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EPIDEMIOLOGY OF WHEAT RUSTS IN THE WESTERN HEMISPHERE

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EPIDEMIOLOGY OF WHEAT RUSTS IN THE WESTERN HEMISPHERE*

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ABSTRACT

Shortly after the turn of the century, devastating wheat rust epidemics in the Great Plains of North America (Northern Mexico, the Plains of the U.S.A. and the Prairie Provinces of Canada), prompted the study of physiologic specialization in stem and leaf rust, the breeding of resistant varieties, and the epidemiology and aerobiology of these rust diseases. No comparable area of the world has been studied so precisely and 50 years data have been systematically presented for the aerobiology and epidemiology of these organisms in this region.

In the present paper, additional evidence is provided to support the hypothesis that this region forms a single epidemiological zone for these two diseases.

Five other major geographical epidemiological zones are delineated in the Western Hemisphere: three in North America and two in South America. Evidence for their existence is based on data available for virulence patterns of the three species viz *Puccinia graminis tritici*, *Puccinia recondita* and *Puccinia striiformis*, either of one or a combination of species.

Epidemics, virulence surveys, virulence patterns on varieties in Five International Spring Wheat Yield Nurseries and two years of the International Stripe Rust Nursery, have been used to provide supporting data indicative of regional groupings.

On the basis of available evidence it appears that the following epidemiological zones for rust exist:

1. The Great Plains of North America.
2. The Pacific Northwest (California, Oregon, Washington)

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3. The Eastern United States and Canada (areas east of the Alleghanys in the U.S. and the Laurentian Shield in Canada).
4. Southern Mexico and Guatemala.
5. The Andean Countries of Colombia, Ecuador, Peru and Chile (there is evidence of sub-epidemiological zones in this region).
6. Southern Brazil, Argentina, Paraguay and Uruguay.

While correlations are high for virulence patterns within these areas, there are indications of occasional interchange of virulence types between the zones. This is likely to occur where the zones come into close proximity, there are gaps in mountain ranges or a narrowing of desert barriers occurs.

EPIDEMIOLOGIA DE LAS ROYAS DE TRIGO EN EL HEMISFERIO OCCIDENTAL

ABSTRACTO

A principios del siglo actual, las devastadoràs epifitias de roya del trigo registradas en las Grandes Planicies de Norteamérica (Norte de México, Planicies de los Estados Unidos de América y las Provincias de las Praderas de Canadá) propiciaron el estudio de la especialización fisiológica de las royas del tallo y de la hoja, el desarrollo de variedades resistentes y la investigación sobre su epidemiología y aereobiología. No existe ninguna otra región en el mundo que haya sido estudiada tan minuciosamente; durante 50 años se han publicado en forma sistemática datos sobre la aereobiología y la epidemiología de las royas del trigo en esta extensa zona.

En el presente trabajo, se aporta evidencia adicional que apoya la hipótesis de que dicha región forma una sola zona epidemiológica para estas dos enfermedades del trigo.

Se delimitan otras cinco zonas geográficas epidemiológicas en el Hemisferio Occidental: tres en Norteamérica y dos en Sudamérica. La evidencia de su existencia se basa en datos sobre los patrones de virulencia de tres especies viz *Puccinia gramis tritici*, *Puccinia recondita* y *Puccinia striiformis*, solas o en conjunto.

Se proporciona información de apoyo indicativa de los agrupamientos regionales, según datos de epifitias, muestreos sobre virulencia y patrones de virulencia sobre variedades incluídas en cinco ensayos internacionales de rendimiento de trigos de primavera. y de dos años del ensayo internacional sobre roya lineal.

Con base en la evidencia actual, existen las siguientes zonas epidemiológicas para royas:

1. Las Grandes Planicies de Norteamérica.
2. El Pacífico Noroeste de los Estados Unidos (California, Oregon, Washington).
3. El Este de los Estados Unidos y Canadá (áreas al Este de los Montes Alleghanys de los Estados Unidos y de la Barrera Laurentina de Canadá).
4. Sur de México y Guatemala.
5. Zona Andina de Colombia, Ecuador, Perú y Chile (hay evidencia de sub-zonas epidemiológicas en esta región).
6. Sur de Brasil, Argentina, Paraguay y Uruguay.

Aún cuando las correlaciones son altas para los tipos de virulencia dentro de estas áreas, hay indicios de intercambio ocasional de tipos de virulencia entre las zonas. Es probable que esto suceda donde las zonas son adyacentes o próximas, donde hay brechas en las barreras montañosas o en lugares donde las barreras desérticas son angostas.

EPIDEMIOLOGIE DES ROUILLES DU BLE DANS L'HEMISPHERE OCCIDENTAL

EXTRAIT

Au début du siècle actuel, les épiphyties dévastatrices de la rouille du blé enregistrées dans les Grandes Plaines de L'Amérique du Nord (Nord du Mexique, Plaines des Etats-Unis d'Amérique, et les Provinces des Prairies du Canada) ont rendu favorable l'étude de la spécialisation physiologique de la rouille de la tige et de la feuille, le développement de variétés résistantes et la recherche sur l'épidémiologie et l'aérobiologie. Il n'existe aucune autre région dans le monde qui ait été étudiée avec tant de minutie; durant cinquante ans il a été publié systématiquement des données sur l'aérobiologie et l'épidémiologie des rouilles du blé dans cette zone étendue.

Dans ce travail, on apporte l'évidence additionnelle qui appuie l'hypothèse que cette région forme une seule zone épidémiologique pour ces deux maladies du blé.

