



Wheat Rust Race Composition Under Warming Winters in South Asia: A Review of the Evidence

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Abstract

Wheat in South Asia is grown through the coolest months of the year, and the three rust fungi that attack it, the stripe, leaf and stem rust pathogens, differ in the temperatures they prefer. Winter and early spring temperatures in the region are rising, which raises the question of whether the races that make up each rust population are changing as a result. This narrative review brings together four bodies of published work that bear on the question: the classical epidemiology of rust survival and spread on the subcontinent, the methods and record of race surveys, experimental studies of temperature adaptation in *Puccinia striiformis*, and the general literature on climate and plant disease. Four pathways are distinguished: selection for heat-tolerant pathogen lineages that carry their virulences with them, altered off-season survival and epidemic length, temperature-dependent expression of host resistance, and incursion of exotic races. The review finds good experimental support for the first pathway outside South Asia, plausible but largely untested reasoning for the others, and a persistent difficulty in separating any climate effect from the much stronger effect of cultivar deployment. It closes by setting out the measurements that would allow attribution.

Keywords: Wheat rusts, *Puccinia striiformis*, Race surveys, Winter warming, South Asia, Temperature adaptation

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1. Introduction

Across the Indo-Gangetic Plain of Pakistan, India, Nepal and Bangladesh, wheat is sown as the monsoon heat recedes in November and harvested before the return of summer in March and April. The crop therefore lives almost entirely inside the cool season, and so do its three rust diseases: stripe or yellow rust caused by *Puccinia striiformis* f. sp. *tritici*, leaf or brown rust caused by *P. tritricina*, and stem or black rust caused by *P. graminis* f. sp. *tritici*. Each fungus has its own range of favourable temperature, and the few degrees that separate a cold January from a mild one can decide which of them builds up, in which districts, and for how many weeks (Roelfs et al., 1992).

Rust populations are not uniform. Each consists of races, also called pathotypes, that differ in which

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host resistance genes they can overcome, a relationship formalised in the gene-for-gene concept (Flor, 1971). Wheat breeding in South Asia has leaned heavily on race-specific genes, and the working life of a cultivar depends on how long the races able to attack it stay rare. The history of the region is one of repeated boom and bust, in which a widely grown cultivar selects the race that defeats it (Wellings, 2011).

Winters in the region are becoming warmer, and heat late in the season is already recognised as a constraint on the crop itself (Lobell *et al.*, 2012). Whether that warming is also changing the race composition of rust populations is a narrower question, and a harder one. This article reviews what the published literature can and cannot say about it. It reports no new survey or experiment.

2. Scope and Approach

This is a narrative review of the published literature. It draws on the classical accounts of rust epidemiology on the subcontinent, on descriptions of how races are identified and surveyed, on experimental work comparing the temperature responses of old and recent isolates, and on general reviews of climate change and plant disease. No formal search protocol was applied and no claim of completeness is made. Stripe rust receives most attention because it is the rust for which adaptation to temperature has been studied most directly. Much of that experimental work was done in North America and Europe, and its relevance to South Asia is argued here, not assumed.

3. The Rust System of the Subcontinent

Two features of the regional system matter for any argument about warming: the thermal niches of the three pathogens, and the fact that none of them survives the summer in the plains.

3.1. Thermal niches of the three rusts

Stripe rust is the rust of cool, moist conditions. Its urediniospores germinate and infect at low temperatures in the presence of dew, and its development slows sharply once days turn warm (Chen, 2005). In South Asia it has been a disease of the northern hills and the north-western plains, where winter is longest. Leaf rust tolerates a wide band of moderate temperatures and occurs wherever wheat is grown (Huerta-Espino *et al.*, 2011). Stem rust needs the most warmth and has mattered chiefly in central and peninsular India, where the season is warmer throughout. The spatial arrangement of the three diseases is thus already a temperature map, and a shift in winter temperature would be expected to redraw it before it changed anything within a single rust population.

