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RHODODENDRON RUST—TAXONOMIC AND HORTICULTURAL IMPLICATIONS

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ABSTRACT. The rust fungi known to occur on the genus *Rhododendron* worldwide are introduced, and the behaviour of *Chrysomyxa rhododendri* de Bary, the commonest species attacking rhododendrons in cultivation is outlined. Investigations of host susceptibility to *C. rhododendri* are reported, and the great extension of host range from the wild to cultivation, where it is now known to attack Vireya species and their hybrids, is emphasized. The pattern of host susceptibility is also assessed in relation to the classification of *Rhododendron*. The history of spread of *C. rhododendri* is traced, with particular reference to Britain and Australia, and implications for effective quarantine measures to restrict further spread are discussed. The results of experimental trials for control of this rust are reported and a programme of combined husbandry and chemical spraying for its eradication described.

INTRODUCTION: THE RUSTS OF RHODODENDRON

The rust fungi are obligate parasites, some 5000 species of which have been described on a wide range of angiosperms, gymnosperms and ferns. Most species are extremely host specific, although in some cases the pleomorphic life cycle, which can include up to five different spore stages, may involve alternation between taxonomically unrelated hosts. To date 16 different rust species have been described on *Rhododendron*. Leppik's (1974) résumé of taxa listed 14 species, ten of which were assigned to the genus *Chrysomyxa*. Recently two new species have been reported from western China (Wang *et al.,* 1980) and, based on his collections from Nepal, Durrieu anticipated describing at least two more (Durrieu, 1980). The status of all these taxa, some of which may prove to be synonymous, is still being resolved.

The natural distribution and probable origins of most of these species of rhododendron rust were reviewed by Leppik (1974), who also indicated their occurrence in cultivation. At present five species of rust are known on cultivated rhododendrons but of these, *Chrysomyxa himalensis* Barclay has only been reported in the Indian sub-continent where the fungus is native on *Rhododendron arboreum* and *R. campanulatum* (Leppik, 1974), and *C. piperiana* (Arth.) Sacc. & Trott, whose behaviour was outlined by Coyier (1978), is confined to selected hybrids of its native host *R. macrophyllum* in western North America (Ziller, 1974). *C. succinea* (Sacc.) Tranz. occurs extensively in eastern Asia, and has been reported on a number of rhododendron species (Leppik, 1974, incl. *C. expansa* Diet.), especially in Japan (Hiratsuka & Sato, 1969) where it is presumed to have extended into cultivation. *Pucciniastrum vaccinii* (Wint.) Jørst. s.l., a species complex whose members parasitize a spectrum of Ericaceae worldwide (Hiratsuka, 1958) includes specialized forms occurring on certain rhododendrons as yet confined to North America (Leppik, 1974), where in cultivation, it is known to be occasionally troublesome on deciduous azaleas (e.g. Bir, Jones & Benson, 1982). The so-called 'European rhododendron rust', *C. rhododendri* de Bary, which is

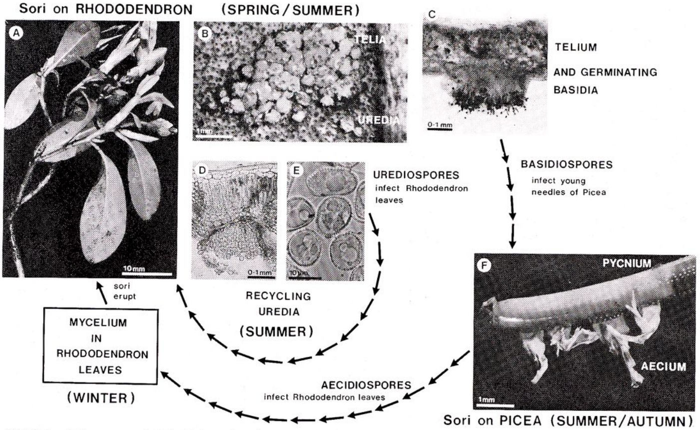

FIG. 1. Life Cycle of *Chrysomyxa rhododendri*. A, sori on the underside of rhododendron leaves; B, detail of sori on rhododendron including ungerminated waxy telia and peripheral uredia; C, t.s. germinating telium showing basidia bearing basidiospores; D, t.s. uredium showing chains of urediospores; E, urediospores showing ornamented walls; F, sori on spruce needle including immersed pycnia, now blackened and declined, and columnar aecia, with conspicuous white peridium; for explanation see text.

sometimes treated as a variety of the small-spored *Ledum* rust (*C. ledi* (Alb. & Schw.) de Bary var. *rhododendri* (de Bary) Savile), is the most widespread species of rust attacking rhododendrons, and is found on native hosts not only in Europe (Gaumann, 1959) but also in North America (Savile, 1955) and Asia (Hiratsuka, 1929). It is also the most widely distributed rust of rhododendrons in cultivation, extending throughout the former continents and beyond into Australasia (e.g. Cunningham, 1931). The preliminary results of extensive researches into the species of *Chrysomyxa* attacking rhododendrons, with particular reference to the USA, were published by Gould (1966), and more recently Coyier (1978) gave a succinct summary of these rusts, also from an American perspective. This paper focuses its attention on *C. rhododendri,* the most common rust of rhododendron, and considers the behaviour, spread and control of the fungus worldwide, in the light of our investigations in Britain.

BEHAVIOUR OF CHRYSOMYXA RHODODENDRI

The life cycle of *C. rhododendri* and the morphology of its major spore stages are illustrated in Fig. 1. A typical heteroecious species of *Chrysomyxa,* it alternates to *Picea* species, on the current season's needles in which immersed golden pycnia develop in mid-summer. As these blacken and decline (Fig. 1F), they are succeeded from late summer to mid-autumn by white columnar aecia (Fig. 1F) whose orange spores are capable of infecting adjacent susceptible rhododendrons. The infection on spruce is accompanied by conspicuous golden banding of diseased needles, which are shed prematurely during the following winter. On rhododendron the rust usually overwinters as dormant mycelium, erupting as dark orange waxy cushions in early spring. These are the telia (Fig. 1B), whose spores germinate *in situ* by late spring to produce basidia bearing basidiospores (Fig. 1C). The latter are capable of infecting young spruce needles which are emerging from the bud at this time. All infections on spruce must be annually re-initiated by these spores from adjacent rhododendron. In contrast, the fungus can persist on rhododendron in the absence of spruce, because of its ability to overwinter in the evergreen leaves, and because of the characteristic recycling uredial stage which produces abundant spores capable of infecting rhododendrons. It is these bright yellow, powdery pustules which are most readily recognized as symptoms of infection; they are clustered or solitary on the underside of the leaves (Fig. 1B), and sometimes accompanied by a red-brown discoloration of both leaf surfaces. These uredia develop concurrently with the telia, on previous seasons' foliage. Sporulation (Fig. 1D, E) coincides with the emergence of the new leaves. These are most susceptible while young, and readily become infected: thereby ensuring continuity of the rust on the rhododendron host.

Throughout the complex life cycle, the co-ordination of sporulation and phenology of the respective alternate hosts should be noted. However, the precise timing and sequence of development of spore stages on rhododendrons varies considerably according to the prevailing climate, host taxon, and probably also pathotype of the rust involved. Five major patterns have been recognized from the populations of *C. rhododendri* studied in Britain (four of which are represented diagrammatically in Fig. 4).

1. Single cycle: in which urediospores, from sori developing on old leaves in late spring, give rise to infections on the new foliage, which in turn only erupt as sori the following year.
2. Recycling: in which uredia develop on the new foliage soon after infection.
3. All year round: in which recycling continues throughout the year. This behaviour is chiefly a consequence of prevailing climate, and occurs in mild, sheltered conditions, especially under glass.
4. Alternating: full cycling behaviour depends on the proximity of susceptible spruce and the ability to produce telia, which may be accompanied by any of the previous patterns of uredial behaviour (1–3).
5. Alternating only: on certain hosts telia only are encountered. In such unusual cases there is no capacity for increase of the fungus on rhododendron, which must be regularly reinfected either from adjacent spruce, or by urediospores from other rhododendrons.

