

## HETEROECIOUS RUSTS AS AGENTS OF INTERFERENCE COMPETITION

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**ABSTRACT:** We suggest that the heteroecious rusts have evolved as agents of interference competition, with one host (the user) tolerating infection by the rust because this has the effect of reducing competition from the other host (the attacked). Several features of rust biology support this idea. In many cases the competitive situation is such that one host clearly has more to gain from damage to the other. The host with most to gain proves to suffer least from the rust, whenever it is possible to assess the relative damage done to the two hosts. This user host is nearly always the telial host, and is infected by the long-range aeciospores. On the other hand aecial (attacked) hosts are infected by short-range basidiospores, hence the individual user host mostly does damage immediately around itself. When a rust restricted to one host evolves from a heteroecious ancestor, the autoecious rust is found on the aecial (attacked) host of the ancestor in most cases, and always for microcyclic autoecious rusts (Tranzchel's Law). The telial (user) host has thus been selected to exclude the pathogen, according to the hypothesis because the benefits of reducing competition no longer outweigh the costs of rust damage. There is some evidence that user hosts can respond to release from shading by becoming more resistant to the rust.

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## INTRODUCTION

Rust fungi (Basidiomycetes, Uredinales) are plant parasites, and many are heteroecious; that is, they use two completely dissimilar hosts in the course of their life cycle. However, this use of two hosts does not necessarily reflect a broad ability to attack many related plant species, such as is common in fungi other than rusts. Very commonly, rusts are unable to attack even close relatives of their hosts. Small genetic (and hence biochemical) changes within individuals of a host species can make them resistant to a given rust race, and conversely a single-gene change in the rust can make it able to attack one strain of the host species rather than another (Flor 1956, Doubly et al. 1960, Person et al. 1962, Ellingboe 1979). Small biochemical changes in one of the hosts could pose problems to a rust race opposite to those it faced on the other host. Such changes would be selected for, because they would make it impossible for the rust race to use both hosts. Why does this not happen? A great deal of work has been done on the physiology and biochemistry of host plant resistance (see Daly and Unitari 1979, Friend and Threlfall 1976, Harborne and Ingham 1978 for recent reviews). However, our purpose here is not to explain heteroecy in terms of rust-host physiology, but to consider what selective pressures on hosts could produce physiologies which allow rusts to continue to use two hosts.

The question we ask is, why should a rust be able to attack two hosts in different families when it cannot attack near relatives of each host? Alternative answers are: (1) because the interactions of the two life-history phases of the rust with their respective hosts have different biochemistries, under the control of completely separate sets of genes in the rust; (2) because the two hosts have in common some biochemical properties which control their resistance/susceptibility reactions. Since there have been no studies looking at the physiology and biochemistry of rust-host interaction in both hosts of a heteroecious rust, the first answer cannot be rejected with data. However, it seems to us unparsimonious

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to suppose that heteroecious rust biochemistry is underlain by two sets of genes which evolve in complete independence of each other. Moreover, this answer leaves one asking why rusts do not have three, four or more hosts attacked by separate rust phases. Supposing the second answer is right, the two hosts could have the relevant biochemistry in common either by chance, or because of selection. Here we suggest how heteroecy could come about by selection.

We propose that one of the hosts of heteroecious rusts is selected to accommodate the rust in its tissues because as a result the rust damages the other host, with which the first competes. In other words, we argue that one host is using the rust as an agent of interference competition against the other. Price (1980) called this form of interaction "biological warfare", and cited (Chapter 7) several examples of it in taxa other than the rusts and their hosts.

To support this argument we put forward some predictions as to the features of rust-host biology (besides heteroecy) which we would expect to find if the agent-of-competition hypothesis were true. We show that the available evidence confirms these predictions. First we describe some essentials of the biology of rusts and their hosts.

RUST LIFE CYCLES

Rusts with the full heteroecious macrocyclic life cycle use three substrates: two plant hosts and the soil or leaf litter (Table 1). There are five spore forms, \*\*\*\*\*  
 Table 1. GENERALIZED LIFE CYCLE OF A HETEROECIOUS RUST.