3.2. Off-season survival and routes of spread

The foundational work of Mehta (1940) established that rust inoculum does not persist through the summer in the plains and that alternate hosts play no practical part in the annual cycle in India. The fungi survive on self-sown and off-season wheat in the hills: the Himalaya in the north, and the Nilgiri and Palni hills in the south. Nagarajan and Joshi (1985) later described how urediniospores from the southern hills are carried northward and deposited with rain, a route they called the Puccinia path, while stripe rust moves down from the Himalayan foothills into the north-western plains during winter.

Each season in the plains therefore begins with a founding population drawn from a small number of upland sources. Race composition in a given year reflects what survived in those sources, what was carried out of them, and what the cultivars in the plains then selected. Temperature can act at each of these three points, which is why its effect is difficult to isolate.

4. How Race Composition Is Measured

A race is identified by inoculating seedlings of a set of differential wheat lines, each carrying a known resistance gene, and scoring the infection types under standard conditions. The approach goes back to the stem rust differentials of Stakman *et al.* (1962) and, for stripe rust, to the nomenclature proposed by Johnson *et al.* (1972); the resistance genes themselves are catalogued by McIntosh *et al.* (1995). National programmes in South Asia maintain their own differential sets and analyse samples sent in from trap

nurseries and farmers' fields every season. A published account of the stripe rust pathotypes found in India over a decade illustrates the kind of record these surveys produce (Prashar et al., 2007).

Three properties of such data limit what they can show about climate. Samples are not random: they come from the cultivars and districts where rust was noticed. Infection types are scored at a fixed seedling temperature, so a race label says nothing about how the isolate performs in a warm or a cold field. And races are defined by virulence alone, although traits such as latent period and spore production are what temperature acts on most directly. Genotyping has begun to fill the gap. Population studies with molecular markers have traced the worldwide lineages of the stripe rust fungus (Ali et al., 2014), and sequencing of infected leaves taken straight from the field can assign samples to lineages without culturing them (Hubbard et al., 2015).

5. Pathways From Warmer Winters to Different Races

The literature suggests four routes by which warmer winters could change race composition. Table 1 sets them out with the kind of evidence available for each, and Figure 1 places them between the climate signal and the survey record. They are discussed in turn.

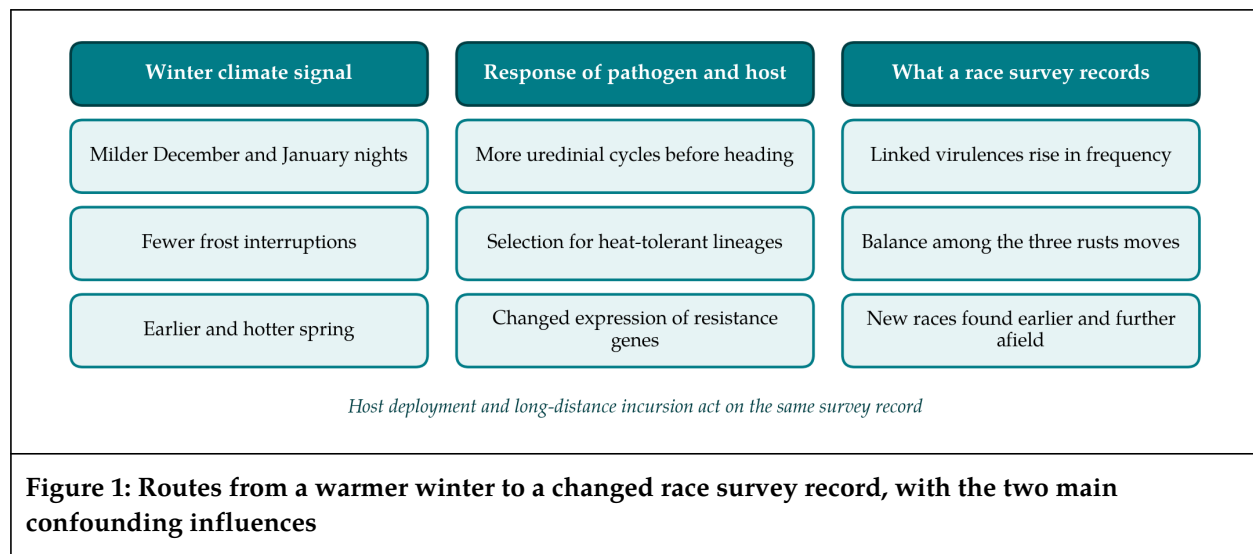
5.1. Selection for temperature tolerance within the pathogen

