1) the Caucasus and its neighboring areas, (2) the Mediterranean regions (Portugal and Israel), and (3) Latin America. In the first two regions, studies dealt with small-grain rusts, whereas in Latin America, maize rusts were investigated. Significantly, conclusions gleaned from the three remote regions have a common pivotal base.

Zhukovsky (1964, pp. 89–92) presented a comprehensive picture of the host–parasite coevolution process in the Caucasus. He found that the most promising sources of defense against diseases can be selected in the home of the host–parasite systems. Both components in the couplet vary continuously and reach dynamic balance, implicating a multiplicity of protection types and virulence forms. The latter are often new and agressive. In those regions is located the center of origin of *Puccinia graminis, P. recondita,* and *P. striiformis.* The spectra of fungus races and biotypes are more heterogenic in Transcaucasia than elsewhere in the Soviet Union.

B. DEFENSE TYPES AND THEIR INTEGRATION IN POPULATIONS

Plant communities in the Caucasus and the neighboring areas are conglomerates of moderate resistance, "field resistance," tolerance, and moderate to high susceptibility. They are devoid of absolute immunity. This is true even of the most resistant *Triticum* species, such as *T. persicum* (*T. carthlicum*) and *T. zhukovskyi.*

Studies in Israel reveal a similar situation. The most common form of protection is slow rusting, with symptoms resembling Zhukovsky's "field resistance." It was further proven that the protection systems comprise, in varying proportions, resistance of low- to intermediate-reaction type, slow rusting, tolerance, and escape. Genetic diversity, in itself, is not a safeguard against epidemics. Effective diversity needs to be "ordered" and "patterned" (Dinus, 1974), or molded by selection pressure of the parasite under specific environmental conditions. Segal's research (1981) has ascertained that "population resistance" (Browning *et al.,* 1979) inherent in indigenousness, which effectively sheltered *A. sterilis* populations from crown rust in northern Israel, was less satisfactory when the populations were maintained in the central coastal plain. Populations from arid regions, where crown rust incidence is very mild and selection pressure inconsequential, develop rust rather seriously in the central coastal plain. Similarly, Borlaug (1972) stressed that "if one moves open-pollinated maize lowland varieties, into higher elevations, they will rust severely." By the same

token, when high-elevation maize varieties are sown in the tropical lowlands, they become seriously infected. Each environment requires a suitable set of genes to mollify disease incidence by damping excessive perturbations.

Studies in Israel have also demonstrated that lush stands of *A. sterilis* are permanently exposed to the *P. coronata* f. sp. *avenae* race group 276-264, which comes close to the conceptual "superrace" as far as hexaploid oats are concerned. These stands do not appear to suffer visibly from the disease. Obviously, the protection associated with indigenousness buffers *A. sterilis* against this race group. This situation seems to dispel the lingering fears of potential hazards that may arise with the increased prevalence of "superraces." The findings in Israel are in agreement with Borlaug's reports on maize rusts, which infect nearly every plant of the crop throughout its natural range. Yet the infection is seldom intense enough to cause appreciable damage. The dilemma presumably starts when humans disturb the natural balance in agroecosystems. "Man domesticated species of small grains, took them from their centers of origin, improved them agronomically, always narrowing their genetic base. . . . Man-guided evolution of the pathogen, boom-and-bust years with the host, the vicious circle of small grain 'improvement,' and low marks of specific resistance as means of disease control, were the all-too-frequent results" (Browning *et al.*, 1979).

C. STABILIZING SELECTION

Van der Plank (1963) introduced the concept of stabilizing selection. He stated that "we take it as axiomatic that simple races are the fittest to survive on simple varieties." Parlevliet (1981) discussed the merits and demerits of the concept and concluded, "although SS [stabilizing selection] sensu van der Plank seems to be an empty concept in crop pathosystems, it need not to be so in wild pathosystems." Studies on crown rust and stem rust of *A. sterilis* do not attest to the applicability of van der Plank's "axiom" to wild pathosystems. Research conducted in Israel for over 30 years has demonstrated a continued and countrywide prevalence of crown rust race 276 and oat stem rust race 72. Both races incorporate many "unnecessary" virulence genes that do not seem to impair the parasitic fitness of the fungi. Brodny's studies on race 276 of *P. coronata* f. sp. *avenae* (1980) demonstrate its adaptability to a wide range of ecologic conditions, high urediospore productivity, and strong infectivity. These findings support Leonard's contention (1977) that "Thus, unnecessary genes for virulence can attain high

frequency in a population if they are introduced in a genotype of superior fitness."

D. PLURIVORITY VERSUS PARASITIC SPECIALIZATION

In agroecosystems "obligate plant pathogens . . . exhibit a great deal of specificity and can grow only on certain varieties of the host" (Sequeira, 1979). Hence, considerable interest if focused on pathogen specificity on the species and cultivar level (Heath, 1981). Specificity has a decisive impact on the achievements of conventional breeding for disease resistance and is responsible for the ephemerality of the attained protection.