The continuity of infection on rhododendrons depends largely on their pattern of leaf retention, which itself varies with climate, and may differ between clones of the same taxon. Completely deciduous plants (e.g. certain azaleas) can only be secondarily infected from adjacent diseased hosts, whereas all evergreen rhododendrons can sustain the rust independently. Small-leaved rhododendrons, and the majority of lepidote forms retain their leaves for just over one year, necessitating annual recycling of the rust. Other rhododendrons which retain some leaves for several (up to 4) years offer limited scope for more protracted persistence of infection on individual plants, even in the absence of new inoculum. It should be noted that in most cases only leaves of the current season are readily infected by either urediospores or aeciospores. Older leaves on the plant are chiefly repositories of previously established infections, few of which remain active after the first year, although old leaves can become infected under optimum conditions (Gould, 1966). The susceptibility of young foliage is particularly significant in the case of rhododendrons that feature a secondary flush of foliage in the early autumn. This late flush coincides with both the production of aeciospores on spruce and the later generations of uredia erupting on the main (earlier) flush on rhododendron, thus leading to high levels of infection on these new leaves. Furthermore, in rhododendrons grown under glass, and given adequate light and warmth, the production of new leaves of some taxa will continue all year, offering scope for sustained recycling of the rust.

Many populations of the rust are reported to lack the ability to produce telia. Savile (1953) has discussed this problem in respect of hosts in the wild, and notes that it is common for many species of *Chrysomyxa* at the northern limits of their range, beyond the range of the alternate spruce host, to persist as uredia-only. Whether this is an environmental restriction as Gould (1966) speculated, or an inherent property of these populations, remains unclear. Significantly in cross-infection experiments, in cultivation under uniform conditions, the same inoculum gave rise to uredia only, uredia with telia, or telia only on different hosts. Thus in this case the ability to produce telia was dependent upon the identity of the host. The nature of the host and its susceptibility to rust also dictates the spread of the fungus within the leaf tissues resulting in different sizes and distributions of sori, from scattered isolated pustules, to extensive clusters (e.g. Fig. 1C). On exceptionally susceptible hosts (e.g. *R. charitopes*) the rust may also extend into petioles, pedicels, bud scales and cataphylls, where sori can also erupt. The major impact of the rust on the rhododendron host is to disfigure and discolour plants grown for their ornamental appeal; the presence of unsightly disease in nursery stock will render it unsaleable. Furthermore severe infections of seedlings and young plants can result in significant loss of vigour, leading ultimately to defoliation and death.

HOST RANGE OF RHODODENDRON RUST

A catalogue of all known hosts of *C. rhododendri* compiled from literature records and herbarium specimens is presented in Appendix 1. Rhododendron nomenclature and the arrangement of species follows the recent revisions of Cullen (1980) and Chamberlain (1982) in conjunction with Philipson & Philipson (1982), with the exception of the Vireya rhododendrons which follow the account of Sleumer (1966). Host species are listed alphabetically by section or subsection and are annotated according to the source of the rust record, whether on plants growing in the wild or in cultivation. Selected hybrid hosts have also been included where their parentage, as documented by Synge & Platt (1964), could be determined. They are listed under the appropriate section of each identified parent species. In the absence of voucher specimens, it has been impossible to check the veracity of the host identification for many of the earlier records. In any case, regrettably, many herbarium collections of the rust simply record the host as 'Rhododendron sp.' and consist of a few detached leaves, which cannot be accurately determined.

From this summary of records it can be seen that of 74 species listed, only 23 are so far known to support the rust in the wild, although it must be acknowledged that few mycologists have yet investigated the majority of rhododendron species in their native habitats. Furthermore, hosts in cultivation represent 19 sections in the genus, whereas in the wild, members of only 5 sections are involved. Leppik's (1974) earlier catalogue of rhododendron rusts demonstrated a similar disparity. Thus in cultivation the rust has been able to attack over 50 new host species. The implications of this dramatic extension in host range are discussed below. More than 100 hybrids are also recorded as hosts of the rust, and their parentage includes another 28 species not otherwise known to support the rust, which represents a further extension of range. Analysis of the hosts indicates that species of certain groups, notably subsects *Cinnabarina, Maddenia, Lapponica* and *Campylogyna* in subgenus *Rhododendron,* and sect. *Fortunea* in subgenus *Hymenanthes,* readily confer susceptibility on their progeny when hybridized with non-host species. It should also be noted that in some instances a hybrid derived from two non-host parent species may prove susceptible to the fungus e.g. *R.* 'Goldsworth Yellow'

(*R. campylocarpum* × *R. caucasicum*). In many instances hybrids are much more heavily attacked by the rust, by comparison to the parents which bear only sparse sori. This apparent 'hybrid weakness' in the context of rust susceptibility has been of great significance to the spread of *C. rhododendri* in Britain (see below).

The pattern of host susceptibility to rusts can also be of taxonomic significance. Many authors, most notably Savile (1979), have begun to examine the host associations of such obligately parasitic fungi in the knowledge that the precise relationship that exists is the consequence of their coevolution, during which the adaptive radiation of the host has been mirrored by that of the fungus. Thus, as Savile (1979) demonstrates, the host affinities of certain rust fungi can be a reflection of the taxonomy of those hosts. In the case of such a vast genus as *Rhododendron,* with over 700 species, even the relatively few rust records accumulated to date may offer valuable insights into the classification especially at the higher levels.

It is noteworthy that certain elements in the genus which have sometimes been considered distinct, and perhaps meriting separate generic status, such as subgenus *Therorhodion,* and section *Vireya* of subgenus *Rhododendron,* both support the rust. The latter represents an important addition to the host spectrum of *C. rhododendri* and is discussed further in the account of rhododendron rust in Australia. The absence of rust records from some sections is probably a reflection of the paucity of collections of the fungus, and may indicate that only a limited range of pathotypes have so far been detected in the wild, or appeared in cultivation. Among the azaleas a number of species and their derivatives of both American and Asian origin, chiefly from subgenera *Pentanthera* ('Luteum' azaleas) and *Tsutsusi* ('Obtusum' azaleas) support the rust. These hosts include both deciduous and evergreen taxa. A large range of lepidote rhododendrons are recorded as hosts, with a concentration of species in certain sections. The presence of the rust may be a guide to closer affinity between the major host groups, e.g., *Edgworthia, Maddenia, Glauca, Cinnabarina*, etc., but cross-infection experiments suggest that most members of subgenus *Rhododendron* are potential hosts of the rust. By contrast representatives of elepidote rhododendrons are concentrated in fewer sections—especially *Arborea, Fortunea, Griersoniana* and *Pontica.* In each case the majority of records concern hybrids, rather than species, and the latter only rarely in the wild.

The restriction of *C. rhododendri* to particular host species may also correlate with the native distributions of these taxa, although many more records from the wild will be needed before any conclusions can be drawn. As further reports of other species of rust on *Rhododendron* accrue, it may also be possible to assess the relative host specializations of each species. This would be of particular interest if any of these other rusts became extensive in cultivation.

RHODODENDRON RUST IN CULTIVATION

In the wild, the prolonged coevolution of host plants and their obligate fungal parasites has usually achieved a condition of balance, in which the pathogen is seldom destructive of its host. In the case of rust fungi, this concept of the 'protection of indigenousness' (Segal *et al.,* 1981) is manifest as sparse infections involving only limited disease sysmptoms, accompanied by restricted sporulation adequate to maintain the fungal population. In the case of rhododendrons in undisturbed natural ecosystems plants of only one, or at most a few species will be present at any locality, and when it occurs the rust is confined to occasional scattered sori on a few leaves. By contrast, in cultivation such constraints on the rust have been eliminated. In a rhododendron nursery or ornamental collection a vast array of species and hybrids are presented in one locality. Taxa previously geographically isolated from exposure to rust, and therefore under no selection pressure to evolve resistance, are readily available for the rust to attempt to infect. In the case of nurseries, or under any circumstances where bulk propagation is undertaken, each species or hybrid is close-planted as blocks of juvenile cloned material. Such physiologically juvenile tissues are known to be more susceptible in combinations involving a rust on an unfamiliar (i.e. other than its major) host, for example the birch rust, *Melampsoridium betulinum* on alder seedlings (Wilson & Henderson, 1966). Furthermore, in nursery plots, or even trays of cuttings of hosts which prove susceptible, conditions are ideal for rapid proliferation of the rust via its recycling uredial stage. In this context it is salutory to note the comments of Gould (pers. comm.) investigating the behaviour of *C. rhododendri* spores, that under conditions of very heavy inoculum even the immunity of apparent non-host rhododendrons begins to break down.