Stage	Name	Karyology and Morphology	Host (AH = aecial host TH = telial host)	Comments
0	Pycnia	n mycelia	AH	
	↓			
	Pycniospores	n spores	AH → AH	Fuse with n hyphae of opposite mating type
	↓	(plasmogamy)		
I	Aecia	n + n mycelia	AH	usually perennial
	↓			
	Aeciospores	n + n spores	AH → TH	light, long range dispersal
	↓			
II	Uredinia	n + n spores	TH	usually not perennial
	↓			
	Urediniospores	n + n spores	TH → TH	multiplication phase
	↓			
III	Telia	n + n mycelia	TH	usually not perennial
	↓	(nuclear fusion)		
	Teliospores	2n spores	TH → soil <sup>1</sup>	usually overwintering
	↓			
IV	Basidia	2n mycelia	soil, litter <sup>1</sup>	
	↓	(meiosis)		
	Basidiospores	n spores	soil → AH	short-lived, short range dispersal

<sup>1</sup> In many Puccinia species teliospores can remain on the telial host and germinate there.

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the pycniospores acting as sperm cells, the urediniospores for reinfection of the telial host, and the aeciospores, teliospores and basidiospores for transfers between different substrates. The five mycelial forms can be differentiated by karyotype, by morphology or by the substrates they occupy. Rust taxonomy and life-cycle terminology have had a tangled history. Peterson (1974) gives a lucid account of the problems, and relates different systems to each other, as does Laundon (1973), whose terms are used in Table 1.

Many rusts occur which are autoecious, using only one host, or which are demicyclic or microcyclic, having only some life-cycle stages. For example, in an autoecious microcyclic life cycle, basidiospores infecting the only host produce short hyphae which quickly fuse to form telial mycelia. Aecial and uredinial stages are bypassed. Heteroecy is universal in the most primitive surviving rusts. Autoecious rusts and those with simplified life-cycles are regarded as derived by most authorities (see Anikster and Wahl 1979, Laundon 1973, Peterson 1974, Savile 1976 for recent reviews).

#### EXPECTED PATTERNS UNDER THE AGENT-OF-COMPETITION HYPOTHESIS

In this section we focus on five features of rust-host biology which ought to follow if the agent-of-competition hypothesis is true. In the next section we assess the evidence for these predictions.

We base our reasoning on the following premises of evolutionary ecology. For a host to be resistant to a rust, it must use resources to make its surfaces inhospitable or to inhibit fungal growth chemically. These resources could otherwise be used for growth or reproduction. Similarly, for a rust to overcome a host's resistance, it must provide its spores with the resources to establish on an inhospitable surface, or its hyphae with the enzymes to overcome chemical resistance; these resources could otherwise be used in producing more spores or in faster hyphal growth. Thus both resistance and the ability to overcome it have costs, as well as benefits. The benefit of resistance depends on whether the rust is present, and the benefit of being able to overcome resistance depends on whether the host is resistant. Both benefits and costs affect the fitness of the hosts and the rust. Over the long haul of evolution we expect those genotypes to predominate in any particular situation which have the best margin of benefits over costs, with respect to resistance or the ability to overcome it. Therefore as between situations which offer different benefits, we expect to find genotypes differing in the costs they incur, that is in their resistance or their ability to overcome resistance.

Our basic hypothesis is that the presence of the rust should confer a net advantage (benefits > costs) on one of the hosts (which we will call the "user" host), and a net disadvantage (benefits < costs) on the other (which we will call the "attacked" host). According to the hypothesis, the rust and the attacked host should have the usual relationship of parasites to their hosts: the attacked host should suffer loss of fitness in proportion to the extent it is infected by the rust, but should not exclude the rust completely because the costs of doing so would outweigh the benefits. The rust's abilities to overcome host plant resistance are primarily selected by the problems the attacked host presents it. If any given rust strain were able to use two attacked hosts, each attacked host would be selected to diverge biochemically from the other so that the rust could not exploit both of them. For this reason, it should be unusual for a rust strain to be able to exploit more than one attacked host.

The user host, on the other hand, could according to the hypothesis exclude the rust at comparatively little cost by presenting it with challenges different from those the rust is adapted to overcome in the attacked host. However, user hosts infected by the rust release into their surroundings an inoculum of the rust, which

damages any attacked hosts in the area and may increase the fitness of the user host by reducing the competition from which it suffers. In this way, according to the hypothesis, user hosts can be selected not to exclude the rust, even though they could do so without the physiological costs of resistance exceeding the physiological costs of damage caused to them by the rust. We will refer to the user host as "accommodating" the rust in this sense. For these reasons, any given rust could have more than one user host, if several potential user species stood to gain from damage to the single attacked host.