Results of studies in natural ecosystems reveal an entirely different picture (Browning, 1979). Gerechter-Amitai's research on *Puccinia graminis* (1973), as well as investigations on *P. coronata* (Eshed and Dinoor, 1981) and on barley powdery mildew (Eshed and Wahl, 1970), show that fungi characterized by strict specificity in agroecosystems possess a wide host range in natural ecosystems. Eshed and Wahl (1970) postulated that the wide host range among indigenous grasses is at least partly accounted for by the major trends in the phylogeny of Gramineae. According to Stebbins (1956), "most of the common species of grasses . . . contain in varying proportions, gene combinations derived from two, three, four or more separate and sometimes widely diverging ancestors." Conceivably wild grasses, as a result of their genetic interrelationships, are less specialized in their rust reaction than cultivated cereals.

Savile (1979) attempted to explain the wide host range of *P. coronata* f. sp. *avenae* in Israel by claiming that "*Puccinia coronata* is an atypical species" and by alluding that "we recognize many genera of festucoid grasses more for their possession of handy key characters than for their genetic diversity." The first explanation is hardly plausible, because *P. graminis* f. sp. *avenae* and the barley powdery mildew fungus, too, have similarly broad host ranges. In our opinion, Savile's second explanation is more convincing and agrees with Stebbins' Gramineae phylogeny concept, which helps in understanding the wide host range of the mentioned parasites on grasses.

Congeniality in host–parasite associations at the centers of their origin becomes obvious also on the intraspecific level of the host. In our studies, interactions of *H. spontaneum* with indigenous powdery mildew cultures, and of *A. sterilis* with native crown rust isolates, were more compatible than in the case of infection with alien cultures (Segal *et al.*, 1980). Incompatible coexistence is characterized by low

reaction and symptoms of hypersensitivity. This may explain the success in various countries in selecting *H. spontaneum* and *A. sterilis* from Israel for low-reaction resistance to barley powdery mildew and oat crown rust, respectively. In these tests, fungus cultures originating in the countries to which the hosts were introduced were used for inoculation. Plants in Israel exhibiting compatible reaction are most likely protected by mechanisms other than low reaction.

Besides, in dealing with the parasitic specialization of modern rust fungi, we have to consider the fact that ancestral rusts were putatively plurivorous (pleophagous), that is, parasitic on a variety of taxonomically remote hosts. Fischer (1898, p. 115) asserted that Uredineae were originally "omni- or plurivorous." Dietel (1899, p. 117) speculated that rust fungi in ancient times were plurivorous. Their specialization was very inconspicuous, and some rust species inhabited a number of plant families. Also Klebahn (1904, pp. 163–165, 179–180) favored the idea of plurivority (pleophagy) in ancestral rusts. He contended that the origin of heteroecious rust organisms should be sought mainly on the alternate host, from which the fungus migrated to numerous species and families. On the latter hosts the fungus became diversified and attained advanced specialization. The concept of evolution of parasitic specialization from unspecialized forms is shared by Ellingboe (1976), Keen (1982), Nelson (1979), and Parlevliet (1979b). Ellingboe (1976) envisioned that specific interactions associated with incompatibility were superimposed upon a "basic compatibility" between host and parasite. In the case of many graminicolous rusts, the fungus expanded from the alternate host to grasses. According to Johnson *et al.* (1967), "most authorities assume that long before cereals came into existence, the rusts were present on grasses ancestral to cereals and that the rusts adapted to cereals as they came into being." On cereal cultivars, which are genetically well-delimited entities, specialization in the host–parasite interaction made great progress. Hence, the transition of hosts to nonhosts on various taxonomic levels may not be less important than the reverse process.

In Israel small grains occupy a limited acreage. Still, their wild ancestors and relatives are ubiquitous and prolific, and they rust annually. These rusts are mostly at the grass-host stage of evolution. The outlined phylogenetic approach may contribute to a better understanding of the plurivorous behavior of rusts on indigenous grasses in the centers of their origin and genetic diversification. The monokaryotic phase in heteroecious rusts is distinctly less specialized than the dikaryotic one (Green, 1971; Wahl and Anikster, 1982) and has thus preserved the attributes of its progenitors. "The relatively unspecialized growth habit of pycnial and aecial mycelia . . . may explain the wide host range of some pycnial and aecial rusts," in contrast to the extreme parasitic specialization of uredial and telial rusts (Rijkenberg and Truter, 1973).

Elucidation and exploitation of factors conditioning host–parasite interaction at the "basic compatibility" stage of evolution (*sensu* Ellingboe, 1976) is expected to stabilize disease resistance since this association does not seem to be influenced by specialization.