The active collecting of rhododendrons for cultivation has inevitably concentrated on the centre of diversity of the genus in the eastern Himalaya and north-western Yunnan (Ming & Fang, 1979). This area is also recognized as the centre of diversity of the rusts of rhododendron (Wang, 1981). As Dinoor (1981) has demonstrated, rusts occurring on wild host plants at their centre of origin exhibit great variability in pathogen virulence towards host resistance. Referring to cereal rusts Dinoor argued that such a reservoir of pathogen variability poses a great threat to new hosts, especially newly developed cultivars, if they are ever introduced to the centre of origin. In the case of collecting wild origin specimens of ornamental rhododendrons for cultivation the situation is reversed and the problem potentially far greater, namely the export of samples of this pathogen variability to locations where many previously unencountered species and hybrids are grown. Furthermore, the importation of rhododendrons carrying damaging new species or pathotypes of rust poses a threat not only to other rhododendrons in a collection, but also, where native or naturalized members of the genus grow in association with *Picea* species, to this adjacent spruce.

THE SPREAD OF RHODODENDRON RUST

The history of the spread of *C. rhododendri* around the world, and the consequent extension of host range, particularly as observed in Britain and recently also Australia, is a graphic illustration of these dangers (see below).

Theoretically the rust could be redistributed by the movement of infected spruce plants. However the conspicuous nature of *C. rhododendri* on *Picea,* coupled to the inability of the fungus to persist on this host (all diseased needles being shed within months of becoming infected), make this most unlikely. Nonetheless, the microcyclic *C. abietis,* which also occurs on the current season's needles but only becomes conspicuous the following winter, is known to have been imported to the United States from Denmark on *P. abies* nursery stock (Spaulding, 1956). Since the rust is quite unknown in association with the seeds of either alternate host (*Picea* or *Rhododendron*), transmission by this means can be excluded.

Natural spore dispersal over long distances is recognized for certain rusts, for example the northwards spread of black stem rust in North America (Rowell & Romig, 1966), but such instances derive from epiphytotics of the fungus generating dense clouds of inoculum within extensive monocultures of a crop, targeted at comparably large areas of the same host. On a smaller scale the exceptional severe outbreaks of *C. rhododendri* on *Picea abies* in Europe (e.g. Biraghi, 1954) alternating from proximal *R. ferrugineum* and *R. hirsutum* will certainly involve very heavy inocula, notably prolific quantities of aeciospores, released in late summer and early autumn, capable of infecting rhododendrons. On a still more localized scale the occasional heavy infections in plantations of *Picea abies* in Britain also generate heavy aeciospore inoculum, which may be implicated in spread of the fungus in parts of Scotland (see below). However, in both these cases the potential target hosts (rhododendrons) do not occur, as in the case of cereal crops, in vast uniform acreages, but rather as either small local populations of individuals on a hillside (native and naturalized plants) or scattered plots consisting of a mixture of taxa (cultivated plants). The probability of initiating a new infection in a nursery or rhododendron collection, other than in the immediate vicinity (i.e. a few miles) of the disease outbreak, is very slight. Thus natural spore dispersal as a means of extending the range of *C. rhododendri* is of negligible significance on an international or regional scale. However, given the nature of interest in cultivated rhododendrons, with visitors moving directly internationally or nationally between famous collections and specialist nurseries, it should be noted that the arrival of stripe rust of wheat in Australia in 1974 is attributed to transport of spores on a tourist's clothing! (O'Brien, Brown, Young & Pascoe. 1980). Rhododendron enthusiasts should exercise caution when visiting sites where the rust is known to be established.

It is concluded that the appearance of rhododendron rust in new localities is most likely to be the consequence of importation of infected, living vegetative rhododenron specimens. The spread of *C. rhododendri* is therefore a reflection of the original collection of rhododendrons from the wild, and their subsequent redistribution by growers.

HISTORY OF RHODODENDRON COLLECTING IN RELATION TO RUST

The history of introduction of rhododendrons to cultivation has been well documented by Leach (1962), Mossman (1975) and most recently for Lepidote species by Davidian (1982), while Mills (1980) has provided a detailed account of early introductions to Britain. In all these works the emphasis is on indicating the date and location of the first cultivation of each species and it is sometimes unclear whether live plants or seeds were involved. It is only with the advent of traffic in cuttings or whole plants that importation of rhododendron rust to new areas becomes a possibility.

All the luminaries of nineteenth century rhododendron exploration, such as Wallich, J. D. Hooker, Fortune and the French missionaries are reported to have handled only seed and herbarium specimens. Mills (1980), however, mentions a few plants of '*Azalea sinensis*' and subsequently at least one plant of '*Azalea indica*' reaching growers in London in the 1820's, but these growers observed that rhododendrons were averse to sea air and the lack of fresh water during transit. Certainly throughout this period many living plants were shipped from the orient, sometimes having been grown on at ports such as Macao or Shanghai, as Bretschneider's (1898) catalogue indicates; however the hot climate in these locations would have been inimical to temperate rhododendrons. In the same treatise Maximowitz is reported as sending many live plants, including some rhododendrons, to St Petersburg from his travels in Mongolia and Japan from 1856. The intense collecting in the Sino-Himalaya by Forrest and others that commenced around the start of the twentieth century is believed to have involved vast quantities of seed only, which in the case of Kingdon-Ward, Rock, Cooper and most other explorers, was obtained from plants previously carefully selected for their quality when in flower (Davidian, 1982). A possible exception is Wilson, collecting latterly for the Arnold Arboretum, who Sargent (1917) describes as despatching 168 lots of plants and cuttings with some 1593 seed lots—although it is uncertain whether any rhododendrons were included amongst the former.

Thus the great periods of oriental rhododendron collecting, which led to the establishment of the large private woodland gardens and the revolution in garden layout, were based almost exclusively on seed imports, and are thus unlikely to have been responsible for introducing the rust to cultivation. Throughout this period, and in some cases considerably earlier, other rhododendron species were being acquired from the new world, and from Europe and the Caucasus, many of which made major contributions to hybridization programmes (Leach, 1962). Most of this traffic is also believed to have involved seed. By the middle of the twentieth century, of the 900 species of rhododendron described over 600 were in cultivation, and with some noteworthy exceptions, were in all probability totally free of rust. In Norway rust had been detected at Bergen Botanic Garden as early as 1896 (Jørstad, 1938), and had already arrived in New Zealand in 1924 (Dingley, 1969).

The first rhododendron to be introduced into cultivation in Britain is considered to have been *R. hirsutum*, catalogued for his garden by Tradescant in 1656. Mills (1980) speculates that this species probably accompanied Huguenot refugees some time earlier. Coming from the relative proximity of the European Alps, it is quite possible that *R. hirsutum*, which hosts *C. rhododendri* throughout its native range, was imported as living plants. Significantly, it was on this host that the first report of the rust in Britain was made (Borthwick & Wilson, 1915). *R. ferrugineum,* its more widespread Alpine companion may also have arrived as live plants on its second introduction to Britain (Mills, 1980). In any case it seems inevitable that these species have been imported as living plants on numerous occasions over the years, and were at some stage accompanied by the rust. Significantly *C. rhododendri* was listed by the SRA Bureau Washington, USA as an intercepted 'pest' on alpenroses on more than 20 occasions involving several European source countries between 1952 and 1955. This confirms these hosts as major disseminators of the rust.

From the earliest period of collecting onwards growers were keenly propagating newly obtained plants and exploiting them in experimental hybridizations, so that well before 1900 a number of nurserymen were actively trading in living plants (Davidson, 1982). Thus a network for redistribution of imported stock, and potentially any accompanying pathogen, became well established.

Davidian's (1982) account of oriental collecting since 1950 again stresses seed as the major medium of importation. However, Cox's (1966, 1978) reports of his rhododendron collecting trips include comments such as: 'again we were lucky to be able to collect a number of seedlings of this plant'; and 'we gathered several collections of seed and a few scions' (woody stems with plenty of foliage, destined for saddle grafting). These recent years have witnessed the advent of readily available air transport, even in remote areas. This affords rapid, direct, inter-regional and inter-continental travel, with the potential for rapid movement of live plants, and consequent dramatic extensions of range for previously localized pathogens associated with these plants. For many years significant quantities of plants were conveyed by ship especially across the Atlantic to supply the spectacular advances in rhododendron cultivation being made in America. But as Frisbie (1969) indicates, air travel has revolutionized this exchange of rhododendrons. In turn it has greatly facilitated the dispersal of *C. rhododendri,* so much so that quarantine measures are now of considerable importance.