On a délimité cinq autres zones géographiques épidémiologiques dans l'Hémisphère Occidental: trois en Amérique du Nord et deux en Amérique du Sud. L'évidence de leur existence s'appuie sur des données des modes de virulence de trois espèces viz *Puccinia graminis tritici*, *Puccinia recondita* et *Puccinia striiformis*, pour chacune d'elle ou ensemble.

On s'est procuré une information d'appui indicative des groupements régionaux, d'après les données des épiphyties, des épreuves sur la virulence et modes de virulence de variétés incluses dans cinq pépinieres internationaux de rendement de blés de printemps et deux ans de pépiniere internationaux de rouille jaune.

Comme base, dans l'évidence actuelle il existe les zones épidémiologiques suivantes pour les rouilles:

1. Les Grandes Plaines de l'Amérique du Nord.
2. Le Pacifique Nord-est des Etats-Unis (Californie, Orégon, Washington).
3. L'Est des Etats-Unis et du Canada (régions de l'Est des Monts Alleghanys des Etats-Unis et l'Est des les Monts Laurencianne du Canada).
4. Sud du Mexique et Guatémala.
5. Zone andine de Colombie, Equateur, Pérou et Chili (il y a une évidence de sub-zones épidémiologiques dans cette région).
6. Sud du Brasil, Argentine, Paraguay et Uruguay.

Même quand les corrélations sont élevées pour les types de virulence dans ces régions, il y a des indices d'échange occasionnel de types de virulence entre les zones. Il est probable qu ceci arrive lorsque les zones sont adjacentes ou voisines, s'il y a des brèches dans les barrières montagneuses ou dans les endroits où les barrières désertiques sont étroites.

EPIDEMIOLOGY OF WHEAT RUSTS IN THE WESTERN HEMISPHERE

INTRODUCTION

The history of cereal rust research has to a large extent been one of challenge and response. One such challenge was the North American Stem Rust Epidemic of 1916 which led to a great effort in the study of the physiological specialization of the rusts and the breeding of resistant varieties. Another was the outbreak of race 15B of wheat stem rust (*Puccinia graminis tritici*) in 1950 in North America which led to an internationalization of the efforts to control the cereal rusts. In this respect the First International Wheat Rust Conference, at St. Paul, Minn., in 1950, was of great significance. This was followed by the more truly international Conferences held at Winnipeg, Canada in 1953 and Mexico City in 1956. The European Colloqui in Black Rust of Cereals, at Versailles 1958, Madrid 1961, and the Cereal Rust Conferences, Cambridge 1964, Lisbon 1968 and Prague 1972, may be considered lineal descendants of the American Meetings. In Europe, a significant event was the resolution passed at the IV International Congress for Plant Protection in Hamburg in 1957 urging effective European cooperation in the study of stem rust of wheat. This led to effective collaboration, especially in the field of epidemiology, among researchers in the countries of Europe. There have been eight North American Leaf Rust Workshops in the last fifteen years, wich led to the understanding of various problems in the field of race identification (virulence survey), epidemiology, and varietal resistance.

A core factor of significance in relation to the distribution and epidemiology of the cereal rusts is their plasticity (18). They adapt. Most authorities assume that long before cereals came into existence, the rusts were present on grasses ancestral to cereals and the rust adapted to cereals as they came into being. Leppik (24) makes this assumption for stem rust, and Hassebrauk (12) supports the suggestion of Humphrey *et al*, (15) that strip rust migrated from its Asiatic gene pool to North America where it became established on American grasses, and much later, when cereals were cultivated in the New World, it adapted to them. Oliviera and Samborski (31) assume that two trends of evolution were followed in the specialization of the sexual stage of leaf rust (*Puccinia recondita* Rob. ex Desm. F. sp. *tritici*), one trend showing adaptation to hosts of the Ranunculaceae and other to species of the Boraginaceae. Within each group