E. PROSPECTS

As put by Dunin (1959), "production of disease resistant crops is not a very difficult problem. The most difficult objective to attain is to insure durable resistance to cultivars in mass production." This is the crux of the problem. According to Kilpatrick (1975), average longevity of conventional resistance to wheat rusts throughout the world was less than 10 years. Borlaug (1978) emphasized that "stable resistance to the three rusts remains the first objective of the wheat scientist."

The studies reported here on the evolution of rust disease in the centers of their host origin in the Caucasus, Israel, and Latin America show that in these regions indigenous wild and cultivated cereals attain a state of balanced coexistence with the rust fungi. The disease cannot be obviated, but it can be tamed and kept within constraints. The regulatory mechanisms stem from the fact that the protection systems in these plant communities consist of various types and levels of defense elements, often including conventional resistance. Their integration patterns are molded by reciprocal host–parasite selection pressure decisively influenced by environmental conditions. This is the essence of Browning's concept (1974) of "protection of indigenousness." The importance of extrapolating this concept to agroecosystems was emphasized (Browning *et al.*, 1982).

Corollary research on rust virulence proves that some strains can be extremely virulent and approach the conceptual "superrace." Yet their destructiveness is buffered by the dynamic balance among the different protection components and the patterns of their integration and cohesion in defense systems. Studies on parasitism may furnish a deeper insight and broader view on their virulence potential and a preview of what can be expected in other regions (Wahl, 1958).

It is postulated that information ferreted out from studies on host–parasite coevolution in their centers of origin can be used to make "shifty" enemies at least partly less shifty and to surmount the "stub-

born biological barrier to rapid progress in increasing and insuring future food supplies" (Stakman, 1968).

Acknowledgments

This chapter is dedicated to the shining memory of Esther Wahl.

We are grateful to Drs. J. A. Browning, G. Fischbeck, J. G. Moseman, and G. Viennot-Bourgin for their most valuable cooperation over the years. Dr. Browning was the pioneering and leading collaborator in studies on "protection of indigenousness." Drs. Z. M. Azbukina, F. Młodzianowski, D. B. O. Savile, and Z. Urban kindly provided important literature and valuable information.

Our studies were supported by the United States Department of Agriculture, under PL 480, and by the United States–Israel Binational Science Foundation (BSF), Jerusalem, Israel.

References

Anikster, Y. (1982). Alternate hosts of *Puccinia hordei. Phytopathology* **72,** 733–735.

Anikster, Y., and Wahl, I. (1979). Coevolution of the rust fungi on Graminae and Liliaceae and their hosts. *Annu. Rev. Phytopathol.* **17,** 367–403.

Arthur, J. C. *et al.* (1929). "The Plant Rusts (Uredinales)." Wiley, New York.

Azbukina, Z. M. (1971). Rust fungi producing aecia on Berberidaceae species in the Far East. *Mikol. Fitopatol.* **5**(5), 420–425 (in Russian).

Borlaug, N. E. (1972). A cereal breeder and ex-forester's evaluation of the progress and problems involved in breeding the rust resistant forest trees: Moderator's summary. *In* "Biology of Rust Resistance in Forest Trees," Mis. Publ. No. 1221. pp. 615–642. U.S. Dept. Agric. For. Serv. Washington, D.C.

Borlaug, N. E. (1978). Stable resistance comes first. *In* "CIMMYT Review 1978," p. 56. Centro Internacional de Mejoramiento de Maiz y Trigo, Mexico.

Brodny, U. (1980). Studies on the nature of mechanisms determining the composition of physiological races populations of *Puccinia coronata* Cda. var. *avenae* Fraser & Ledingham on *Avena sterilis* L. in Israel. Ph.D. Thesis, Tel Aviv University, Tel Aviv (in Hebrew, with English summary).

Brodny, U., Briggle, L. W., and Wahl, I. (1976). Reaction of U.S. crown rust resistant oat selections and Israeli *Avena sterilis* selections to *Puccinia coronata* var. *avenae. Plant Dis. Rep.* **60,** 902–906.

Browder, L. E. (1980). A compendium of information about named genes for low reaction to *Puccinia recondita* in wheat. *Crop Sci.* **20,** 775–779.

Browning, J. A. (1974). Relevance of knowledge about natural ecosystems to development of pest management programs for agroecosystems. *Proc. Am. Phytopathol. Soc.* **1,** 191–199.

Browning, J. A. (1979). Genetic protective mechanisms of plant-pathogen populations: Their coevolution and use in breeding for resistance. *In* "Biology and Breeding for Resistance" (M. K. Harris, ed.), pp. 52–75. Texas A&M University, College Station.

Browning, J. A., and Frey, K. J. (1969). Multiline cultivars as a means of disease control. *Annu. Rev. Phytopathol.* **7,** 355–382.

