

Isaak Wahl

Disease Resistance from Crop  
Progenitors and other Wild Relatives



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## DISEASE RESISTANCE FROM CROP PROGENITORS AND OTHER WILD RELATIVES

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## Chapter 1

### Introduction

#### Definition of "Wild Plants"

Webster (1977) defined "wild" as "living in a state of nature and not ordinarily tame or domesticated." He referred also to wild plants as "related to or resembling a corresponding cultivated or domesticated organism." According to Bos (1981), wild plants are plants that develop without human aid, e.g. in natural habitats. Bos maintained that inbreeding with related cultivars may enhance genetic variation. Harlan (1970) considered "wild" as races or species neither cultivated nor markedly encouraged by human disturbances. Some researchers distinguish between "wild plants" and "weeds." Harlan (1970) regarded "weed" as a race or species adapted to habitats disturbed by man. Bos (1981) emphasized that the terms "weed" and "wild plants" are not exactly equivalent. We shall make no such distinction, because it often is not essential, and may only reflect differences in the growth habitat. For example, wild oats *Avena sterilis* is a significant component in the natural flora in Israel but a noxious weed in the USA. The wild barley species *Hordeum spontaneum*, too, is an important constituent of Israel's natural flora, and widespread in Azerbaijan and Turkestan both in natural coenoses and as weeds (Zhukovsky 1965). Regardless of the growth habitat, both species are valuable sources of disease resistance germplasm and will be treated as such herein.

#### Importance of Wild Plants as Sources of Protection against Diseases

There is general agreement that "the ideal way of controlling all plant diseases would be the use of resistant varieties" (Stakman and Harrar 1957). Regrettably, the genetic resources of major crops are "vulnerable" and founded on a narrow and rapidly dwindling genetic base (National Academy of Sciences 1972). Wild relatives constitute vast gene pools that contain abundant and very diversified genetic reservoirs for gene improvement (Zohary 1991).

According to Stalker (1980), "by far the most common reason for attempts of utilizing wild species is to transfer factors for disease resistance." In his comprehensive review of the utilization of genetic material from wild relatives to improve disease resistance, Harlan (1976) stated that wild plants "have been used for this purpose in almost every crop grown by man."

Wienhues (1969) stated that the main value of using primitive - or wild species is the transfer of particularly effective genes for disease resistance to susceptible crops. Knott and Dvorak (1971) presented comprehensive information on utilization of alien germplasm in breeding crops for disease resistance. Frey (1983) described in detail the use of wild relatives of rice, sugarcane, tomatoes, and oats for improvement of the corresponding cultivated crops, because the wild material is a very important source of genetic variation. Gale and Miller (1987) provided information on transfer from *Aegilops* spp. and *Agropyron* spp. to wheat of genetic factors controlling stem rust, leaf rust, stripe rust and eye spot. In the case of maize only limited efforts were made to introgress genes from wild sources like teosinte (*Zea mexicana*) and *Tripsacum* (Reeves 1950, Reeves and Bockholt 1964). Significant improvements were achieved by breeders from utilizing cultivated gene pools (Frey 1983). Zeller and Fischbeck (1974) concluded, a final solution of the different problems of breeding for resistance is, therefore, in all probability not attainable by means of introducing alien resistance genes into the germplasm of wheat. There can, however, be no doubt whatsoever that this work can be expected to provide valuable additions to the genetic potential of resistance breeding."

### **Types of Resistance to Plant Pathogens**

Resistance to many diseases, like the highly epidemic powdery mildews and rusts of cereals or late blight of potatoe is ephemeral and thwarted by new virulent strains of a pathogen. The disappointments of the past and the threat of depleting the already limited resources of conventional resistance, effectively acting only against specific pathogen races ("vertical resistance" *sensu* Vanderplank 1963), gave impetus to the development of new concepts of more durable resistance (Johnson 1981), putatively not influenced by changes in pathogen populations, and described by different terms, e.g. "horizontal resistance" (Vanderplank 1963), "partial resistance" (Parlevliet 1985), "dilatory resistance" (Browning et al 1977), "slow-rusting" and "slow-mildewing" (Wahl et al 1978, 1984), and "race non-specific resistance" (Wood 1982).

In this review of plant disease resistance used world-wide, particular attention is given to conventional, race-specific resistance because of its common use in breeding and ease in manipulation (Burdon and Jarosz 1989), and because of its documented transfer to crop cultivars from crop progenitors and other wild relatives.