If the evolutionary pressures outlined above are in fact operating, we would expect the following patterns:

(1) The user host, but not the attacked host, should suffer substantially from competition relative to the damage it suffers from the rust. Competition between the two hosts could be asymmetrical so that damage to the attacked host would help the user while the converse would not be true. Alternatively the rust could do less damage to the user than to the attacked host. When there is a difference between the two hosts both in the importance of competition from the other host, and in the damage caused by the rust, we expect one of the hosts (the attacked) to be both the competitive dominant and the host more damaged by the rust.

(2) We would expect the rust often to disperse over long distances from attacked host to user host, but only over relatively short distances from user host to attacked host. Using the rust would not be stable as an evolutionary strategy if it were possible for individual user hosts to reap the benefit of damage to the competing attacked host without themselves accommodating the rust. User hosts should therefore be selected to accommodate strains of rust which mainly damage attacked hosts near to, i.e. competing with, the user individual.

(3) The attacked host should always benefit from the absence of the rust, but should be unable economically to exclude it. On the other hand the user host should only be selected to accommodate the rust when the circumstances of its competition with the attacked host favor this. If these circumstances change in the course of evolution, the user host could be selected to exclude the rust. Therefore, when rusts are reduced through evolutionary time to using only one host, it should usually be the user host that disappears from the life cycle.

(4) For the same reason, user hosts should be selected to adjust their own resistance to the rust according to the benefit they can obtain, i.e. according to whether they are suffering from the competition of the attacked host. Such selection could produce both genetic differences between populations of user hosts, and also an ability for individuals to adjust their resistance phenotypically.

(5) An individual user host which accommodated the rust would only reap a benefit if the few other plants shading that individual, or otherwise competing with it, included at least one attacked host. Now according to the hypothesis it should be unusual for a rust strain to be able to exploit more than one species of attacked host. Understory user hosts should therefore profit relatively little from accommodating a rust where the overstory is made up of many interspersed species. Heteroecy should be less common, relative to autoecy, in vegetation with a diverse overstory.

#### EVIDENCE FOR THE EXPECTED PATTERNS

The first question we can ask is: which of the two hosts is likely to gain most from damage to the other?

The heteroecious rust genera of North America, with their hosts, are listed in Table 2. (This sample of the world's rust flora is representative in that most heteroecious genera are present in North America, and the genera such as Puccinia represented by many species in North America are also important elsewhere.)

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 Table 2. NORTH AMERICAN HETEROECIOUS RUST GENERA AND THEIR HOSTS.  
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Genus	Number of Species	Aecial Host	Telial Host
<b>Melampsoraceae</b>			
<u>Uredinopsis</u>	5	<u>Abies</u> <sup>1</sup>	Ferns (Osmundaceae, Polypodiaceae)
<u>Milesia</u>	7	<u>Abies</u> <sup>1</sup>	Ferns (Polypodiaceae)
<u>Hyalopora</u>	3	<u>Abies</u> <sup>1</sup>	Ferns (Polypodiaceae)
<u>Pucciniastrum</u>	12	<u>Pinaceae</u> <sup>1</sup>	Deciduous shrubs, herbs
<u>Melampsorella</u>	1	<u>Abies</u> , <u>Picea</u> <sup>1</sup>	Herbs (Caryophyllaceae)
<u>Melampsoridium</u>	3	<u>Larix</u> <sup>1</sup>	Deciduous trees & shrubs (Betulaceae, Corylaceae)
<u>Cronartium</u>	7	<u>Pinus</u> <sup>1,2</sup>	Dicot trees & shrubs, herbs
<u>Chrysomyxa</u>	9	<u>Picea</u> <sup>1</sup>	Dicot shrubs, herbs
<u>Coleosporium</u>	21	<u>Pinus</u> <sup>1</sup>	Dicot herbs, deciduous shrubs
<u>Melampsora</u>	9	<u>Pinaceae</u> except <u>Pinus</u>	Deciduous shrubs, dicot herbs
<u>Cerotelium</u>	2	<u>Dicentra</u>	<u>Laportea</u> ( <u>Urticastrum</u> )
<b>Pucciniaceae</b>			
<u>Tranzschelia</u>	1	<u>Ranunculaceae</u>	<sup>1</sup> Shrubs (Rosaceae)
<u>Puccinia</u>	78	Many families <sup>1</sup>	Grasses primarily (Poaceae)
<u>Gymnosporangium</u>	32	Several families	Gymnosperms (Juniperaceae)