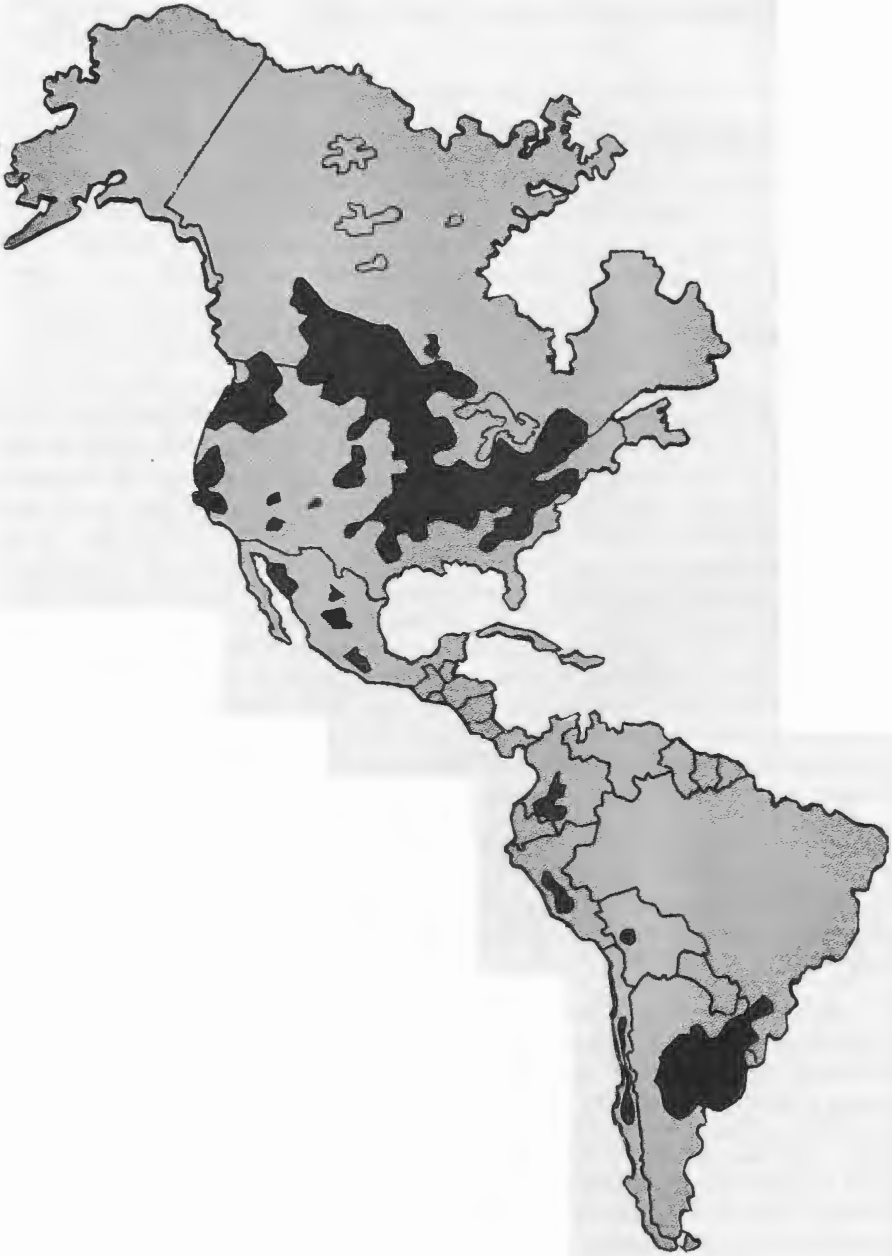

Fig. 1. Wheat areas in the Western Hemisphere.

further differentiation has taken place, and a variety of combinations of gametophytic and sporophytic hosts now occur in nature. This is illustrated by the presence on wheat of two strains of *P. recondita* in Portugal, one adapted to *Thalictrum* spp. and the other to *Anchusa italica* Rtz. Another strain adapted to *Isopyrum fumarioides* occurs in Siberia. A relatively late introduction to the Americas of wheat leaf rust from its Eurasiatic home may perhaps account for its non adaptation to American species of *Thalictrum*, but the report of Young, Saari and Curtis (51) suggets the possibility that the rust may gradually be acquiring ability to infect some of these American species.

The plasticity of the rusts is most evident in their host-pathogen relations; it is less evident in their environmental responses. Each rust has its particular climatic adaptation and there is little evidence of change in that regard (18). The incursion of stripe rust into the Great Plains of the United States in 1957 and 1958 (50, 34, 36, 37, 39, 8, 7, 14, 9) was probably a response to weather conditions favorable to rust rather than, as first feared, to a change in climatic requirements. The climatic requirements, and therefore the distribution of the three rusts of wheat was probably fixed long before cereal crops were developed: stripe rust predominated as it does today, in the cool climates of littoral regions and high elevations; stem rust in the warmer, lower lying continental areas; and leaf rust, with its intermediate temperature adaptation, took some toll in both types of climates (18).

That spores of fungi are disseminated by air currents, has been known almost as long as the spores themselves. Micheli in 1729, (29) published the results of epoch-making investigations on the reproduction of fungi by means of spores and showed that clouds of them might be liberated into the air. Prevost in 1807, (40) not only showed that bunt of wheat was caused by a fungus but also suggested that the spores sometimes might be disseminated by the wind at threshing time. After DeBary furnished general ly accepted evidence in 1853 that fungi could cause plant diseases, there gradually developed the realization that many of the fungal pathogens of plants were disseminated, at least locally, by wind. But still there was no conclusive evidence for long distance diseemination, although Klebahn (21) and others postulated that this was so because of the epidemic occurrence of certain rust diseases at considerable distances from known sources of inoculum.

One of the most widely studied and documented case histories on aerial dissemination of a plant pathogen over a distance of 4,000 kilometers covering the areas of Northern Mexico, the Great Plains of the United States and the Prairie Provinces of Canada is that of wheat stem rust moving south to north and then north to shouth (4, 5, 42, 43, 44). No similar area in the world has been studied as throughly in relation to aerobiology and epidemiology of wheat stem rust as the Great Plains of North America. The present review and interpretation will follow the presentation on some selected history cases of reported wheat rust epidemics in North America. In addition, studies on physiological specialization and virulence surveys made in the present decade are compiled to arrive at conclusions in grouping the various epidemiological and sub-epidemiological zones in both North and South America. Representation of similar virulence genes in a particular pathogen in different adjoining areas which would be considered as one epidemiological zones irrespective of different countries involved, has arisen from the authors' experience, and from similar interpretations, elsewhere (Saari personal communications), (48).