Browning, J. A., Frey, K. J., McDaniel, M. E., Simons, M. D., and Wahl, I. (1979). The biologic of using multilines to buffer pathogen populations and prevent loss. *Indian J. Genet. Plant Breed.* **39,** 3–9.

Browning, J. A., Manisterski, J., Segal, A., Fischbeck, G., and Wahl, I. (1982). Extrapolation of genetic and epidemiologic concepts from indigenous ecosystems to agroecosystems. *In* "Resistance to Diseases and Pests in Forest Trees" (H. M. Heybroek, B. R. Stephan, and K. von Weissenberg, eds.), pp. 371–386. Pudoc Cent. Agric. Publ. & Doc., Wageningen.

Chabelska, H. (1938). Life-cycle of the rust on *Anchusa strigosa Lab. Palest. J. Bot., Jerusalem Ser.* **1,** 101–103.

Coons, G. H. (1953). Breeding for resistance to disease. *In* "Plant Diseases," The Yearbook of Agriculture 1953, pp. 174–192. U.S. Dept. Agric., Washington, D.C.

Cummins, G. B. (1959). "Illustrated Genera of Rust Fungi." Burgess, Minneapolis, Minnesota.

de Bary, A. (1879). *Aecidium abietinum. Bot. Centralbl.* **37**(49), 777–789.

Dietel, P. (1899). Waren die Rostpilze in früheren Zeiten plurivor? *Bot. Centralbl.* **79,** 81–85, 113–117.

Dietel, P. (1904). Betrachtungen über die Verteilung der Uredineen auf ihren Nährpflanzen. *Zentralbl. Bakteriol., Parasitenkd. Infektionskr., Abt. 2, Naturwiss.: Allg. Landwirtsch. Tech. Mikrobiol.* **12,** 218–234.

Dinoor, A. (1967). The role of cultivated and wild plants in the life cycle of *Puccinia coronata* Cda. var. *avenae* F. & L. and the disease cycle of oat crown rust in Israel. Ph.D. Thesis, Hebrew University, Jerusalem (in Hebrew, with English summary).

Dinus, R. J. (1974). Knowledge about natural ecosystems as a guide to disease control in managed forests. *Proc. Am. Phytopathol. Soc.* **1,** 184–190.

D'Oliveira, B. (1940). Notas sobre a produção da fase aecidica de algumas ferrugens dos cereais em Portugal. *Rev. Agron.* **28**(2), 201–208 (in Portugese, with English summary).

D'Oliveira, B. (1951). The centers of origin of cereals and the study of their rusts. *Agron. Lusit.* **13**(3), 221–226.

D'Oliveira, B. (1960a). Ideas concerning the evolution and distribution of cereal rusts. *Port. Acta Biol. Ser. A* **6**(2), 111–124.

D'Oliveira, B. (1960b). Host range of the aecidial stage of *Puccinia hordei* Otth. *Malhoramento* **13,** 161–188.

Dunin, M. S. (1959). Preface to the Russian edition of the book by E. C. Stakman and J. G. Harrar. "Principles of Plant Pathology." Innostrannoi Literatury, Moscow.

Ellingboe, A. H. (1976). Genetics of host-parasite interactions. *Encycl. Plant Physiol., New Ser.* **4,** 761–778.

Eshed, N. (1978). The genetical basis of the pathogenicity of *Puccinia coronata* Cda. in Israel. Ph.D. Thesis, Hebrew University, Jerusalem (in Hebrew, with English summary).

Eshed, N., and Dinoor, A. (1981). Genetics of pathogenicity in *Puccinia coronata:* The host range among grasses. *Phytopathology* **71,** 156–163.

Eshed, N., and Wahl, I. (1970). Host ranges and interrelations of *Erysiphe graminis hordei, E. graminis tritici,* and *E. graminis avenae. Phytopathology* **60,** 628–634.

Feldman, M., and Sears, E. R. (1981). The wild gene resources of wheat. *Sci. Am.* **244,** 102–112.

Fischer, E. (1898). Entwicklungsgeschichtliche Untersuchungen über Rostpilze. 1. Über Beziehungen zwischen Uredineen, welche alle Sporenformen besitzen und solchen

von reduziertem Entwicklungsgang. *Beitr. Kryptogamenflora Schweiz* **1**(1), 109–121.

Flor, H. H. (1971). Current status of the gene-for-gene concept. *Annu. Rev. Phytopathol.* **9**, 275–296.

Gäumann, E. (1959). Die Rostpilze Mitteleuropas. *Beitr. Kryptogamenflora Schweiz* **12,** 7–1407.

Gerechter-Amitai, Z. K. (1973). Stem rust, *Puccinia graminis* Pers. on cultivated and wild grasses in Israel. Ph.D. Thesis, Hebrew University, Jerusalem (in Hebrew, with English summary).