<sup>1</sup> Dominant over other host because overstorey species; <sup>2</sup> precedes other host in successional series; species counted from main text of Arthur and Cummins (1962).  
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In many cases one host is clearly an overstorey species and the other an understorey species. Presumably the understorey species would have more to gain from damage to the overstorey than vice versa. In one case (some Cronartium species) where the two hosts are of similar stature, Pinus typically precedes Quercus in succession (Spurr 1964). It is now recognized (e.g. Connell and Slatyer 1977) that late-successional species may be unable to increase until the dominance of space by early-successional species breaks up. It is easy to imagine the advantage of fostering a rust which would thin out the canopy of species established earlier, or prevent continuing establishment of their seedlings. In nearly all the cases in Table 2 the presumed user is the telial host, and the presumed attacked host is the aecial host.

Generally we would expect that where one host is damaged more seriously by the rust than the other, the attacked host would suffer more damage and the user less. We have found it very difficult to use the literature to attribute degrees of damage to the different hosts, for a number of reasons. The first is that few comments are made about the impact of the rust on the host which is not the economic crop. Even in a case such as Cronartium ribicola, where great efforts have gone into the eradication of Ribes, we have found only qualitative information on the damage done by the rust to Ribes. The second reason is that it can be very difficult to decide to what extent the physiological damage to a host constitutes a loss of fitness. For example, the effect of Melampsoridium on both its aecial (Larix) and its telial (Salix, Betula, Populus) hosts is to cause premature leaf drop. In Britain, the premature leaf dropping causes severe damage to the telial hosts because as a side-effect it prevents them from becoming cold-hardened (Peace 1962). It is unclear, though, whether the telial hosts are more severely damaged throughout the range of Melampsoridium. A similar case is that of Coleosporium tussilaginis in nurseries of Pinus sylvestris (the aecial host) with Senecio vulgaris (the telial host) present,

in Britain. The pine needles are affected and are shed the spring following infection; in severe cases branches are pruned as well. The Senecio seems morphologically to be more badly damaged than the pine, with shoot deformation and stunting in cases of severe infestation. However, infection on Senecio "tends to hasten flowering and seeding, so that far from lessening the necessity for weeding it makes it even more urgent" (Peace 1962, p. 276). It may be that the radius over which the pine canopy will open up next spring favours seed production rather than vegetative growth in Senecio, and that Senecio has evolved to use the rust as an indicator of these conditions.

Puccinia, perhaps the most-studied rust genus, presents a third problem in assessing damage. The telial hosts, hypothetically the users, are grasses, particularly annuals now planted as economic crops. The damage to crops has been described in detail; generally the plants are stunted and the seeds are unable to develop to full weight (Arthur 1929). It is unclear how such changes would affect fitness in a self-propagating population. Moreover, this is in a situation where the user host is being grown as a monoculture with increased opportunity for epidemic population growth of the rust, and with the presumed attacked hosts (e.g. Berberis, Mahonia, Rhamnus) posing no competitive threat. Segal et al. (1980) comment that despite severe infection by P. coronata, wild Avena populations in Israel do not seem to suffer from the disease, and show excellent tolerance. Similarly, serious disease outbreaks have not been observed in wild Hordeum spontaneum harboring P. graminis. In other cases studied in Israel, the damage by Puccinia to wild grass populations is limited because of the early maturation of the wild grasses. A number of wheat varieties are tolerant of stem rust (Mussell 1980). Mechanisms include good seed yield despite heavy infestation, and stimulation of the rust toward early telial formation. Puccinia damage to any of the aecial hosts has been described relatively rarely, and we have found no descriptions of damage to whole plants which would enable us to judge, how much wild grass populations might benefit from infecting these aecial hosts.

In those cases where there is evidence that one host is more damaged than the other (Table 3), a clear pattern emerges. In every case, the host which suffers less damage is the one with most to gain by reducing competition from the other, as the agent-of-competition hypothesis would predict. If we take as null hypothesis the prediction that the dominant competitor of the two hosts is equally likely to suffer more, or less, from the rust, the probability that the pattern in Table 3 would arise by chance is  $1/2^7$  or about 0.008. The result is thus highly significant. In all cases but Tranzschelia, the user host is the telial host; Tranzschelia is also unusual in that the telial mycelium is perennial. Gymnosporangium, another major genus in the Pucciniaceae, also has perennial telial mycelia, and may prove to have aecial user hosts as in Tranzschelia.