PROPOSED EPIDEMIOLOGICAL ZONES

From the illustrative point of view, six major geographical areas, four involved in North and Central America and two in South America are discussed in relation to rusts of wheat (*Puccinia graminis tritici, Puccinia recondita*, and *Puccinia striiformis*). Historical events of epidemics and data from virulence surveys are presented to clarify and substantiate the hypothesis put forward. Data will be presented to illustrate the possibility of sub-epidemiological zones within the area. Six zones are listed below:

1) The Great Plains of North America constituting Northern Mexico, the Mississippi Basin of the United States and the Prairie Provinces (Manitoba, Saskatchewan, and Alberta) of Canada.
2) The Pacific North West Area the United States (States of California, Oregon and Washington), i.e. the area generally west of the Rocky Mountain System. Stripe rust is the major wheat rust, and there is the possibility of sub-epidemiological zones in the area.
3) The Eastern United States and Canada (Areas East of the Alleghanys in the U.S.A. and the Laurentian Shield in Canada).
4) Southern Mexico and Guatemala.
5) The Andean Countries of Colombia, Ecuador, Peru and Chile. (Area generally West of the Andean Mountain System). Sub-epidemiological zones may also be present.
6) Those areas comprising Southern Brazil, Northern Argentina, Uruguay and Paraguay where stem and leaf rust are major diseases of wheat.

I GREAT PLAINS OF NORTH AMERICA

Studies on Rust Aerobiology in Canada

Geographical barriers are among the factors of importance in determining the distribution of physiological races. There are two barriers of this type in Canada: The Rocky Mountains, which separate the province of British Columbia from the Prairie Provinces; and the extensive area of forest and lakes that separates the Prairie Provinces from the arable land of Eastern Canada. To a certain extent, both act as barriers to the spread of rust races.

Fig. 2. Suggested epidemiological zones for wheat rusts: I. The Great Plains of North America; II. The Pacific Northwest; III. The Eastern U.S.A. and Canada; IV. Southern Mexico and Guatemala; V. The Andean Countries (Colombia, Ecuador, Peru and Chile); and VI. Southern Brazil, Argentina, Paraguay and Uruguay.

Craigie (6) studied the relationship in Western Canada between the various factors influencing rust increase and the amount of rust present each year for the period 1926-1939. No one factor could be singled out as being chiefly responsible for the abundance or scarcity of rust. However, of the several factors studied he found that early arrival of abundant rust inoculum, plentiful moisture, particularly during July, and late seeding were associated with the heavy rust years. High summer temperatures on the other hand were less closely associated with severe rust development. He concluded that initial inoculum consists largely, if not entirely, of wind borne spores that originated outside of the Prairie Provinces of Canada. Local sources of infection are virtually absent. The disease regularly appears first in Southern Manitoba, more often than not in the Red River Valley, and later further northward and westward, the time of first appearance in Manitoba being late June or early July and in Alberta a month or more later. In any given district, inoculum has always been found present in the air in advance of infections in the field.

Peturson (39) indicated the following factors which determine the course of rust development:

1) The amount and time of arrival of wind borne rust inoculum which initiates rust each spring in Western Canada; 2) The degree of rust resistance of the predominant varieties grown, to the rust races present; 3) The amount and distribution of precipitation and intensity of dew formation during the crop season (April to August inclusive); 4) The temperature during the crop season; and 5) The time of seeding of the crop. He concluded that all these main factors must be present and at least some of them must be operative throughout the season and must occur over vast areas of the Great Plains of North America in years when major rust epidemics occur in Western Canada.

Green (10) writes that stem rust development is initiated in Western Canada each spring by air-borne inoculum from the South. Climatic conditions and the varieties grown in the United States help to determine the kind and the amount of primary inoculum. Similarly, rust development in Canada influences the races that develop during the winter months and early spring in Southern United States. This cycle returns to Canada inoculum of the races that predominated there the previous year. Consequently, races found in the Canadian race survey are indicative of which races can survive the hazards of unfavorable host varieties and climatic conditions during their annual migration. Hence, they are most likely to be the main components of the North American rust population.

B. Case History: Aerobiology and Epidemics Over the Area Involving Northern Mexico, the Mississippi Basin of the United States and the Prairie Provinces of Canada

Stakman and Harrar, (45) in their book "Principles of Plant Pathology" have presented very clearly and systematically, all the aerobiological studies and epidemiological events, which occurred in the Great Plains of North America over a period of 50 years. A similar story is further expended in another publication by Hamilton and Stakman (11). In addition, many other reports of major epidemics of stem and leaf rust in various areas of the Mississippi Basin have been epidemiological data (1, 19, 38, 3, 28, 27, 20, 32, 33, 35, 36, 2). Lambert, (22) in a voluminous publication, has given the details of the relationship of weather to the development of stem rust in the Mississippi Valley.

The following paragraphs refer briefly to certain case histories based on the studies of those epidemics which resulted in catastrophic reduction in wheat production, and the aerobiological data gathered later which it was hoped would form the basis of effective control measures.

Mexico, the Mississippi Basin of the United States, and the Prairie Provinces of Canada constitute an exceptionally suitable area for studying effective spore dissemination. Wheat is grown from South Central Mexico to the Prairie Provinces of Canada, a distance of about 4,000 kilometers. Because of differences in latitude and elevation, plants of wheat, barley, or susceptible wild grasses are growing somewhere in this great area throughout the year. There are no effective topographic barriers between the South and North. The wind, therefore, has a free field and a vast one. There are mass air movements from South North and from North to South, often carrying countless numbers of spores and other minute objects hundreds of miles within a few days.

During the first half of the century stem rust frequently was so destructive in the spring wheat area of Northern U.S.A. and the Prairie Provinces of Canada that it became imperative to ascertain the source of rust as a basis of control measures. Some studies were begun soon after the destructive epidemics of 1904, and more detailed observations and experiments were begun in Minnesota in 1909. The scope if this study was expanded and more progress was made prior to the epidemic of 1916. Following this economic disaster, epidemiology studies were begun on a wide regional basis in the spring of 1917, and studies have been made continously since that time by the United States Department of Agriculture in cooperation with Minnesota and several other experimental stations. Cooperative studies with the Mexican Ministry of Agriculture and similar studies by Canadian investigators have elucidated the general features of rust development in North America and have convicted the wind of responsibility for rapid and wide spread dissemination of inoculum.