The clearest evidence concerns stripe rust outside South Asia. Milus et al. (2009) compared isolates collected in the United States before and after 2000 and showed that the recent ones had shorter latent periods and produced more spores at the warmer of two test temperatures. The same period saw two closely related aggressive strains spread across several continents within a few years (Hovmöller et al., 2008), and the authors of both studies linked the expansion of the disease into formerly marginal, warmer areas to this change in the pathogen. In France, Mboup et al. (2012) found that northern and southern populations differed in their temperature responses in a way that matched the local climate.

Table 1: Pathways by which warmer winters could alter rust race composition in South Asia, and the evidence for each			
Pathway	Expected effect on races	State of the evidence	Key sources
Selection for heat-tolerant lineages	Virulences carried by tolerant clones increase together	Experimental support from North America and Europe	Milus et al., 2009; Mboup et al., 2012
Off-season survival and earliness	Larger and more varied founding population in the plains	Inferred from classical epidemiology; not measured	Nagarajan and Joshi, 1985
Shorter cool period in spring	Stripe rust curtailed; leaf and stem rust favoured	Consistent with thermal niches; regional data sparse	Chen, 2005
Temperature-sensitive host resistance	Different genes effective, so different races selected	Gene behaviour known; population effect untested	McIntosh et al., 1995
Incursion of exotic races	Abrupt appearance of new virulence combinations	Well documented; link to climate weak	Singh et al., 2011
Cultivar deployment (confounder)	Race matching the dominant cultivar rises	Strong and repeatedly observed	Wellings, 2011

The relevance to race composition lies in the clonal structure of rust populations. Where the fungus reproduces only asexually, every virulence gene in a successful lineage is carried along with the trait that made it successful. A lineage favoured by warm winters would therefore raise the frequency of its whole virulence profile, whether or not those virulences are of any use against the cultivars being grown. The near-Himalayan region complicates this picture, because it has been identified as a centre of diversity of the stripe rust fungus where signatures of recombination are found (Ali et al., 2014), and barberry species are now known to serve as alternate hosts (Jin et al., 2010). Where sexual recombination occurs, tolerance

of heat and virulence can be reshuffled, and the simple hitch-hiking argument weakens. The same region has since been shown to be the source of races that replaced the established European population (Hovmöller *et al.*, 2016).



5.2. Survival, earliness and the founding population

Cold slows rust in midwinter. On mild nights the stripe rust fungus keeps cycling on the lower leaves of early-sown crops, and each additional uredinial generation before stem elongation multiplies the population from which new mutants can arise. Milder conditions in the hills could also widen the altitude band over which volunteer wheat carries rust through the off-season. Both effects would be expected to enlarge and diversify the founding population, and a larger population explores more virulence combinations in a season. The reasoning follows directly from the classical epidemiology (Nagarajan and Joshi, 1985), but the literature reviewed here contains no measurements of off-season inoculum made over a long enough period to test it.

Warming at the other end of the season works in the opposite direction for stripe rust. An earlier and hotter spring shortens the weeks in which the disease can progress, and may hand the later part of the season to leaf rust and, further north than before, to stem rust. A general poleward movement of crop pests and pathogens has been inferred from historical records at global scale (Bebber *et al.*, 2013). For South Asia these are expectations to be tested, not established regional trends.