Gerechter-Amitai, Z. K. (1982). Major and minor genes for resistance to stripe rust in wild emmer wheat, *Triticum dicoccoides* Körn. p. B/4. *In* "Gifrid Workshop on Wheat and Barley Breeding and Cultivation under Semi-arid and Arid Conditions," pp.

Gerechter-Amitai, Z. K., and Wahl, I. (1966). Wheat stem rust on wild grasses in Israel. Role of wild grasses in the development of the parasite and in breeding for resistance. *In* "Cereal Rust Conference," pp. 207–217. Plant Breed. Inst., Cambridge, England.

Gerechter-Amitai, Z. K., and Loegering, W. Q. (1977). Genes for low reaction to *Puccinia graminis tritici* in *Aegilops* and *Triticum. Crop Sci.* **17,** 830–832.

Gerechter-Amitai, Z. K., Wahl, I., Vardi, A., and Zohary, D. (1971). Transfer of stem rust seedling resistance from wild diploid einkorn to tetraploid *durum* wheat by means of a triploid hybrid bridge. *Euphytica* **20,** 281–285.

Golan, T., Anikster, Y., Moseman, J. G., and Wahl, I. (1978). A new virulent strain of *Puccinia hordei. Euphytica* **27,** 185–189.

Goulden, C. H., Newton, M., and Brown, A. M. (1930). The reaction of wheat varieties at two stages of maturity to sixteen physiologic forms of *Puccinia graminis tritici. Sci. Agric.* **11,** 9–25.

Green, G. J. (1971). Hybridization between *Puccinia graminis tritici* and *Puccinia graminis secalis* and its evolutionary implications. Can. J. Bot. **49,** 2089–2095.

Harder, D. E. (1980). Virulence and distribution of *Puccinia coronata avenae* in Canada in 1979. *Can J. Plant Pathol.* **2,** 249–252.

Harlan, J. R., and Zohary, D. (1966). Distribution of wild wheats and barley. *Science* **153,** 1074–1080.

Hassebrauk, K. (1965). Nomenklatur, geographische Verbreitung und Wirtsbereich des Gelbrostes, *Puccinia striiformis* West. *Mitt. Biol. Bundesanst. Land- Forstwirtsch., Berlin-Dahlem* **116.**

Heath, M. C. (1981). A generalized concept of host-parasite specificity. *Phytopathology* **71,** 1121–1123.

Hooker, A. L. (1973). Maize. *In* "Breeding Plants for Disease Resistance" (R. R. Nelson, ed.), pp. 132–154. Pennsylvania State Univ. Press, University Park.

Johnson, T., Green, G. J., and Samborski, D. J. (1967). The world situation of the cereal rusts. *Annu. Rev. Phytopathol.* **5,** 183–200.

Keen, N. T. (1982). Specific recognition in gene-for-gene host–parasite systems. *Adv. Plant Pathol.* **1,** 35–82.

Kilpatrick, R. A. (1975). New wheat cultivars and longevity of rust resistance, 1971–75. *U.S., Agric. Res. Serv., Northeast. Reg. [Rep.] ARS-NE* **64.**

Kim, S. K., and Brewbaker, J. L. (1977). Inheritance of general resistance in maize to *Puccinia sorghi* Schw. *Crop Sci.* **17,** 456–461.

Kislev, M. E. (1982). Stem rust of wheat 3300 years old found in Israel. *Science* **216,** 993–994.

Klebahn, H. (1904). "Die wirtswechselnden Rostpilze." Borntraeger, Berlin.

Leonard, K. J. (1977). Selection pressures and plant pathogens. *Ann. N.Y. Acad. Sci.* **287,** 207–222.

Leppik, E. E. (1961). Some viewpoints on the phylogeny of rust fungi IV. Stem rust genealogy. *Mycologia* **53,** 378–405.

Leppik, E. E. (1965). A pathologist's viewpoint on plant exploration and introduction. *U.S., Agric. Res. Serv., Plant Introd. Invest.* **1,** 1–5.

Leppik, E. E. (1967). Some viewpoints on the phylogeny of rust fungi. VI. Biogenic radiation. *Mycologia* **59,** 568–579.

Leppik, E. E. (1970). Gene centers of plants as sources of disease resistance. *Annu. Rev. Phytopathol.* **8,** 323–344.

Littlefield, L. J. (1981). "Biology of the Plant Rusts." Iowa State Univ. Press, Ames.

Luke, H. H., Barnett, R. D., and Chapman, W. H. (1975). Types of horizontal resistance of oats to crown rust. *Plant Dis. Rep.* **59,** 332–334.

Lumbroso, E., Anikster, Y., Moseman, J. G., and Wahl, I. (1977). Completion of life cycles of *Puccinia hordei and Uromyces scillarum* on detached leaves of their hosts. *Phytopathology* **67,** 941–944.