Widespread Wheat Stem Rust Movement in 1923, 1925 and 1935. In 1923 rust moved from Northern Mexico and Southern Texas to Canada in five successive waves during a period of two months. This was clear from results of systematic spore trapping at 38 stations, direct observations on the sequence of rust development, and the distribution of physiologic races 11, 17 and 21 throughout the area.

Because of cool weather the northward movement of stem rust was slower in 1924 than in 1923; it required theree months to extend in seven successive waves from Central Texas to Canada. However, rust sometimes moves far faster than in 1923 and 1924 and this was true in 1925.

The special feature of rust development in 1925 was the fact that spores were disseminated within a few days from a rusted area to a rust free area of more than a quarter of a million square miles. A huge spore shower moved northward 600 miles over a front more than 400 miles wide. In 1925 the rust wrote its own aerobiological story with un usual lucidity and legibility. There have been more catastrophic rust movements and development in this area, but few were as clearly defined. Indeed, the wheat growing area northward from Kansas in 1925 was like a vast agar plate on which the number of fungus colonies decreased proportionately with distance from a given source of spores.

From the aerobiological standpoint, the stem rust epidemic of 1935 in the U.S.A. and Canda is especially significant because the ground work, or air work, was laid in the fall of 1934, when spores were carried southward from Northern United States on October 10 and again from November 10 to 12. Rains followed these North to South movements, and 64 percent of the winter wheat fields in Oklahoma became infected. In Texas, the uredial stage survived the winter only on barley and there was very little rust in the early spirng. Then super abundant rainfall in Northern Texas in May, and unusually late ripening of wheat, led to an extraordinary development of rust. Spores were disseminated early and encountered favorable conditions on late wheat in parts of Kansas and northward. Weather conditions also were favorable for rust development in the spring wheat regions; and one of the worts epidemics on record destroyed about 135 million bushels of wheat in Minnesota, South Dakota, and North Dakota, despite the fact that a hitherto resistance variety, Ceres, had largely replaced the susceptible variety, Marquis, in that region. Race 56 was principally involved.

Because of the obvious desirability of knowing whether races of rusts in one country or area are likely to become established in another, comprehensive and persistent regional studies on spore dissemination are essential. There always is a question regarding adequacy of sampling as a basis for valid generalizations. Nevertheless, extensive studies for about 40 years in the United States and 35 years in Mexico indicate that some races are exchanged frequently, some occasionally, and some only rarely between the wheat regions. The interchange of races of wheat stem between Northern Mexico, the United States, and Canada roughly in a zone between longitude 90° and 100° +, occurs in so many seasons that it may be considered normal. However, East-West movements, especially across mountains such as the Rocky Mountain System, apparently do not occur commonly.

C. History of Race 15B and Destructive Stem Rust Epidemic of 1950

Dr. E. C. Stakman, (47) in his recommendations to the Rockefeller Foundation and CIMMYT concerning need for intensified and integrated campaigns against pests and pathogens of economic plants, cited two case histories to illustrate the origin and wide spread establishment of new races in North America: race 56, responsible for the stem rust epidemic of 1935 in the U.S.A., Northern Mexico and Southern Canada; race 15B, responsible for the great epidemics of 1950 and 1954 in the Great Plains of North America.

In the following paragraphs the history of race 15B is illustrated in relation to the epidemic of 1950. Dr. Stakman in his recommendation writes that race 15B of wheat stem rust illustrates a sudden, unexpected, simultaneous and catastrophic explosion of a virulent physiologic race affecting wheat. In the U.S.A., the first collection of this race was made from rusted barberries in Iowa in 1939. Subsequently, this race was found occasionally, principally on or near barberries in North Eastern U.S.A. But it never became established outside the barberry area prior to 1950; in fact, it appeared that it did not have good survival ability. But 1950 proved that it did. For two successive years prior to 1950, race 15B had been found only in barberry areas a thousand miles away from where it appeared in Texas in the spring of 1950. Circumstantial evidence indicated very strongly that the original source of the rust in Texas was in the Eastern U.S.A. barberry area. The rust from Texas then clearly had moved northward some 1,300 miles before the end of the Northern growing season. In Northern United States and Southern Canada it caused heavy demage to late fields of wheat varieties that had been almost immune from rust for a decade or longer. The autumnal air mass movement then carried clouds of spores southward to infect fall sown wheat in Southern United States and Mexico, where the rust survived the winter of 1950-51 in the uredial stage. It then moved northward again more than 2,000 miles in the spring and summer fo 1951 and comprised 40 percent of the 1,000 isolates of wheat stem rust identified in the United States that year.

Between spring and fall, then, race 15B travelled at least 4,000 miles; first about a thousand miles from the Eastern barberry areas of the United States to Texas, then northward about 1,300 miles through the United States and into Southern Canada, and finally southward and southwestward about 1,700 miles from Canada and Northern United States into Southern United States and Mexico. It moved northward a distance equivalent to the from Istanbul to Helsinki and southward from Finland to Cyprus. The area in which 15B caused infection during the year 1950 comrpised some two million square miles.