That active import of new samples from wild populations of the rust are occurring, is indicated by the results of the 1981 Sino-British expedition to W Yunnan, one of the first major rhododendron collecting expeditions to avail itself of the efficiency of air travel. Of approximately 100 living specimens brought to Edinburgh from China, no fewer than seven, involving four different host species, subsequently developed rust infections, all identified as *C. rhododendri.* Three plants were evidently rusted on arrival in Britain in June (*R. heliolepis, R. lacteum* and *R. brachyanthum*), and sori erupted on *R. sinogrande* within two weeks. Careful scrutiny of the material of *R. brachyanthum* revealed scars of old sori on the leaves, but not on any other specimens. After originally gathering these seedlings in the wild, their roots were packed in sphagnum and enveloped in polythene according to standard procedures, then many collections were packed together, with their foliage in mutual contact. The specimens were in transit in this condition for up to four weeks, sufficient time for incubation of the rust. The proximity of potentially infected leaves to susceptible leaves of other species, maintained in warm humid conditions ideal for proliferation of the rust, make it quite possible that some of these interceptions became infected during transit, possibly from rust on *R. brachyanthum*. This highlights the advisability of isolating individual specimens whenever they are packed for export.

RHODODENDRON RUST AND QUARANTINE MEASURES

The aim of quarantine procedures is to prevent the introduction of injurious pathogens not known to be established in an area. In its most rigorous form it will involve a pre-export inspection in the country of origin (to certify that stock is disease free) and a post-entry inspection followed by controlled growing-on of plants in isolation for a defined period. Certification is obviously inapplicable to rhododendron collecting in the wild, but contemporary explorers should be encouraged to exercise great vigilance in selecting cuttings, seedlings and other live specimens. Rigorous pre-export inspections, involving registration and regular nursery checks currently operate in respect of Chrysanthemum white rust in Europe, and constitute a model for disease regulation in other nursery stocks. In any case most countries demand an International Plant Health (Phytosanitary) Certificate from the country of origin. In the absence of such documentation, consignments are customarily destroyed, as in Britain, for example, under the terms of the Import and Export (Plant Health) (Great Britain) Order, 1980. Countries may also impose precise restrictions on the numbers of specimens that may be imported. In this context, it is interesting that New Zealand, where *C. rhododendri* is already established, has recently introduced stringent controls in respect of mildew and the somewhat host-restricted *Pucciniastrum vaccinii* on rhododendron, reducing the permitted annual import of rhododendron cuttings from 1000 to 100, and demanding an endorsement on the health certificate that the nursery of origin is rust free (Rainbow, 1982). Ironically a far greater threat to rhododendron cultivation is posed by the importation of new pathotypes of *C. rhododendri,* with its much more extensive host range. Even when a species is already present in a region, it is important, in the case of physiologically variable fungi such as rusts, that quarantine controls are also applied to prevent the introduction of new foreign races, with their different virulences, and likely extension of existing host ranges. This point is stressed by Yde-Anderson (1981) in his survey of potential conifer pathogens in northern Europe, but even here, although the alien *Chrysomyxa arctostaphyli* is cited as a harmful organism, no mention is made of *C. rhododendri,* new races of which could, for example, prove harmful to the extensively planted *Picea sitchensis* in Britain.

Post-entry quarantine measures involve the growing-on of plants either at specified government establishments or, subject to stringent requirements, at a grower's own premises, as in New Zealand (Anon., 1981). However as Savile (1973) has explained, the behaviour of *Chrysomyxa* species may make them quite undetectable at import inspection. Thus *C. rhododendri* can infect foliage without causing any perceptible symptoms for many months, remaining as dormant mycelium before giving rise to conspicuous sori in the late spring. Only by growing-on imported stock under quarantine conditions will the absence of rhododendron rust be confirmed. However, the first appearance of *C. rhododendri* in the United States (Gould, Eglitis & Doughty, 1955) at a nursery in western Washington undoubtedly involved imported plants (probably from Europe), which had been subject to Federal post-entry quarantine. Ironically this quarantine requirement was lifted in 1960, 'once it was found that the rust does not produce telia' (i.e. poses no threat to Spruce) as Ziller (1974) stated. However, investigations of this rusts's behaviour (see above) suggest that this may not be a constant characteristic. In any case Savile (1955) believed the Washington outbreak to have originated from a very limited inoculum, only partially representing the natural variation of the parent rust. Future uncontrolled imports may well have the potential to produce telia.

Clearly to be successful, any rhododendron quarantine operation must outlast the protracted latent phase of infection in the fungus life cycle. In the context of nursery stock in Britain, plants are usually lifted for dispatch in the early autumn (e.g. September). At this stage, with the exception of highly susceptible hosts on which the rust recycles producing sori all year, the current season's foliage may only support cryptic infection, and the previous year's leaves, on which the rust had sporulated in spring and early summer, will have abscised. Rust, if present on the extant foliage may not erupt as sori for up to 9 months (e.g. May/June, the following year). Thus to guarantee freedom from infection, quarantine measures would have to last at least this long. The prescribed standard 3 or 6 month holding period would be of no value under these circumstances. It is interesting to note here that Frisbie (1969) advocated importing stock in the early spring, when new growth is about to commence. If practicable for the purposes of plant husbandry, this procedure would greatly reduce the required quarantine period against rust, since any infection present would be expected to erupt as sori within 3 months of a March importation. Furthermore, as outlined under control measures (q.v.) removal of all older leaves just prior to the new foliage emerging, virtually guarantees rust free stock, and could be readily undertaken during the quarantine period. It is concluded that all rhododendron imports, whether wild collections or plants from cultivation, should ideally be grown-on until they have produced new foliage, and all previous foliage (which must be checked for absence of rust) has fallen, or if necessary been prematurely removed.

It is equally important to limit the spread of rust diseases within a country or region. This may be achieved by adopting similar procedures to those outlined above when stocks of plants are exchanged between nurseries or other growers. In the United States, by the time the original rust outbreak had been recognized in Washington several thousand plants had been distributed (Gould, Eglitis & Doughty, 1955), and the disease subsequently extended to California (Stout & Alstatt, 1960). Similarly in Britain the indiscriminate distribution of infected plants has contributed to disseminating the rust to many different localities (Fig. 2).

RHODODENDRON RUST IN BRITAIN

The early records of *C. rhododendri* in Britain were summarized by Wilson & Henderson (1966), who report that following the first discovery of rust on *R. hirsutum* in SW Scotland in 1915, alternate stages were soon discovered on plantation trees of *Picea abies* in the same area, and shortly afterwards in Aberdeenshire and Northern Ireland. Such scattered records suggest that the fungus may have been present for some years in these locations, but remained undetected. In 1937 rust was observed in Cornwall on plants of *R. cinnabarinum* var. *roylei* (Ashworth, 1938). It subsequently became established on a range of *R. cinnabarinum* hybrids in a number of important rhododendron collections in SW England, until by 1960 Johnstone (1960) reported the rust from 10 different gardens in the area. By this time the hosts affected included *R. trichocladum* (*oulotrichum*), *R. scabrifolium* (*spiciferum*) and hybrids involving Maddenia rhododendrons. On one of the latter *R.* 'Rosy Bell' (*ciliatum* × *glaucophyllum*) the disease appeared in Northern Ireland. In the intervening years rust on cultivated rhododendrons had also been found at nurseries in Cheshire, Surrey and Kent, where the hosts included *R. keleticum.* More recently it has been found at a number of gardens throughout Scotland, where apart from the familiar hosts cited above it also infects *R. charitopes* and *R. tephropeplum.*

This dispersal of *C. rhododendri* around Britain can be traced to a few sources, which have inadvertently exchanged infected rhododendrons. Thus the records in SW England on a uniform range of hosts are all associated, and the subsequent outbreaks in Scotland on identical hosts probably also derive from there. Similarly, some of the records in SE England derive from a single nursery at which rust has been recorded regularly over a period of 15 years! In 1980 a new range of hosts, especially *R. campylogynum* and its hybrids, became infected at a locality in central Scotland. On investigation this proved to have originated from the importation of a few live plants from western USA, the previous year. Not only were new hosts involved, but rhododendrons known to be highly susceptible in other situations (e.g. *R. cinnabarinum* hybrids) did not become infected. Clearly a new pathotype of the fungus, not previously represented in Britain, was introduced on this occasion.