The second expectation outlined above was that spores infecting user hosts should disperse over longer distances. This is true; aeciospores are generally relatively light and long-range, teliospores are usually heavy, and basidiospores are short-lived and disperse over short distances (Boyce 1961, Peace 1962). This is a qualitative observation not susceptible to statistical testing.

The third pattern which was predicted from the agent-of-competition hypothesis is that where a formerly heteroecious rust has been reduced to one host, i.e. become autoecious, through evolutionary time, it should be the user (hypothetically telial) host of the ancestral heteroecious rust which no longer accommodates the parasite. For rusts which have become microcyclic as well as autoecious, this is so true that

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 Table 3. CASES WHERE ONE HOST IS CLEARLY MORE DAMAGED BY A HETEROECIOUS RUST THAN THE OTHER.  
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Rust	Aecial Host	Telial Host	Source
<u>Pucciniastrum padi</u>	1,2 <u>Picea</u> spp.	<u>Prunus</u> spp.	Peace (1962)
<u>Cronartium comptoniae</u>	1,2 <u>Pinus</u> spp.	<u>Myrica</u> spp.	C.H. Driver, pers comm
<u>C. quercuum</u> & <u>C. fusiforme</u>	1,2 <u>Pinus</u> spp.	<u>Quercus</u> spp.	Hedgecock & Siggers (1949)
<u>C. ribicola</u>	1,2 <u>Pinus</u> spp.	<u>Ribes</u> spp.	Mielke (1943)
<u>Chrysomyxa pyrolae</u>	1,2 <u>Picea</u> spp.	<u>Pyrola</u> spp.	D.E. Stuntz, pers comm
<u>Chrysomyxa</u> spp.	1,2 <u>Picea</u> spp.	<u>Rhododendron</u> spp., <u>Ledum</u> spp.	D.E. Stuntz, pers comm
<u>Tranzschelia pruni-spinosae</u>	<u>Anemone</u> spp.	1,2 Rosaceae	Arthur (1929)

<sup>1</sup> Host which is overstory, or precedes the other in succession (see Table 2).

<sup>2</sup> Host which suffers more damage from the rust.

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 it has the status of an empirical rule, known as Tranzschel's Law (Tranzschel 1904 cited by Laundon 1973). This rule is now considered so well established that it can safely be used to interpret phylogeny. Some autoecious rusts which are macrocyclic or demicyclic do occur on the telial host of the presumed heteroecious ancestor, but even this is rare. In the rusts of North America as described by Arthur and Cummins (1962), roughly 11% of autoecious Puccinia species and 3% of other autoecious species occur on the telial hosts of their ancestors, the remainder occurring on the ancestral aecial hosts (Table 4). If we take as null hypothesis that a rust which  
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Table 4. REDUCTION OF NORTH AMERICAN RUSTS TO ANCESTRAL TELIAL OR AECIAL HOSTS ON BECOMING AUTOECIOUS.

	Number of Species <sup>1</sup>	
	<u>Puccinia</u>	Other Genera
Heteroecious rusts	78 <sup>2</sup>	139
Autoecious rusts		
Microcyclic (all on aecial host)	131	18
Macro/Demicyclic		
On aecial host	132	57
On telial host	32	2
Percentage of autoecious species on telial host of presumed ancestor	11%	2.6%

<sup>1</sup> Calculated from Arthur and Cummins (1962).

<sup>2</sup> Plus at least 40 species which were thought to be heteroecious but had been found only on the grass host.

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 has become autoecious is equally likely to be found on telial or aecial host of the ancestor, the probability of Tranzschel's Law arising by chance is a vanishingly small  $1/2^{149}$ , considering only North American species and including Puccinia. If macrocyclic and demicyclic species are included, the pattern of Table 4 has a  $X^2$  of 248 (df = 1, P << .001).