Stakman and Rodenhiser (46) wrote that race 15B wheat stem rust has become notorious to everyone interested in wheat improvement in North America. In 1950 this race suddenly and without warning extended its geographical range over most of North America, increased abruptly and alarmingly in prevalence, attacked previously resistant bread wheat and durums, proved to be complex in composition, and has continued to be one of the principal obstacles to the production of resistant varieties of wheat since that time. That 15B finally became widely established is not surprising in itself, but it is surprising that it increased and spread so suddenly and spectacularly in a single season, after it been watched carefully during the

Fig. 3. Slide Exposure Stations in the U.S.A. in 1955 to determine the movements of spores in the air (Photo: USDA)

previous decade without showing any tendency to increase in prevalence or to extend geographically.

II PACIFIC NORTHWEST OF NORTH AMERICA: AREA WEST OF ROCKY MOUNTAINS SYSTEM

Stripe rust (*Puccinia striiformis*) is the major rust disease prevalent in the Pacific Northwest (California, Oregon, Washington). This fungus according to accepted opinion, is capable of withstanding extended periods of subfreezing weather but is intolerant to prolonged periods of high temperature. The tendency for the fungus to subside and indeed, seemingly to disappear during the hotter monts, has posed a question of where, how and under what circumstances it survives the summer. Careful investigations of this phase of the biology of *Puccinia striiformis* in the Eastern Hemisphere, have revealed a number of ways in which oversummering is accomplished. In India and Africa oversummering is mainly accomplished at high elevations (25, 26 and 23).

In the Pacific Northwest the period from July to September is critical in the disease cycle of stripe rust. Under the influence of hot, dry weather which prevails at the time wheat reaches maturity, grasses typically brown off and exceedingly few surviving volunteer wheat plants are to be found over much of the wheat acreage of the Columbia Basin. Concomitantly strip rust recedes rapidly and essentially disappears at lower elevations.

In 1923, Hungerford (16), investigated the oversummering of stripe rust at Corvallis, Oregon. He observed conditions similar to those described above and reported that the period from July 20 to the return of the rains in the fall was characterized by few or no new rust infections.

Hendrix *et al* (13) noted oversummering of stripe rust in a few rare cases on spring planted winter wheat employed as ground cover in Central Washington.

Tollenaar and Houston (49) established that stripe rust of wheat was found to oversummer in the Sierra Nevada at altitudes of 6,000 feet or above on wild grasses belonging to *Elymus* spp., *Hordeum* spp., and *Sitanion* spp. The similarity of infection types of stripe rust isolate from various locations and hosts on a differential set of wheat cultivars suggests that only one race of *Puccinia striiformis* occurs in California. A mean temperature of 22.3°C or mean maximum temperature of 32.4°C measured over a 10 days period is lethal to stripe rust, thus accounting for the absence of this fungus during the summer in all regions of California but the Sierra Nevada and the Coastal Area. In late autumn, recurrence of the rust in the wheat growing areas is initiated when east winds carry uredospores from the Sierra Nevada into the Central part of the Sacramento-San Joaquin Valley infecting volunteer wheat plants and early sown wheat.

Shaner and Powelson (41) investigated possible summer reservoirs of inoculum which are found in Oregon: (1) Residual green wheat; and (2) Perennial grasses. Rust was found on residual green wheat during the summer, although not in abundance. On grasses, rust appeared later in the spring and disappeared as early (or earlier) in the summer as the rust on wheat. Grasses at high elevations have been suggested as oversummering host for *Puccinia striiformis* (13, 49); however, in Northern Oregon, rust was found less frequently on grasses at high elevations than on grasses in the wheat land. Rust also appeared at high elevations later, and disappeared earlier each summer than it did in the wheat lands. Therefore they (4) feel grasses in the mountains are of no importance in the epidemiology of the disease on wheat in contrast to the conclusions of others (13, 49). Grasses in the wheat land may also be unimportant in the epidemiology of the disease on wheat. Had the grasses surrounding wheat fields been the source of primary inoculum in the fall, it would have been expected to see the first infections near field borders. However, the initial infections were scattered throughout the field.

The historical study of aerobiology such as that done for stem rust in the Great Plains of North America is relatively limited in the case of wheat stripe rust. This results from the fact that mechanical spore-trapping devices

Fig. 4. The northward movement of wheat stem rust in the U.S.A. (Photo: USDA)

are of little use for the study of the uredospore flights, since uredospores of *Puccinia striiformis* are visually indistinguishable from the uredospores of other rusts. However, the International Yellow Rust Trial coordinated by R.W. Stubbs of the Netherlands, which is essentially a trap nursery has given good information on the virulence patterns of stripe rust populations in particular geographical areas.

Zadoks (52), using the results of the International Yelow Rust Nursery and subsequent race identifications made at Braunschweig showed that a strip rust race (Tupe Heines VII) spread over large parts of Northwest Europe, covering distances up to 800 kilometers to establish the epidemic of 1956. No such aerial dissemination data is available to strengthen the hypothesis that the whole region of the Pacific Northwest of North America can be considered one epidemiological zone. However, limited data of virulence analysis of stripe rust based on 50 varieties taken from the 5th International Spring Wheat Yield Nursery indicate a very high virulence correlation between the races of stripe rust in California and Washington. Of 50 varieties, 40 varieties showed identical field reaction in both locations.

Because of this similarity of virulence on test varieties it is probable that the same physiologic race or races are operative in both areas. Oversummering of stripe rust has been suggested in the higher altitudes of the Sierra Nevada (California), Blue Mountains (Washington and Northeast Oregon), Cascada Mountains (range of mountains extending southward through West-Central Whashington from Canada to Oregon), and Nez Perce National Forest (Idaho). The rust inoculum present in these locations infects the wheat in the valleys, and then recedes back to the high altitudes when summer arrives.