Some years earlier a more dramatic extension of host range was also reported from Scotland when R. W. G. Dennis identified *C. rhododendri* on specimens of *R. ponticum* sent from Ayrshire. Within a few years records of rusts on this host had accumulated from a series of sites throughout Scotland (Wilson & Henderson, 1954) associated in each case with alternation to *Picea abies.*

R. ponticum is now extensively naturalized throughout Britain, following its original planting as game cover during the 18th and 19th centuries (Cross, 1975) and its use as hardy breeding and grafting stock for ornamental purposes. In parts of its range it occurs as understorey or peripheral thickets to spruce plantations, artificially recreating the natural juxtaposition of hosts on which the rust flourishes in the wild. Today this particular rust is known to persist in more than 20 localities in northern Britain (Fig. 2), where it is recognized as a minor disease problem in forest plantations of Norway spruce (Phillips & Burdekin, 1982).

R. ponticum, however, is an enigmatic host which has never been reported to support the rust in either its native range (chiefly the Caucasus, but also Iberia and Lebanon) or more surprisingly, despite

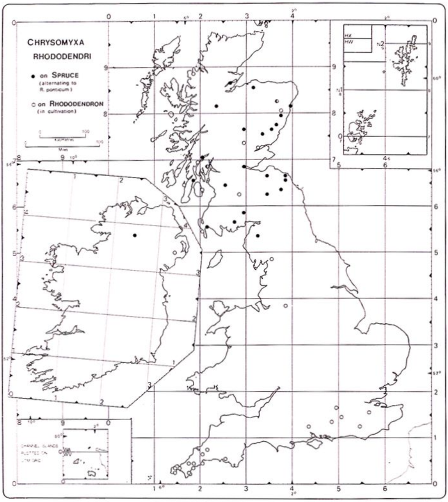

FIG. 2. Distribution of *Chrysomyxa rhododendri* in Britain.

extensive use by rhododendron growers, anywhere outside Britain. Significantly, J. Cullen (pers. comm.) considers the British populations of this host to be thoroughly introgressed following many generations of free hybridizing with other hardy rhododendrons from America and Asia, notably *R. caucasicum, R. catawbiense,* and *R. maximum.* Indeed, in cross-infection experiments at Edinburgh inoculum from a range of sources has repeatedly failed to infect any wild origin stocks of *R. ponticum* from both the Caucasus and Portugal. By contrast, samples from the naturalized British populations (*R.* '*ponticum*') are readily infected, although only by aecidiospores from spruce, never by urediospores from other rhododendrons. Furthermore, no uredia develop on infected *R. ponticum,* only telia, constituting an abbreviated life cycle (see Fig. 1) which offers no scope for increase of the rust on this host, but demands annual reinfection from adjacent spruce. It should be noted that the same aecidiospore inoculum readily infects a range of cultivated rhododendrons, producing telia and uredia; and in complementary experiments aecidiospore inoculum derived from previous cross-infection of spruce by telia on *R. hirsutum* in cultivation, also readily infected *R. 'ponticum'*.

It is suggested that original introductions of the rust on *R. ferrugineum* and *R. hirsutum* alternated readily to *Picea abies* which is frequently planted on the estates where rhododendron gardens are established. *R. 'ponticum'* in the vicinity inevitably received aeciospore inoculum and proved partially susceptible, albeit with a restricted life cycle. It should be remembered from the survey of host ranges of *C. rhododendri* (see above) that many species of rhododendron that seem immune to the rust are readily infected if hybridized, even to other non-host species, which seems to be the case with *R. 'ponticum'*. Thus an imported rust, brought into the country on ornamental rhododendrons has escaped onto a widespread naturalized host, and now poses a threat to commercial forestry in some areas.

Although the occurrence of this rust at a range of sites could be in part the consequence of long distance spore dispersal, it is more likely that the cross-infection to *R. 'ponticum'* via spruce from cultivated rhododendrons has occurred on several occasions. It is noteworthy that with few exceptions, all of the reports of disease in forest plantations alternating from *P. abies* to naturalized *R. 'ponticum'*, are on estates immediately adjacent to country houses. These have established woodland gardens featuring many rhododendrons, as at Duns, Inglesmaldie, Drumtochty, Benmore, Skipness, Setmurthy, Skene, Insch, Airlie, Drumlanrig, and Kindrogan. So far rust has been detected on cultivated rhododendrons at only two of these locations (Benmore and Skene), but the coincidence is striking.

At present the threat to spruce is only slight because of the absence of a uredial stage on *R. 'ponticum'*. However continuing import of new samples of the rust, and the possibility of further escapes from nurseries and gardens where the rust is allowed to flourish uncontrolled, may yet lead to the establishment of a pathotype capable of recycling on this rhododendron host and also perhaps of overcoming the resistance so far shown by the more widely planted *Picea sitchensis* (sitka spruce).

RHODODENDRON RUST IN AUSTRALIA

C. rhododendri was first encountered in cultivation near Sydney on an indeterminate lepidote host in 1932 (Noble, Hynes, McCleery & Birmingham, 1935), and was subsequently identified from a series of localities in this area of New South Wales during the 1960s (J. Walker, pers. comm.). Among the hosts were a number of hybrids known to be susceptible to rust in Britain and America (e.g. *R.* 'Racil'). More recently the rust became established in Victoria, particularly in the key rhododendron growing region of the Dandenong Ranges. For over 15 years it is said to have flourished on a range of hybrids of either *R. cinnabarinum* or *R. ciliatum* (e.g. *R.* 'Lady Chamberlain' and *R.* 'Rosy Bell'), and in 1975 appeared on such hybrids at Olinda (R. Withers, pers.

comm.). Although said not to attack the young leaves, it is this young flush that becomes imperceptibly infected, although abundant sori do not erupt until the following winter when the leaves have hardened off. On the more susceptible plants infection is so heavy that rusted leaves are shed prematurely and the plants seem almost deciduous.

As already stated such heavy inoculum in a collection of rhododendrons poses a threat to previously unrusted taxa. Within 200 yards of the rusted *R. cinnabarinum* hybrids at Olinda a range of Vireya rhododendrons are grown, partially covered in a slatted house. In 1979 rust was noted for the first time attacking selected hybrids especially of the native Australian *R. lochae* (e.g. *R.* 'Princess Alexandra'). It must be stressed that *C. rhododendri* is quite unknown on any Vireya rhododendron in the wild. The suspicion that rust on Vireya arose *in situ* as a result of cross-infection from *R. cinnabarinum* hybrids is strongly supported by experimental inoculations carried out in Edinburgh. Inoculum from *R.* 'Lady Chamberlain' in a Scottish garden readily infected wild origin specimens of *R. lochae* and *R. javanicum,* producing abundant uredia, although a number of other Vireya species seemed immune.

It is alarming to conclude from these inoculations and from examination of Australian collections, that a range of Vireya species and their hybrids are highly susceptible to the rust (see Appendix I). On these hosts the fungus spreads very rapidly, single infection foci expanding radially and producing circinate rings of sori on both surfaces of the leaves. Such profuse amphigenous sporulation is otherwise unknown for *C. rhododendri,* but seems to be a property of the anatomy of the leaves. As with all other reports of the rust in Australia, to date only uredia have been found.

Vireya rust has subsequently been reported from further localities in Victoria, including a nursery and a private collection and is now known on 4 species and a range of hybrids (see Appendix I). In most cases the plants are being reared under cover, e.g. polythene tunnels, or in glasshouses, under which conditions vegetative growth is sustained virtually all year, providing a continuous supply of young leaves for the rust to exploit. The programme of rust control (see below), devised for more seasonal circumstances, must be adapted accordingly.

Although it is impossible to pinpoint the original importation of rust to Australia, the correlation of susceptible hosts with those involved in disease outbreaks in Britain, makes this a likely source. In all probability the rust was introduced on at least two occasions, to New South Wales and Victoria respectively. Such imports are continuing however, rust being intercepted on a series of *R. campylogynum* hybrids from America in 1979 and from Britain in 1981. Furthermore, the disease is also spreading within Australia, having recently appeared in Tasmania, on plants received from Victoria (J. Walker, pers. comm.)*.