Marková, J., and Urban, Z. (1977). To the knowledge of the brown rust of couch grass in Bohemia and Moravia. 2. *Ceska Mykol.* **31,** 72–80 (in Czech, with English summary).

Mode, C. J. (1958). A mathematical model for the coevolution of obligate parasites and their hosts. *Evolution* **12,** 158–165.

Moseman, J. G., Baenziger, P. S., and Kilpatrick, R. A. (1980). *Hordeum spontaneum*—an overlooked source of disease resistance. *Proc.—Eur. Mediterr. Cereal Rusts Conf., 5th, 1980* pp. 91–94. Bari and Rome, Italy.

Murphy, H. C., Wahl, I., Dinoor, A., Miller, J. D., Morey, D. D., Luke, H. H., Sechler, D., and Reyes, L. (1967). Resistance to crown rust and soilborne mosaic virus in *Avena sterilis. Plant Dis. Rep.* **51,** 120–124.

Nelson, R. R. (1973). The meaning of disease resistance in plants. *In* "Breeding Plants for Disease Resistance" (R. R. Nelson, ed.), pp. 13–25. Pennsylvania State Univ. Press, University Park.

Nelson, R. R. (1978). Genetics of horizontal resistance to plant diseases. *Annu. Rev. Plant Pathol.* **16,** 359–378.

Nelson, R. R. (1979). Some thoughts on the coevolution of plant pathogenic fungi and their hosts. *In* "Host-Parasite Interfaces" (B. B. Nickol, ed.), pp. 17–25. Academic Press, New York.

Parlevliet, J. E. (1979a). Components of resistance that reduce the rate of epidemic development. *Annu. Rev. Phytopathol.* **17,** 203–222.

Parlevliet, J. E. (1979b). The co-evolution of host–parasite systems. *Symb. Bot. Ups.* **22**(4), 39–45.

Parlevliet, J. E. (1981). Stabilizing selection in crop pathosystems: An empty concept or a reality? *Euphytica* **30,** 259–269.

Peterson, R. F. (1965). "Wheat." Leonard Hill Books, London.

Rijkenberg, F. H. J., and Truter, S.J. (1973). Haustoria and intracellular hyphae in the rusts. *Phytopathology* **63,** 281–286.

Robinson, R. A. (1980). New concepts in breeding for disease resistance. *Annu. Rev. Phytopathol.* **18,** 189–210.

Santiago, J. C. (1968). Physiologic specialization of the oat crown rust fungus in Portugal. *Cereal Rusts Conf., 1968* pp. 89–91. Oeiras, Portugal.

Savile, D. B. O. (1979). Fungi as aids to plant taxonomy: Methodology and principles. *Symb. Bot. Ups.* **22**(4), 135–145.

Savile, D. B. O., and Urban, Z. (1982). Evolution and ecology of *Puccinia graminis. Preslia* **54,** 97–104.

Schmidt, R. A. (1978). Diseases in forest ecosystems: The importance of functional diversity. *In* "Plant Disease: An Advanced Treatise" (J. G. Horsfall and E. B. Cowling, eds.), Vol. 2, pp. 287–315. Academic Press, New York.

Segal, A. (1981). Elements of resistance against *Puccinia coronata* Cda. var. *avenae* F. & L. and their integration in the defense structures of *Avena sterilis* L. populations in natural ecosystems undisturbed by man in Israel. Ph.D. Thesis, Tel Aviv University Tel Aviv (in Hebrew, with English summary).

Segal, A., Manisterski, J., Fischbeck, G., and Wahl, I. (1980). How plant populations defend themselves in natural ecosystems. *In* "Plant Disease: An Advanced Treatise" (J. G. Horsfall and E. B. Cowling, eds.), Vol. 5, pp. 75–102. Academic Press, New York.

Segal, A., Manisterski, J., Browning, J. A., Fischbeck, G., and Wahl, I. (1982). Balance in indigenous plant populations. *In* "Resistance to Diseases and Pests in Forest Trees" (H. M. Heybroek, B. R., Stephan, and K. von Weissenberg, eds.), pp. 361–370. Pudoc Cent. Agric. Publ. & Doc., Wageningen.

Sequeira, L. (1979). Recognition between plant hosts and parasites. *In* "Host–Parasite Interfaces" (B. B. Nickol, ed.), pp. 71–84. Academic Press, New York.

Simons, M. D. (1969). Heritability of crown rust tolerance in oats. *Phytopathology* **59,** 1329–1333.

Simons, M. D. (1972). Crown rust tolerance of *Avena sativa*—type oats derived from *Avena sterilis. Phytopathology* **62,** 1444–1446.