Our studies of over 40 years in Israel have ascertained that slow leaf-rusting

resistance and slow mildewing resistance in natural populations of *Hordeum spontaneum*, or slow crown rusting resistance in *Avena sterilis*, are the predominating forms of genetic protection from the corresponding diseases. Yet, our experience corroborates the opinion of Person and Sidhu (1971), Browning et al (1977), Wood (1982), and Burdon and Jarosz (1989) that conventional, race-specific resistance associated with necrotic-chlorotic lesions, is a natural phenomenon that also provides important protection from pathogens.

### **Centers of Development and Accumulation of Disease Resistance**

Coons (1953) postulated that common experience has shaped our thinking and forced recognition of the first and most fundamental principle of breeding for disease resistance, namely, that where host and parasite developed in continual association, the evolutionary process chose resistance forms by natural selection. Vavilov (1949-50) formulated the concept that gene centers of cultivated crops are the places to search for disease resistance. Based on his own studies and Bodenheimer's entomologic research in Israel, Vavilov (1939) advanced the hypothesis that the evolution of the fungus parasites parallels that of their hosts. Maximum pathogen diversity coincides with that of its hosts and the host's indigenous wild relatives. Their interaction and reciprocal selection pressure have resulted in "balanced polymorphism" (Mode 1958). Nelson (1978) contended that coepicenters, geographic areas in which both host and parasite have evolved, most accurately depict the story of the long process of covevolution that resulted in the accumulation of many resistance and virulence genes. Flor (1971) envisioned that the primary gene centers of host-parasite coevolution have been and probably will continue to be the plant breeder's source of both vertical and horizontal resistance. Leppik (1970), D'Oliveira (1940, 1960), Krivchenko (1983), Wahl et al (1984), and Browning (1991) furnished evidence that epicenters of origin and genetic diversification of cereal rust fungi are situated in the geographic regions where the centers of origin and genetic diversification of the main and alternate hosts are located. Zhukovsky (1961) presented a broad scope of host-pathogen associations embracing cereals, potato, tomato, sunflowers, tobacco, apples, pears, grapes, and other crops. He concluded that resistance to pathogens should be sought at the centers of coevolution of the respective host-pathogen systems.

Burdon and Jarosz (1989) maintained that the antiquity of the origin of the host or its relatives is not necessarily an indication of the presence of disease resistance. This is

true when the center of the host's origin is void of the pathogen concerned. "Nevertheless the fact remains that natural selection for resistance within the endemic area is of greatest importance, which explains the fact that the occurrence and frequency of genes for resistance is closely connected with the habitat of the origin of a species (Rudorf 1959, Rudorf's italics). Furthermore, in such habitats one might expect to find forms of wild plants with broad spectra of resistance ("group resistance") or race non-specific resistance ("field resistance," "incubation resistance," or "generalized resistance.")

### Disease Control Strategies

Diseases in natural plant communities seldom assume serious proportions. In such ecosystems the host-pathogen association has reached dynamic balance in the process of prolonged coevolution. Vanderplank (1975) described the situation in the statement "endemicity implies both balance and coexistence." Person and Sidhu (1971) postulated that understanding the regulatory mechanisms in natural ecosystems could be the first step toward learning how to achieve long-term solutions to disease problems in agriculture. De Neergaard (1986) maintained that "the best possible agricultural stable strategy should be based on a simulation of the wild pathosystems." Browning (1974) labeled protection from disease in natural plant populations "protection of indigenousness." He envisioned relevance of the knowledge gleaned from studies of natural ecosystems to the development of pest management programs for agroecosystems. The defense systems and strategies in natural stands offer many modes of patterned diversity" (Dinus 1974). The choice of a suitable model depends on the crop, disease, and environment (Segal et al 1980). The nature and significance of "protection of indigenousness" is elaborated by Browning in our final chapter.

### REFERENCES

- Bos, L. 1981. Wild plants in the ecology of virus diseases pp. 1-33. In: Plant Diseases Academic Press, New York.
- Browning, J.A. 1974. Relevance of knowledge about natural ecosystems to development of pest management programs in agro-ecosystems. Proc. Am. Phytopathol. Soc. 1:191-199.
- Browning, J.A. 1991. Conserving crop plant-pathogen coevolutionary processes *in situ* pp. 59-85 In: Biodiversity, Culture, Conservation and Ecodevelopment (M. L. Oldfield and J. B. Alcorn, eds.). Westview Press, Boulder, CO.