CONTROL OF RHODODENDRON RUST

The damage caused by the fungus to host species of *Rhododendron* and *Picea* and the potential threat posed by the continued spread of the

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*See note added in proof—p. 52.

disease to spruce plantations and nurseries, and rhododendron collections and nurseries, necessitates establishing effective measures for control. Three major approaches, which might contribute to an integrated control programme are appropriate: exclusion of susceptible hosts, sanitation measures, and chemical control. In contrast to the control of many crop diseases, e.g. cereal rusts, where the aim is to reduce disease occurrence to an acceptable level, the ultimate aim of control of *Chrysomyxa rhododendri* is to completely eradicate the disease at a particular location.

Investigations of host range indicate that many species of *Rhododendron* will support *C. rhododendri* (see Appendix I). The use of known host species in large breeding programmes should be considered ill-advised, especially in the knowledge that in many cases resultant hybrids have proved more susceptible to rust than either parent. Although specific selection for rust resistance is unlikely to be important, it is a criterion that could usefully be considered when assessing the progeny of new hybridizations. Where the disease is a threat, large plantings of rhododendron hybrids known to be susceptible to the rust, whether for amenity purposes or as nursery stocks, should be avoided, and alternative plants selected.

Sanitation involves both tailoring the husbandry of the host plants as individuals or in group plantings to combat the disease, and screening host plants wherever they are being distributed to exclude the disease (see above under 'Rhododendron rust and quarantine measures').

Study of the life cycle of *C. rhododendri* (see Fig. 1) established that continuity of the disease on spruce for successive seasons depends on annual reinfection from *Rhododendron*. Similarly, on *Rhododendron* infection must be transferred to the new season's foliage, either directly from the previous season's leaves or via the alternate host, from spruce needles. Diseased stock or plants under threat of infection should therefore be managed according to a programme designed to break the continuity of the disease cycle, or at least to minimize the opportunities for transfer of infection. This can be achieved at two levels: by removing the infected tissues from diseased plants, or in severe cases, eliminating the whole plant; and by eliminating the alternate host from the vicinity of valued plantings.

The latter approach has a long history in the control of rust fungus diseases, most notably in control of black rust, *Puccinia graminis* in wheat growing areas, where the eradication of all Barberry bushes, hosts of the pycnial and aecial stages, resulted between 1915 and 1929 in almost 80% improvement in the average annual American wheat yield (Van der Plank, 1963). For disease control on *Rhododendron* removal of adjacent spruce will only break one avenue of continuity of infection, but it is undoubtedly a wise precaution in the vicinity of a rhododendron nursery. The results of cross-infection experiments clearly demonstrated the greater host range infection potential of an aeciospore inoculum, derived from the *Picea* host, in contrast to the recycling urediospore inoculum from *Rhododendron*. Removal of all adjacent spruce also eliminates the least accessible, and therefore least controllable potential source of reinfection.

A number of authors have stressed the importance of spacing of susceptible individuals to the spread of pathogens, for example Burdon

(1978) who demonstrated that the reduction in spore concentration between widely spaced hosts was the main factor in decreasing spread of a disease. This situation is echoed in *C. rhododendri* in the wild where infection levels reduce dramatically with increasing spacing between rhododendrons and spruce. Greater spacing of host plants cannot be contemplated in commercial operations where land is at a premium, nor indeed in private gardens. However, the horticultural habit of closely interplanting dwarf ornamental spruce trees and rhododendrons should be critically appraised where rust is a problem. Essentially this recreates in miniature the Spruce Forest/Rhododendron understorey juxtaposition which exists in the wild, greatly facilitating host alternation, leading to heavy infection levels and a dangerous concentration of inoculum.

Removal of diseased foliage is the most direct means of eliminating sources of inoculum. Where a rust outbreak occurs on rhododendrons in a large ornamental collection or among nursery stock, the continued presence of a heavily infected plant on which the rust readily proliferates poses a threat to the adjacent plants. The regular recycling of the rust on such a host offers an opportunity for the appearance and establishment of new virulences in the rust population, perhaps with the potential to infect a new range of hosts. Under these circumstances such heavily infected plants should be discarded. Alternatively, selective removal of all infected leaves of the previous season, carried out just before emergence of new flush in the spring, can virtually eliminate all infection from individual plants. The possibility of infected foliage persisting on the plant for long periods before the rust becomes detectable, as sori develop, not only poses problems for quarantine control but also suggests that only complete defoliation of all older leaves just prior to flushing, will eliminate infection. The effect of such defoliation procedures will vary according to the phenology of the host as some rhododendrons retain their leaves for up to 3 years, and premature removal of two-thirds of the foliage in one season is likely to cause a significant check to plant growth. By contrast, pre-flush defoliation of rhododendrons, which only retain their leaves for 12 to 15 months will be just a matter of weeks premature, and only deprives the plant of leaves that are already declining, with commensurately less effect on plant vigour. In all cases the effects can be minimized by carefully timing the removal of leaves just prior to bud break as tested on a limited range of hosts in experimental beds at Edinburgh. Meticulous defoliation in this way, is also recommended for all cuttings raised where there is a risk of the parent plant supporting rust. It can also be readily practised on individual plants in a large ornamental collection and on selected high-risk stock in a nursery, although on the scale of a commercial nursery such intimate husbandry becomes impractical. It should be noted that even where comprehensive defoliation is carried out the rust may occasionally be able to persist in other tissues of the plant. On certain highly susceptible plants mycelium has been observed to spread into the petiole and thence into parenchymatous stem tissues adjacent to the leaf axil. Thus on *R. charitopes,* even after detaching an infected leaf, sori can erupt around the leaf scar on the stem and provide a means of continuity of infection to the next generation of leaves.

In accordance with normal horticultural practice, and as advised by Coyier (1978) in his account of rhododendron diseases, all infected plants or tissues gathered should be burned to guarantee destruction of the rust. When such measures are being carried out, it is vitally important not to overlook the fallen leaves. These often sustain large populations of sori, usually associated with persistent green islands of tissue, and can remain active for several weeks, thus constituting a dangerous source of inoculum. At the time of defoliation it is recommended that these are also gathered and burned. The fact that this approach to control can only be effectively applied on a limited scale, and cannot guarantee eradication of the disease makes it necessary to have recourse to complementary chemical methods.

A range of fungicides are now available with a proven capacity for rust control. Although most research has been directed towards cereal rusts, some compounds have been tested on a limited number of host-pathogen combinations (e.g. Gjaerum, 1975), but apart from the generalized comments of Coyier (1978) and Gould (1966) there is no literature on fungicidal application to combat *C. rhododendri.*

The following four fungicides were selected for testing at Edinburgh against rhododendron rust; made up in distilled water according to the manufacturer's specification:

1. Zineb (formerly Dithane) supplied as a wettable powder containing 70% active ingredient (a.i.) applied at a recommended dose rate of 2gms/litre (1400μgms a.i./ml). This dithiocarbamate fungicide was chosen as representative of traditional non-systemic fungicides.
2. Benomyl (as Benlate), wettable powder, 50% a.i.; application rate: 1gm/litre (500μgms a.i./ml). This systemic benzimidazole was chosen because it is readily available to the public, and regularly applied against a spectrum of horticultural fungus diseases.
3. Oxycarboxin (as Plantvax 75) 75% a.i.; application rate: 1gm/litre (750μgms a.i./ml), with surfactant (AGRAL) added: 150μ litres/litre made up fungicide. This systemic carboxamide fungicide was chosen for its proven ability against a number of rusts of ornamentals.
4. Triadimefon (as Bayleton 25) wettable powder, 25% a.i.; application rate 0·5gms/litre (125μgms a.i./ml), chosen as representative of the recently developed triazole systemic fungicides, which are currently much exploited in cereal disease control programmes.

   (*Note*: it has recently been demonstrated that triadimefon is rapidly transformed by fungi to triadimenol. The manufacturers are now replacing Bayleton with 'Bayfidan', a 25% a.i. formulation of triadimenol. Supplied as an emulsifiable concentrate this has the advantage, over a wettable powder, of leaving no unsightly residues on the foliage which might detract from the appearance of ornamental plants).