Since the advantage to a user host of accommodating the rust will depend on

whether it is actually suffering under competition from an attacked host, we might expect to find some variation in how much the user host accommodates the rust. A phenotypic response of user host resistance would ideally be keyed to the presence of the attacked host specifically. However, plants have few methods to sense what species they are competing with. Moreover, if a user host were to be selected to adjust its resistance according to the incidence around it of some secondary chemical released by the attacked host, the attacked host would in turn be selected to release different chemicals. The most likely response of user hosts is therefore that they will be more resistant to the rust in the sun than where they are shaded. Such a pattern has been observed in Ribes infected by Cronartium ribicola (Kimmey 1938, Mielke 1943). Furthermore, the Ribes can suffer extensive dieback during the period when there are infected pines nearby, but after the pines are killed by the rust the Ribes soon recovers vigor (Lachmund 1934). These phenomena fit the agent-of-competition hypothesis well, but could also be explained as by-products of increased humidity in the shade, and of such responses to shading as thinner cuticles and open stomates. It would therefore be very useful to have information on the mechanisms which decrease resistance of user hosts in the shade.

Lachmund (1934) also found that a less shade-tolerant Ribes species was more susceptible to the rust than a more shade-tolerant Ribes. The field ranking of susceptibility was confirmed under more controlled conditions by Mielke (1943).

Since using a heteroecious rust should usually only be effective against one attacked host, heteroecy should be less common relative to autoecy in forests with diverse overstories. We have found no systematically assembled information on the geographical distribution of heteroecy and autoecy with which to test this prediction. It is encouraging, though, that many attacked hosts of north American rusts (Table 2) are gymnosperm trees which commonly grow in extensive stands of one or a few species. Further, autoecy may be relatively concentrated in the tropics<sup>1</sup>. Savile (1976) implies this in arguing that heteroecy is particularly an advantage in seasonal environments away from tropical moist forest. Many tropical forests are particularly rich in tree species (Whittaker 1977).

#### DISCUSSION

We have shown that several important features of rust biology make sense on the hypothesis that the rust is being used as an agent of interference competition by one of its hosts against the other. The most convincing kinds of evidence are Tranzschel's Law, and the relatively short range of dispersal to the aecial hosts, because these are patterns known to be true across the rusts as a whole.

Features such as Tranzschel's Law have previously been regarded as purely empirical rules, and we believe the agent-of-competition hypothesis is a potential explanation. The pattern of Table 3, whereby hosts which are superior competitors are more damaged by the rust, represents a more direct test of the actual machinery of the agent-of-competition hypothesis. The test is weaker, however, (though still highly significant statistically) due to shortage of evidence. We have only been able to say with confidence that one host is more damaged than another for seven cases, a small subset of all the rusts. Only much more work in many rust-host systems will make it possible to say whether the cases we cite are a representative sample or not.

The deficiencies of the evidence are our second reason for publishing the hypothesis. Present knowledge of rust-host biology testifies impressively that a

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<sup>1</sup> An anonymous referee for another journal asserted so, unfortunately without source; we can find no literature documenting the pattern. The referee thought this pattern destroyed our argument, but we thank him or her anyway.



question must be asked before data which answer it will be collected. Despite a century of very extensive work on rust biology, there exist no measurements of rust damage to host plants which quantify its effects on the host's fitness, and for hosts which are not economic crops even qualitative descriptions of damage are rare. There have been no comparative studies of the physiology or genetics of resistance and virulence in both hosts and both life-history phases of a heteroecious rust.

Since heteroecy is primitive in rusts, we would expect the balance of selective forces implied by the agent-of-competition hypothesis to be widespread in rust biology. This is not to say, however, that all features of the biology of all rusts can be explained by the agent-of-competition hypothesis. Many modern rusts are autoecious. Since competition is a two-edged sword, we would not be surprised to find cases where the original user has become the attacked host. (Perhaps Tranzschelia is an example of this.) And the actual costs and benefits of using the rust may be rather different in crop situations compared to what they are in natural vegetation.

The three-species interaction hypothesized here may seem like a novel and elaborate variety of coevolution. However, it is not really surprising. Species suffering loss of fitness from competitors or predators will be selected to use any available device to defend themselves, and naturally some of the available devices will be other organisms. Perhaps the best-known case of this kind is the way plants use ants to defend themselves against predators (e.g. Janzen 1966, Bentley 1977). There are a number of animal parasites which obligately alternate between two hosts [e.g. many trematodes, cestodes and protozoa, and some aphids (Dogiel 1964, Little 1972)]; perhaps some of these are being used as agents of interference competition.

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