## Chapter 2

### The Protection of Indigenousnes

by J. Artie Browning

A coevolutionary model for the presence and the wide range of resistance germplasm in populations from small graine progenitors from  
**Israel's natural ecosystems**

Our original plan was for this introductory chapter to describe a generic indigenous ecosystem from which any resistance gene mentioned in this book might have coevolved. Then we read Groth and Christ's (1992:184) statement that "with the possible exception of the groundsel-mildew example, even at the more accessible phenotypic level, there exist today no published detailed or quantitative studies of diversity of any pathogen as it occurs on a wild or weedy species." Previously, Leppik (1970:325-326) had written similarly: "Although the origin and history of our main field crops and most garden plants are extensively studied today, little or nothing is known about the genetics and evolution of plant pathogens. Gene centers of cultivated plants are only partially explored pathologically. We do not yet know which pathogens or physiologic races attack plants in their natural habitats, and what conditions are responsible for development of inherited resistance." And Zadoks (1999:5) added that "Progress in [studies of] wild pathosystems is made in ecological rather than phytopathological research institutions." In 1974 I responded to Leppik (1970), and now to all three, that "A notable exception to this is the ecosystem that includes the progenitors of cultivated species of barley, oat, and wheat in southwest Asia where they are indigenous and where they and their pathogens have been studied intensively, especially by the Soviets and, more recently, the Israelis" (Browning, 1974:191).

Obviously, it is time for a current review of the referenced, most researched indigenous ecosystem, which also is the most relevant indigenous ecosystem because it has been such a rich source (i) of resistance genes for crop improvement, and (ii) knowledge (a) of host-pathogen coevolution and (b) of how plants protect themselves in an indigenous ecosystem. The last is relevant to managing those genes after they are transferred through crop improvement methodology from their well-buffered center of diversity to the harsh, unnatural world of agriculture so as to maximize their useful effective life of protecting plants in an agroecosystem. Therefore, this review will focus on the ecosystem from which small grains and their pathogens coevolved in that part of

the Fertile Crescent that is tiny Israel. The model systems described herein will enable workers on other crops and/or in other regions to apply them to those crops and regions by projecting their thinking or, better, running experiments these models suggest.

For a broader, sometimes more ecological treatment, the reader is referred to Burdon (1987), Dinoor (1974), Dinoor and Eshed (1984), Fritz and Simms (1992), and Harper (1977).

### **Israel's indigenous ecosystems of small graines progenitors and relevant populations of wild barley, wild oat and wild emmer wheat**

Mediterranean-type climate. Ravin (1971) includes a map of these areas and a description of the climate and the floras it facilitates. This climate type, which is characterized by hot, dry summers and cool, moist winters, favors annual plants. They achieve preeminence there, often constituting half of the total plant species in comparison to rarely 10% elsewhere.

The variable climates and topography of southwest Asia "are powerful factors leading to racial differentiation in crop plants and the formation of agroecotypes." In southwest Asia about 10,000 years ago, people first began the deliberate cultivation of plants, which hastened the formation of ecotypes. Every case of domestication had, "as a universal response, a veritable explosion of genetic variation." When selection pressures fell, e.g. when spike disarticulation was selected, "variation and variability increased; . . . a flood of evolution was released." As cultivation expanded among wild plant communities that, themselves, are "remarkably stable," hybridization was "conducted unwittingly by primitive man in the midst of their primitive agriculture on a scale that modern man can no longer expect to repeat" (Bennett, 1971:222-224).

Every habitat [became] distinguished by its own agroecotypes. Innumerable races of cultivated plants have evolved wherever agriculture has been practiced." But the enormity of the diversity cultivation created "was totally unsuspected until Vavilov undertook his monumental work of exploring and studying cultivated species on a global scale" (Bennett, 1971:223). Vavilov and his associates were the first to study and describe the whole complex (Zohary, 1971, in discussion after Bennett, 1971:232)

"Ecotypic differentiation in cultivated plants affects many characteristics. Agroecotypes differ in their adaptation to soil type and fertility; they vary in their resistance to drought, cold and diseases [and arthropods] according to the habitats in which they evolved. Agroecotypes offer, therefore, a wide range of characters to the