It has been postulated on the basis of the fact that spores of stripe rust are unable to tavel long distances and remains viable, that many sub-epidemiological zones may exist in the Pacific North West, each located close to the center of oversummering sites.

III. THE EASTERN U.S.A. AND CANADA (AREAS EAST OF ALLEGHANYS IN THE U.S.A. AND LAURENTIAL SHIELD IN CANADA)

Johnson (17) working with leaf rust over the period 1931 to 1955 concluded that there are three epidemiological zones in Canada: 1) The Province of British Columbia; 2) Prairie Provinces and 3) Eastern Canada. Races 1 and 11 of leaf rust, the predominant races of British Columbia, were very rarely found in the Eastern parts of the Prairie Provinces, but occurred frequently in certain years in Southern Alberta. As the area in which these races are found is a northward extension into Canada of the winter wheat belt, it is not clear whether the presence of these races is due to air-borne spores carried across the mountains or is merely the result of a northward extension of the rust flora congenial to the winter wheat varieties that are grown in areas just East of the Rocky Mountain. The Great Lakes and the contiguous forested area no doubt form an effective barrier against the distribution of races between the Prairies and Eastern Canada. This extensive uncultivated region is probably one of the reasons for the scarcity in Western Canada of races 58 and 76 which have long been the characteristic races of Eastern Canada and the adjacent areas in the United States.

IV. SOUTHERN AREAS INVOLVING SOUTHERN MEXICO AND GUATEMALA

Based on the virulence gene analysis for stripe rust and stem rust, the Toluca Valley of Mexico and Guatemala (Xelaju Valley) showed a very high correlation. Data are presented in Table 1. Forty, 33 and 40 entries of the 50 varieties of the 3rd, 4th and 5th ISWYN, respectively, showed parallel reactions. It si evident that many virulence genes are common in the population of stripe rust present in these two regions. Similar results were obtained for the population of *Puccinia graminis tritici*. Twenty-four varieties of the 25 in the 1st ISWYN, 36 of the 50 in the 3th ISWYN, and 38 of

Table 1. Results of Five International Yield Nurseries showing the epidemiological relationship between wheat growing areas related to *Puccinia striiformis* and *Puccinia graminis tritici*.

	1st ISWYN 25 varieties		2nd ISWYN 25 varieties		3rd ISWYN 50 varieties		4th ISWYN 50 varieties		5th ISWYN 50 varieties	
	Resist.	Suscept.	Resist.	Suscept.	Resist.	Suscept.	Resist.	Suscept.	Resist.	Suscept.
Mexico-Guatemala (*P. graminis*)	24	0	—	—	33	3	—	—	35	3
Mexico-Guatemala (*P. striiformis*)	12	9	—	—	23	17	24	9	33	7

the 50 in the 5th ISWYN had similar reactions to stem rust in both centers (Table 1).

Again we suggest, even in the absence of aerobiological and climatological data, that Southern Mexico and Guatemala share common rust races.

V. ANDEAN CUNTIES OF COLUMBIA, ECUADOR, PERU AND CHILE: (AREAS WEST OF THE ANDES MOUNTAINS SYSTEM)

Stripe rust is prevalent in all Andean Regions of South America at higher altitudes; at lower altitudes, stem rust is the more prevalent. No aerobiological studies have been conducted to correlate the data on meteorology and the epidemiology of wheat rust in this area.

We have gathered virulence data for both stripe rust and stem rust to substantiate our hypothesis that the wheat regions of Ecuador and Colombia are contiguous insofar as the inoculum of stripe rust and stem rust are concerned. The virulence data on five International Spring Wheat Yield Nurseries consisting of 25 varieties was collected from two Nurseries in previous years, and 50 varieties in the last three years. The data for *Puccinia striiformis* West. reactions are presented in Table 2. It is interesting to note that there is a very high correlation between the virulence genes of races of stripe rust in Colombia and Ecuador. Of 25 varieties in the First and Second ISWYN, 16 and 19 varieties, respectively, gave parallel reaction in both countires. In the 3rd, 4th and 5th ISWYN, where 50 varieties were analyzed, 35, 38 and 35 entries, respectively, had similar reactions. The genetic bases for resistance in these varieties are very diverse, as they represent varieties from all six continents where wheat is major crop.

With this as evidence, we suggest that, even in the absence of aerobiological data, there seems every likelihood that the virulence gene spectrum is similar for the races of *Puccinia striiformis* West. in the geographical area from Ecuador to Colombia. Oversummeing of stripe rust probably occurs in the higher altitudes of the mountains which would provide a common source of inoculum to be disseminated to the wheat fields in both countries (Personal communications, E.C. Stakman). Dr. J.W. Gibler (Personal communication) wrote that in 1962 a new race of stripe rust was found in the Department of Nariño, Colombia, just North of Ecuador which attaked the wheat variety Nariño. Due to the earth rotation, air mass movements are clockwise in the Northern Hemisphere and counter clockwise in the South, but the climatological equator moves North or South depending on time of year also low and high pressure areas are developed. He was able to follow the spore movements both South and North by observing the attack on the Nariño variety in Ecuador (South) and other wheat zones in Colombia (North). As he recalls the attack moved first into Ecuador infecting the variety as far South as Cuenca and Loja. It was not until later that the race was found in the savanna of Bogota and further

Table 2. Results of Five International Yield Nurseries showing the epidemiological relationship between wheat growing areas related to *Puccinia striiformis*, and *Puccinia graminis tritici*.