5.3. Temperature-sensitive resistance in the host

Resistance genes do not all behave alike across temperatures. Some seedling genes lose their effect as it gets warmer; the stem rust gene *Sr6* is the textbook example (McIntosh *et al.*, 1995). Others work the other way. High-temperature adult-plant resistance to stripe rust is expressed more fully as the crop ages and the weather warms (Chen, 2005), and slow-rusting resistance based on several genes of small effect has proved lasting in CIMMYT-derived wheats grown across the region (Singh *et al.*, 2005). A warmer winter therefore changes which of the genes in a cultivar are doing the work, and with it the selection placed on the pathogen. A race survey run at one seedling temperature would not see this.

5.4. Incursions along changing routes

Some of the largest changes in race composition have arrived from outside. Virulence for the stripe rust gene *Yr9* moved from eastern Africa through western Asia into the subcontinent, and virulence for *Yr27* later overcame cultivars that occupied very large areas in India and Pakistan (Wellings, 2011). The stem rust race known as Ug99, first detected in Uganda with virulence for *Sr31* (Pretorius *et al.*, 2000), spread through eastern Africa to Yemen and Iran and gave rise to a family of variants (Singh *et al.*, 2011). These events follow prevailing winds and the movement of people and goods. Warmer winters might make an

arriving race more likely to establish, particularly a stem rust race in the northern plains, but the reviews cited treat incursion chiefly as a matter of wind-borne connectivity and host susceptibility (Wellings, 2011; Singh *et al.*, 2011).

6. What Can and Cannot Be Attributed to Climate

The dominant cause of race change is the host. When one cultivar or one resistance gene covers a large share of the wheat area, the race able to attack it increases, and this has been seen so often that it serves as the default explanation for any shift. A climate effect has to be detected against that background. General reviews of climate and plant disease have warned for many years that responses measured in growth chambers do not translate simply into field outcomes, because host, pathogen and management all adjust at once (Garrett *et al.*, 2006; Chakraborty and Newton, 2011).

For South Asia specifically, the published record supports three statements. Stripe rust lineages with greater tolerance of warmth exist and have spread widely. The regional epidemiology offers several points at which winter temperature could change the make-up of the founding population. And no study reviewed here has separated a temperature effect on race frequencies from the effect of cultivar turnover in the same years. The proposition that warming winters are shifting race composition in the region is thus reasonable, mechanistically grounded and not yet demonstrated.

7. Gaps and Priorities for Research

Attribution would need data that survey programmes do not routinely collect. The most direct step is to phenotype isolates for temperature response as well as virulence: latent period, lesion growth and spore production at a cool and a warm regime, following the design of Milus *et al.* (2009). Applied to isolates kept in national collections from earlier decades, this would show whether thermal traits have moved, and whether they moved with particular races. A second step is to tie every survey sample to a location, a date, a cultivar and the nearest weather record, so that race frequencies can be analysed with cultivar area as a covariate.

Genotyping should accompany pathotyping as a matter of course, since lineage identity is what links a South Asian isolate to the experimentally characterised strains elsewhere (Hubbard *et al.*, 2015). Monitoring of off-season wheat and barberry in the hills would test the survival pathway directly. On the host side, the practical response does not depend on resolving attribution: resistance that combines several partial genes, and that holds at the higher temperatures now expected late in the season, is a sound objective whatever the cause of race change (Singh *et al.*, 2005).

8. Conclusion

Race composition in the wheat rusts of South Asia is shaped first by the cultivars grown and by races arriving from elsewhere. Warmer winters add a further influence whose mechanisms are well understood in outline: selection among pathogen lineages for performance in the warmth, changes in survival and epidemic timing, and altered expression of host resistance. Experimental evidence for the first is strong in other regions. Evidence that any of them has measurably altered race frequencies in South Asia is still lacking, mainly because surveys record virulence and not thermal traits. Adding temperature-response phenotyping, genotyping and weather records to the existing survey system would turn a plausible hypothesis into a testable one.

Conflict of interest

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