The effect of each fungicide was assessed on spore germination *in vitro,* and in terms of protectant action (applied prior to infection) and curative action (applied after establishment of infection), and involved both excised leaf discs in the laboratory and whole plants in field plots. Fig. 3 shows the effect of each compound on percentage spore germination, or

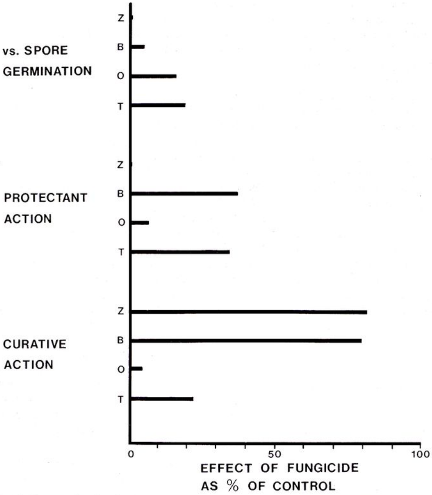

FIG. 3. Comparative fungicidal control of *Chrysomyxa rhododendri*. Z—Zineb; B—Benomyl; O—Oxycarboxin; T—Triadimefon; for explanation see text.

percentage infection (leaves or discs bearing sori) in comparison to untreated controls: the shorter the column, the more effective the treatment. These experiments refer only to infections derived from urediospore inoculum (cross-infection between rhododendrons), but similar results were obtained against aeciospore inoculum (cross-infection from spruce).

Zineb was identified as the most effective protectant fungicide, affording powerful control of spore germination and the initiation of new infections, but having negligible curative effect. Futhermore as a surface-acting non-systemic compound, to be effective in field use it must be applied directly to the underside of the rhododendron leaves, where infection takes place, and be present before any inoculum arrives. Thus Zineb is only of value in a control programme if sprayed intensely at regular intervals throughout the period of risk. Benomyl was only partially successful as a protectant agent, and relatively ineffective as a curative agent. By contrast the other systemic fungicides not only exhibited a potential to kill off the fungus in established infections, but also offered good protection against newly arrived inoculum, with Oxycarboxin conspicuously more successful than Triadimefon at these concentrations.

Uptake of such fungicides across the cuticle is reported to be around 5% of the surface accumulation (Edgington, 1981). Such a figure derived from cereals may be further reduced in plants such as rhododendrons with their thick upper cuticles, and confirms the need to maximize spray coverage of the leaf undersides, even with systemic compounds. Although duration of the antifungal activity has not yet been defined in rhododendrons, Rathmell & Skidmore (1982) report from cereals that a single fungicide application will be effective for up to four or six weeks, in the cases of Oxycarboxin and Triadimefon respectively. Neither compound produced any detectable phytotoxic effects on the limited range of hosts treated. Nonetheless, use of such systemic fungicides should always be restricted, both because as yet we have no understanding of their potential effects on rhododendron mycorrhizae, and particularly to minimize the risk of promoting fungicide-tolerant strains of the rust, as has already been reported for e.g. Chrysanthemum white rust in respect of Oxycarboxin (Montfort, Grouet & Leroux, 1981). For the latter reason, both Oxycarboxin and Triadimefon should be used in a control programme for rhododendron rust. As members of separate classes of fungicides, operating at different metabolic sites, their alternate application will reduce this risk. Both compounds have already been employed to good effect against an outbreak of the rust in a commercial nursery in Britain. Comparable results have also been obtained in America (Coyier, pers. comm.) where it was found that Triadimefon was best used in a protectant role.

It is therefore possible to recommend that for chemical control of *C. rhododendri* on rhododendrons, a programme utilizing alternate sprays of Triadimefon and Oxycarboxin, at manufacturers' recommended dose rates be followed. These fungicides must be applied as foliar sprays, taking care to maximize coverage of the leaf undersides. The timing of application is related to the phenology of the rhododendrons and the behaviour of the rust. A suggested schedule based upon experiences in Britain is outlined in Fig. 4. Recommended timings are indicated by arrows, commencing with an initial curative spraying: (1) in late spring, to restrict or prevent sporulation on old foliage prior to emergence of the new season's leaves. The requirement for this spray is obviated if a programme of husbandry, removing such leaves, is being undertaken. In either case it is important to apply a protectant spray; (2) to the new foliage promptly, once it has fully unfolded, repeating coverage of old foliage, where it is still extant. Optional further sprays at 3–4 weekly intervals through the summer (3 & 4) are advised in the event of any sporulating rust being detected in the locality. Further fungicide application in the autumn (5 & 6) serves to protect foliage, especially of rhododendrons producing a secondary (late) flush against aeciospore infection from adjacent spruce. It is also necessary to spray if the rust produces subsequent generations of uredia

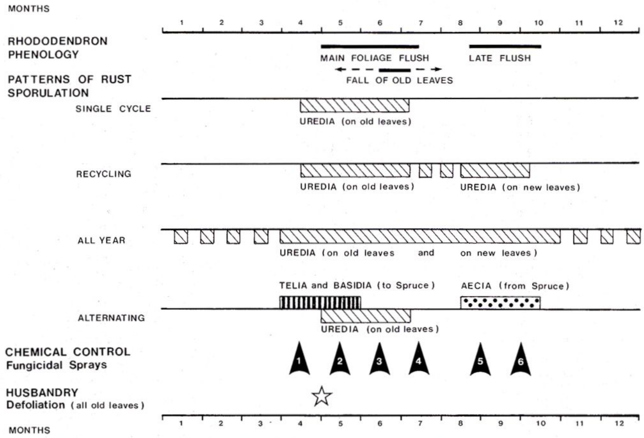

FIG. 4. Programme for control of Rhododendron rust, in relation to host phenology and cycle of rust sporulation; for explanation see text.

on the new foliage. Diligent pursuit of such a spray programme, responding quickly to any signs of rust, and coupled to selective defoliation has successfully eradicated the fungus in trials, within two seasons.

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APPENDIX I

Hosts of *Chrysomyxa rhododendri*

W—recorded in the wild: C—recorded in cultivation

SUBGENUS RHODODENDRON

SECT. POGONANTHUM: R. sargentianum C; R. sargentianum × R. myrtifolium C; R. trichostomum × Ledum groenlandicum C.

SECT. RHODODENDRON

Subsect. Campylogyna: R. campylogynum C; R. campylogynum × R. calostrotum C; R. campylogynum × R. ferrugineum C; R. campylogynum × R. racemosum C.

Subsect. Caroliniana: R. minus C; R. minus × R. calostrotum C; R. minus × R. ciliatum C; R. minus × R. hirsutum C.

Subsect. Cinnabarina: R. cinnabarium ssp. cinnabarinum C; R. cinnabarinum ssp. xanthocodon C; R. keysii C; R. cinnabarinum × R. ambiguum C; R. cinnabarinum × R. keysii C; R. cinnabarinum × R. maddenii C; (R. cinnabarinum × R. maddenii) × R. flavidum C; R. cinnabarinum × R. maddenii ssp. crassum C.

Subsect. Edgeworthia: R. edgeworthii C; R. edgeworthii × R. ciliatum C; R. edgeworthii × R. ciliicalyx C; R. edgeworthii × R. formosum C; R. edgeworthii × (R. ciliatum × R. virgatum) C.

Subsect. Glauca: R. brachyanthum W., C; R. charitopes C; R. glaucophyllum C; R. schweliense C; R. brachyanthum × R. fletcheranum C; R. brachyanthum × R. ludlowii C; R. glaucophyllum × R. ciliatum C; R. glaucophyllum × R. ludlowii C.

Subsect. Heliolepida: R. heliolepis W (?).

Subsect. Lapponica: R. fastigiatum C; R. hippophaeoides C; R. impeditum C; R. lapponicum W; R. russatum C; R. setosum W; R. yungningense C; R. fastigiatum × R. augustinii C; R. flavidum × (R. cinnabarinum × R. maddenii) C; R. hippophaeoides × R. racemosum C; R. impeditum × R. hanceanum C; R. rupicola × R. ludlowii C.

Subsect. Lepidota: R. lepidotum × R. lowndesii C; R. lowndesii × R. trichocladum C.

Subsect. Maddenia: R. burmanicum C; R. ciliatum C; R. horlickianum C; R. maddenii C; R. maddenii ssp. crassum C; R. parryae C; R. ciliatum × R. dalhousiae C; R. ciliatum × R. edgeworthii C; R. ciliatum × R. glaucophyllum C; R. ciliatum × R. minus C; R. ciliatum × R. racemosum C; R. ciliatum × R. veitchianum C; R. ciliatum × R. virgatum C; (R. ciliatum × R. virgatum) × R. edgeworthii C; R. ciliicalyx × R. edgeworthii C; R. fletcheranum × R. brachyanthum C; R. fletcheranum × R. ludlowii C; R. maddenii × R. cinnabarinum C (very many hybrid selections); R. maddenii ssp. crassum × R. cinnabarinum C.