	1st ISWYN 25 varieties		2nd ISWYN 25 varieties		3rd ISWYN 50 varieties		4th ISWYN 50 varieties		5th ISWYN 50 varieties	
	Resist.	Suscept.	Resist.	Suscept.	Resist.	Suscept.	Resist.	Suscept.	Resist.	Suscept.
Colombia-Ecuador (*P. striiformis*)	10	6	12	7	20	15	20	18	18	17
Colombia-Ecuador (*P. graminis tritici*)	20	1	22	0	39	3	46	1	48	0

North at the Bonza Station near Sogamosa. Linked with the same movement was the spread of the "dwarfing" virus transmitted by the leafhopper *Cicadulina pastucae*. Native barley varieties with resistance were found in the Department of Nariño in Colombia, indicating that the virus had been present there for several hundred years. The virus was also found as far as Cuzco, Peru but never neached Bogota in the north even though the vector was present.

In Table 2, are also presented the data on the reaction to *Puccinia graminis tritici* for Ecuador and Colombia. These data further verify the hypothesis put forward in relation to *Puccinia striiformis* that Colombia and Ecuador share similar races of rust pathogens, and hence can be considered one epidemiological zone. Of 25 varieties in the 1st and 2nd ISWYN, 21 and 20 entries, respectively, had parallel reactions. Similarly, 42, 47 and 48 entries of the 3rd, 4th and 5th ISWYN, respectively, gave similar reactions in both Ecuador and Colombia.

Stubb's (48) data from the International Stripe Rust Trial for Ecuador, Peru, Chile and Mexico, are presented in Table 3. The data are based on 14 varieties having at least ten genes for stripe rust resistance. His data basically puts Ecuador, Peru and Chile in one epidemiological area in the broad sense. It is interesting to note, however, that there is a higher correlation between the data of Ecuador and Peru than that Ecuador and Chile. There is even less correlation between the data of Peru and Chile. This suggests that though Chilean and Ecuadorian races of stripe rust carry some similar genes for pathogenecity, there is less similarity than exists in the races of Ecuador and Colombia, Dr. J.W. Gibler (Personal communication) writes that there are more stem rust races in Peru than anywhere in the world, with the possible exception of Kenya. Nevertheless, this broad race range has never been found to the North in Ecuador and Colombia nor does it apparently pass on South to Argentina, Brazil or Chile. In this region there is a vast area lying between the regions where little wheat is grown. Rust from Peru does not ordinarily move North into Ecuador possibly because of the wind movements.

On the basis of the above analysis and interpretation, we suggest that there occur two or possibly three sub-epidemiological zones in respect to wheat rust: one occurs in Ecuador and Colombia one in Peru and the third in Chile.

VI. AREAS COMPRISING SOUTHERN BRAZIL, NORTHERN ARGENTINA AND PARAGUAY

In a personal letter, Dr. J.W. Gibler states that the common stem rust races 11, 15 and 17 and their sub-races are common in Brazil and Argentina. indirect evidence of wind movements, is available from the pattern of aphid attack of *Macrosiphum avenae* and another species. In 1971 aphids moved from Argentina to Brazil and into Paraguay. Additional evidence may be derived from movement of stripe rust in Argentina and Brazil. Each year stripe rust is found in such cool areas in Argentina as Bolson near Bariloche.

Table 3. Specific reation of twelve differential wheat cultivars in four countries to the attack of yellow rust **Puccinia striiformis***

	Heines Kolben Yr 6	Lee Yr 7	Chinese 166 Yr 1	Moro (PI 178383)	Compair (AEG. Comosa Yr 8	Swong 92 Omar Yr	Vilmorin 23 Yr 3	Strubes Dikkoph	Casterns V	Spaldings prolific	Heines VII Yr 2	Hybrid 46 Yr 4	Selkirk	Michigan Amber
Ecuador	S	R	S	R	R	S	S	S	S	S	S	R	R	S
Peru	S	R	S	R	R	S	S	S	S	S	S	R	S	S
Chile	S	S	R	R	R	S	S	S	S	S	S	S	R	S
Mexico	R	R	R	R	R	R	R	R	R	R	R	R	S	S

* From Stubbs, R. W. Regional Wheat Workshop, Beirut, Lebanon, 1972, ALAD. The Ford Foundation.

Table 4. Results of four International Yield Nurseries showing the epidemiological relationship between wheat growing areas related to *Puccinia recondita*.

	3rd ISWYN 50 varieties		4th ISWYN 50 varieties		5th ISWYN 50 varieties		6th ISWYN 50 varieties	
	Resist.	Suscept.	Resist.	Suscept.	Resist.	Suscept.	Resist.	Suscept.
Argentina-Brazil	—	—	—	—	27	7	24	11
Argentina-Uruguay	28	13	—	—	—	—	—	—
Mexico-Argentina	16	10	17	6	—	—	11	16

In the cooler years, stripe rust extends to the North and when Argentina has a heavy outbreak, stripe rust is very prevalent in Brazil.

We have analyzed the varietal reaction to leaf rust of wheat on 50 entries of the 3rd, 4th and 5th ISWYN (Table 4) to support the hypothesis that the areas of Southern Brazil, Argentina and by inference Paraguay and Uruguay, constitute a single epidemiological zone. In Table 4, 34 and 35 varieties of 50 from the 3rd and 4th ISWYN, respectively, had similar reactions in Argentina and Brazil.

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