Simons, M. D., Martens, J. W., McKenzie, R. I. H., Nishiyama, I., Sadanaga, K., Sebesta, J., and Thomas, H. (1978). Oats: A standardized system of nomenclature for genes and chromosomes and catalog of genes governing characters. *U.S. Dep. Agric., Agric. Handb.* **509.**

Simons, M. D., Rothman, P. G., and Michel, L. J. (1979). Pathogenicity of *Puccinia coronata* from buckthorn and from oats adjacent to and distant from buckthorn. *Phytopathology* **69,** 156–158.

Stakman, E. C. (1968). What are the prospects for permanent control of cereal rusts? *Cereal Rusts Conf., 1968* pp. 217–230. Oeiras, Portugal.

Stebbins, G. L. (1956). Cytogenetics and evolution in the grass family. *Am. J. Bot.* **43,** 890–905.

Sztejnberg, A., and Wahl, I. (1976). Mechanisms and stability of slow stem rusting resistance in *Avena sterilis. Phytopathology* **66,** 74–80.

Tranzschel, W. A. (1939). Sovremiennoe sostaianie znanii po biologii rshavchin khlebnykh zlakov (Present status of knowledge about the biology of cereal rusts). *In* "Rshavchina Zernovykh Kultur" (Rusts of Ceral Crops) (N. A. Naumov and A. K. Zubareva, eds.), pp. 21–28. Selkhosgiz, Moscow.

Urban, Z. (1961). Zur Schwarzrostfrage in Böhmen. *Z. Pflanzenkd.* **27,** 67–68.

Urban, Z. (1968). Zum Artbegriff bei Rostpilzen. *In* "Das Art-und Rassenproblem bei Pilzen," Int. Symp. Werrningerode am Harz (1967), pp. 19–25.

Urban, Z. (1969). Taxonomie der parasitischen Pilze und die Widerstandsfähigkeit der Kulturpflanzen. *Ceska Mykol.* **23,** 236–242.

Urban, Z. (1980). Rust ecology and phytocenology as aids in rust taxonomy. *Rep. Tottori Mycol. Inst.* **18,** 269–273.

Van der Plank, J. E. (1963). "Plant Diseases: Epidemics and Control." Academic Press, New York.

Van der Plank, J. E. (1968). "Disease Resistance in Plants." Academic Press, New York.

Vavilov, N. I. (1939). Selekstia ustoichovykh sortov kak osnovnoi metod borby s rshavchinoi (Selection of resistant varieties as a basic method for rust control). *In* "Rshavchina Zernovykh Kultur" (Rusts of Cereal Crops) (N. Z. Naumov and A. K. Zubareva, eds.), pp. 3–20. Selkhozgyz, Moscow.

Viennot-Bourgin, G. (1969). Mission phytopathologique en Iran en 1968. *Ann. Phytopathol.* **1,** 5–36.

Wahl, I. (1958). Studies on crown rust and stem rust on oats in Israel. *Bull. Res. Counc. Isr., Sect. D* **6,** 145–166.

Wahl, I. (1959). Physiologic races of oat crown rust identified in Israel in 1956–59. *Bull. Res. Counc. Isr., Sect. D* **8,** 25–30.

Wahl, I. (1970). Prevalence and geographic distribution of resistance to crown rust in *Avena sterilis. Phytopathology* **60,** 746–749.

Wahl, I., and Anikster, Y. (1982). Role of the alternate host in evolution of some cereal rusts. *Garcia de Orta, Ser. Estud. Agron.* (Volume dedicated to Professor B. D'Oliveira) (in press).

Wahl, I., Dinoor, A., Halperin, J., Schreiter, S., (1960). The effect of *Rhamnus palaestina* on the origin and persistence of oat crown rust races. *Phytopathology* **50,** 562–567.

Zadoks, J. C. (1965). Epidemiology of wheat rusts in Europe. *FAO Plant Prot. Bull.* **13,** 97–108.

Zhukovsky, P. M. (1959). Interrelation between host and parasite in their origin and beyond it. *Vestn. S-kh. Nauki (Moscow)* **4**(6), 25–34 (in Russian, with English summary).

Zhukovsky, P. M. (1961). Grundlagen der Introduktion der Pflanzen auf Resistenz gegen Krankheiten. *Zuechter* **31,** 248–253.

Zhukovsky, P. M. (1964). "Kulturnye Rasteniia i ikh Sorodichi" (Cultivated Plants and their Wild Relatives), 2nd ed. Publ. Kolos, Leningrad.

Zhukovsky, P. M. (1965). Main gene centers of cultivated plants and their wild relatives within the territory of the U.S.S.R. *Euphytica* **14,** 177–188.

Zillinsky, F. J., and Murphy, H. C. (1967). Wild oat species as sources of disease resistance for the improvement of cultivated oats. *Plant Dis. Rep.* **51,** 391–395.