Subsect. Micrantha: R. micranthum W.

Subsect. Moupinensia: R. moupinense × R. ferrugineum C.

Subsect. Rhododendron: R. ferrugineum W, C; R. hirsutum W, C; R. myrtifolium W, C; R. ferrugineum × R. hirsutum C; R. ferrugineum × R. campylogynum C; R. ferrugineum × R. moupinense C; R. hirsutum × R. minus C; R. myrtifolium × R. sargentianum C.

Subsect. Rhodorastra: R. dauricum, W, C; R. ledebouri W; R. mucronulatum W; R. sichotense W.

Subsect. Saluenensia: R. calostrotum C; R. calostrotum ssp. keleticum C; R. saluenense C; R. calostrotum × R. campylogynum C; R. calostrotum × R. minus C; R. calostrotum × R. racemosum C.

Subsect. Scabrifolia: R. hemitrichotum C; R. scabrifolium C; R. racemosum × R. ciliatum C; R. racemosum × R. hippophaeoides C; R. racemosum × R. tephropeplum C; R. spinuliferum hybrid C.

Subsect. Tephropepla: R. tephropeplum C; R. hancearum × R. impeditum C; R. tephropeplum × R. racemosum C.

Subsect. Trichoclada: R. lepidostylum C; R. mekongense C; R. trichocladum C; R. trichocladum × R. lowndesii C.

Subsect. Triflora: R. augustinii C; R. oreotrephes C; R. yunnanense C; R. zaleucum C; R. ambiguum × R. cinnabarinum ssp. xanthocodon C; R. augustinii × R. fastigiatum C; R. davidsonianum × R. pemakoense C; R. keiskei × R. ludlowii C.

Subsect. Uniflora: R. ludlowii C; R. pemakoense C; R. uniflorum C; R. ludlowii × R. brachyanthum C; R. ludlowii × R. fletcheranum C; R. ludlowii × R. keiskei C; R. ludlowii × R. rupicola C; R. pemakoense × R. davidsonianum C.

Subsect. Virgata: R. virgatum C; R. virgatum × R. ciliatum C; (R. virgatum × R. ciliatum) × R. edgeworthii C.

Subsects Afghanica, Baileya, Boothia, Camelliiflora, Fragеriiflora, Genesterana, Monantha: NO RUST RECORDED.

SECT. VIREYA: R. javanicum C; R. lochae C; R. multicolor C; R. orbiculatum C; R. brookeanum × R. javanicum × R. zoelleri C; R. javanicum × R. brookeanum C; R. lochae × R. christianae C; R. lochae × R.(?) leucogigas C.

SUBGENUS HYMENANTHES

SECT ARBOREA: R. arboreum ssp. cinnamomeum C; ([(R. arboreum × R. griffithianum) × R. thomsoni] × R. arboreum) × R. forestii C; R. arboreum × (R. sanguineum ssp. didymum × R. griersonianum) C.

SECT. BARBATA: R. barbatum W(?).

SECT. CAMPYLOCARPA: R. souliei C; R. campylocarpum × R. caucasicum C; R. campylocarpum × R. fortunei C; (R. campylocarpum × R. fortunei ssp. discolor) × R. wardii C; R. campylocarpum × R. griersonianum C; R. wardii × R. molle hybrid C.

SECT. FORTUNEA: R. decorum W; R. fortunei ssp. discolor C; R. fortunei × R. campylocarpum C; (R. fortunei ssp. discolor × R. campylocarpum) × R. wardii C; R. fortunei × R. griffithianum C; (R. fortunei × R. griffithianum) × (R. maximum × R. griffithianum) C; R. fortunei × R. griersonianum C: ([(R. griffithianum × R. arboreum) × R. thomsoni] × R. arboreum) × R. forrestii C.

SECT. GRANDIA: R. sinogrande W(?).

SECT. GRIERSONIANA: R. griersonianum C; R. griersonianum × R. campylocarpum C; R. griersonianum × R. facetum C; R. griersonianum × R. fortunei ssp. discolor C; R. griersonianum × R. neriiflorum C; R. griersonianum × R. sanguineum ssp. didymum C; (R. griersonianum × R. sanguineum ssp. didymum) × R. arboreum C.

SECT. IRRORATA: R. aberconwayi C.

SECT. MACULIFERA: R. pseudochrysanthum C.

SECT. NERIIFLORA: R. dichroanthum ssp. scyphocalyx C; R. forrestii C; R. forrestii × (R. arboreum × [R. thomsoni × (R. arboreum × R. griffithianum)]) C; R. neriiflorum × R. griersonianum C; R. sanguineum ssp. didymum × R. griersonianum C.

SECT. PARISHIA: R. elliotii hybrid C; R. facetum × R. griersonianum C.

SECT. PONTICA: R. brachycarpum C; R. catawbiense C; R. degronianum C; R. macrophyllum C; R. smirnowii C; R. caucasicum × R. campylocarpum C; R. macrophyllum hybrid C; R. maximum hybrid C; (R. maximum × R. griffithianum) × R. fortunei C; R. 'ponticum' (see text p. 38).

SECT. TALIENSIA: R. bureavii C; R. faberi W; R. lacteum W(?); R. sphaeroblastum C.

SECT. THOMSONIA: ([R. thomsoni × (R. arboreum × R. griffithianum)] × R. arboreum) × R. forrestii C.

SECTS: ARGYROPHYLLA, AURICULATA, CAMPANULATA, FALCONERA, FULGENSIA, FULVA, GLISCHRA, LANATA, SELENSIA, VENATORA, WILLIAMSIA: NO RUST RECORDED.

SUBGENUS TSUTSUSI

SECT. TSUTSUSI: R. kaempferi W; R. kiusianum W; R. macrosepalum W, C; R. obtusum W; R. oldhamii W; R. serpyllifolium W; R. tosaense, W; R. 'indicum' C; R. macrosepalum × R. ripense C.

SECTS: BRACHYCALYX, TSUTSIOPSIS: NO RUST RECORDED.

SUBGENUS PENTANTHERA

SECT. PENTANTHERA: R. molle C; R. occidentale C; R. prunifolium C; R. molle hybrid × R. wardii C; indet. Ghent hybrid C; indet. Knaphill hybrid C.

SECT. SCIADORHODION: R. schlippenbachii C.

SECTS: RHODORA, VISCIDULA: NO RUST RECORDED.

SUBGENUS THERORHODION

R. camtschaticum C.

SUBGENERA: Azaleastrum, Candidastrum, Mumeazalea: NO RUST RECORDED.

QUESTIONS

Leach: If you reduced the shade and increased the air circulation, can you minimise the disease?

Bennell: Where the rust is already present on a plant, its rate of proliferation will be reduced at lower temperatures. Efficient air movement around the plants may be of greater significance, since urediospores are only capable of germinating and initiating new infection under conditions of high (>95%) relative humidity.

Bump: In a friend's garden in America many Chinese rhododendrons are growing adjacent to Sitka Spruce, but remain free from rust.

Bennell: Two important points must be made here. Firstly, although *C. rhododendri* is known to alternate to various species of *Picea* in the wild and also in cultivation in Europe and Asia, this species of rust has never been reported on spruce in North America. Secondly, from our cross-infection experiments on a range of *Picea* species it is clear that *P. sitchensis* (sitka spruce) is somewhat resistant to the pathotypes of the fungus so far tested. The populations of *C. rhododendri* present in the United States are not known to produce telia and basidiospores, and thus are incapable of infecting spruce. However as our investigations have shown, on a different rhododendron host, or under a different climatic regime, or else as the result of importation of new samples of the fungus, this may no longer be the case. Measures to eradicate this rust, whenever possible, and to prevent its continuing geographic and host range extensions are strongly advised.

Anon. Speaker (USA): Will the defoliation of a plant followed by fungicidal treatment eradicate the rust?

Bennell: On individual specimens the combination of meticulous husbandry and a programme of chemical spraying, as outlined, will eradicate the rust. To remain disease free, all other sources of inoculum in a locality must be eliminated.

NOTE ADDED IN PROOF: *Rust on Vireya rhododendrons*

Chrysomyxa rhododendri has recently also been observed on species and hybrids of section Vireya (incuding *R. christianae* and *R. lochae × virgatum*) in New Zealand. Although it has been detected on plants reported from Australia, these infections may also have arisen *in situ* by the cross infection from other susceptible hosts (e.g. *R. cinnabarinum* hybrids). See p. 40.