Zohary, D. (1971). Origin of south-west Asiatic cereals: Wheats barley, oats and rye. *In* "Plant Life of South-West Asia" (P. H. Davis *et al.*, eds.), pp. 235–263. Botanical Society of Edinburgh.

Zohary, D. (1973). The origin of cultivated cereals and pulses in the Near East. *Chromosomes Today* **4,** 307–320.

Zohary, D., and Brick, Z. (1961). *Triticum dicoccoides* in Israel: Notes on its distribution, ecology and natural hybridization. *Wheat Inf. Serv.* **13,** 6–8.

association has decisively influenced its counterpart. This reciprocal impact is reflected in a multiplicity of morphologic and biologic traits (Anikster and Wahl, 1979). Dietel's idea has spawned into various fields of science, such as taxonomy, cytology, genetics, and plant protection.

The main purpose of this chapter is to elucidate some problems of rust diseases and their evolution at the centers of their origin. Special interest is focused on the evolution of different forms and levels of host defense correlated with the evolution of virulence in a broad spectrum of ecosystems undisturbed by humans. The analysis not only deals with the protection of individual plants but also embraces the nature of defense systems of plant populations in unmanaged ecosystems, their constituents, and patterns of their interaction and cohesion. Browning (1974) labeled this phenomenon "protection of indigenousness," and Schmidt (1978), "ecosystem disease resistance." It is akin to the "evolutionary stable strategy" concept (Robinson, 1980).

The graminicolous plants are characterized at their centers of origin by extreme genetic variability and heterozygosity ascribed by Zhukovsky (1961) and also to the high rate of open pollination even in self-pollinated plants. On the basis of his own studies and Bodenheimer's entomological research in Israel, Vavilov (1939) advanced the hypothesis that the evolution of fungus parasites and insect pests parallels that of their hosts. Maximum diversity coincides with that of the host and its indigenous wild relatives. Their interaction and reciprocal selection pressure has resulted in "balanced polymorphism" (Mode, 1958), as expressed by a multitude of protection types in the hosts, matched by broad virulence specialization of their parasites. Nelson (1978) postulated that "coepicenters, geographic areas in which both host and parasite have evolved, most accurately depict the story of evolution of genes for virulence and resistance." In such areas "the long process of coevolution resulted in the ultimate accumulation of many resistance and virulence genes." In Flor's opinion (1971), "the primary gene center [of host–parasite coevolution] has been and probably will continue to be the plant breeder's principal source of both vertical and horizontal resistance." Coons (1953) contended that common experience has "shaped our thinking and forced recognition of the first and fundamental principle of breeding for disease resistance, namely, that where host and parasite are long associated, then in the evolutionary process resistance forms are developed by natural selection."

Obviously, there seems to be a broad consensus that protection from disease should be sought in the centers of host–parasite coevolution and introduced from those regions (Leppik, 1970). D'Oliveira (1940, 1951, 1960a) provided ample evidence that epicenters of origin of cereal rusts are situated in the geographic regions where the centers of origin and genetic diversification of the main and alternate hosts coincide. In such regions teliospores are produced abundantly and germinate readily at least in some of the fungus strains. "The absence of an aecidial host from regions where a given rust exists, seems only to indicate that the sporophytic host, as well as the rust, have been introduced recently" (D'Oliveira, 1951).

II. Evolution of Cereal Rust Diseases

A. PLANT DEFENSE AND PARASITE VIRULENCE AT THE ORIGIN CENTERS

The problem of wheat and wheat rusts origin and coevolution was discussed by Leppik (1961, 1965, 1970), Vavilov (1939), and Zhukovsky (1959, 1961, 1964, 1965). According to Leppik (1970), the rust resistance of wheat, a classic case, demonstrates most convincingly the importance of gene center of hosts and sources of disease resistance. Zhukovsky (1959) was of the same opinion. He emphasized that "wild relatives of cultivated plants usually do not possess absolute immunity. This can be considered as a rule." Their defense is based on "field resistance" and tolerance. Ordinarily, the fungus parasitizes only certain plant parts, causing some necrosis and reduced sporulation. Thus the survival of the host and the parasite lasts over millennia. In their common center of origin, hosts and their parasite undergo parallel evolution resulting in development of a plethora of new protection types and fungus strains with increased virulence.

B. CENTERS OF WHEAT ORIGIN

Zhukovsky (1959, 1961) postulated that the home of wheat is Transcaucasia, the central and western parts of Asia Minor, the eastern Mediterranean areas, and the western part of Iran. These regions abound in endemic wild and cultivated wheat and store the variation potential of the genera *Triticum*, *Aegilops*, and *Secale*. Vavilov (1939) maintained that in the mentioned regions are the world's richest concentration of wild relatives of small grains. Zhukovsky (1965) reported that "Transcaucasia (Georgia, Azerbaijan, and Armenia) is a primary gene centre of speciation of the genus *Triticum*."