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A NOTE ON THE OCCURRENCE OF INTERNAL SORI IN RUST FUNGI

A. P. BENNELL

ABSTRACT, The formation of rust fungal sori inside the tissues of host organs is outlined with particular reference to aecidia of *Puccinia graminis* within fruits of *Berberis* and *Mahonia*. The first reports are made of internal aecidia of *Puccinia caricina* var. *pringsheimiana* in fruits of *Ribes grossularia,* and of *Phragmidium rosae-pimpinellifoliae* in swollen receptacles of *Rosa pimpinellifolia*.

The abnormal development of rust fungal sori inside their host tissues, maturing centripetally before erupting from an internal surface and discharging spores into a lumen within the host organ, was first reported in fruits of *Mahonia ilicifolia* infected with *Puccinia graminis* Pers. (Buchenau, 1884). Buchenau noted with evident surprise that aecidia were present not only on the outside of the fruit but also on the inside.

At the time of this observation there was intense interest in the behaviour of the notorious black rust of cereals. De Bary (1866) had already shown by inoculation that the aecidia on the barberry (*Berberis vulgaris*) were an alternate stage in the life cycle of *P. graminis,* but this connection was still doubted by some British authorities twenty years later. Worthington G. Smith (1885) described and illustrated the development of teliospores inside the seed of oats. The following year he recounted the observations of George Brebner who sent him a collection of infected barberries from Aberdeen in which the aecidium was 'growing centripetally within the seed' (Smith, 1886). Smith's illustrations show aecidia with mature spores developing inside the single seed while normal aecidia develop externally on the outer wall of the fruit. Brebner's original slide preparation on which these drawings were based is housed at the British Museum (Natural History) and has been examined to check the veracity of these observations. Smith's articles contain the first thorough accounts of internal sori in the Uredinales, and indicate that they can involve different stages in the rust fungus life cycle. Ironically, despite this careful observation, in these same articles Smith ridicules any connection between the two infections: 'all the writings and illustrations produced in favour of the at present purely suppositious connection of the two fungi are not worth the paper they are printed on'.

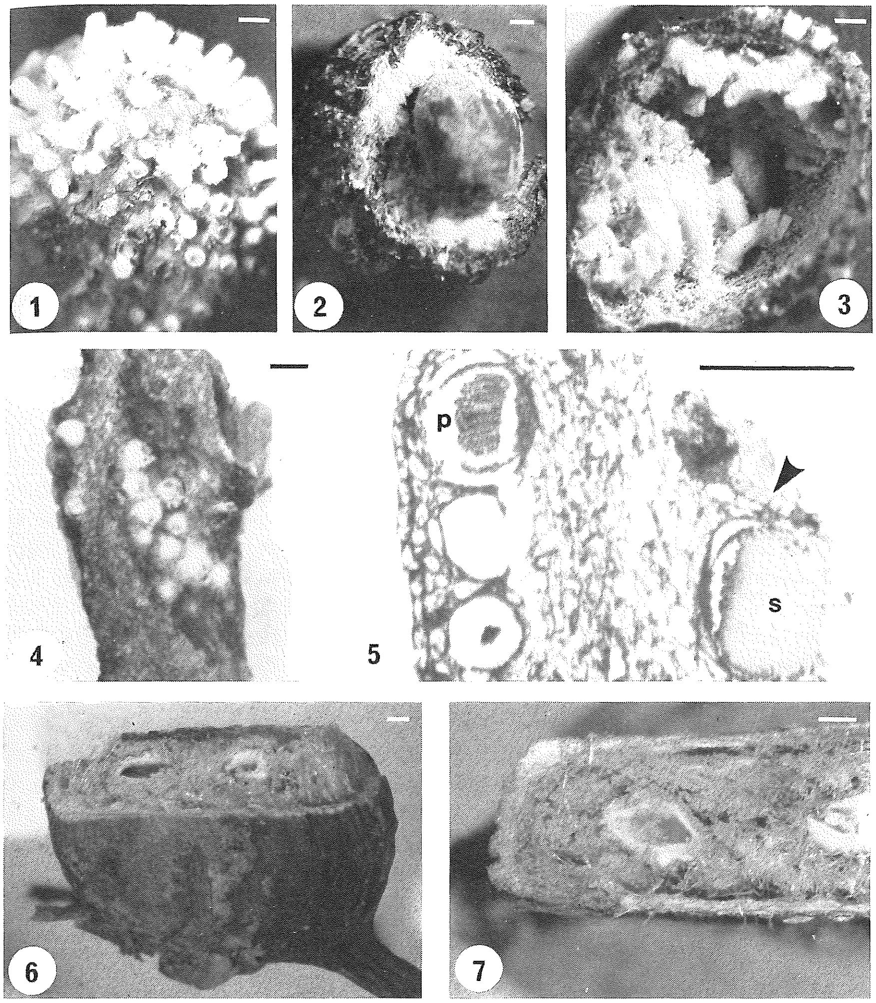
Less sceptically C. B. Plowright was conducting a range of cross-infection experiments to establish the identity of an aecidium found in abundance on the fruits of *Mahonia aquifolium* (Plowright, 1883). Although he successfully demonstrated that this was also attributable to *Puccinia graminis* he must have obtained his inoculum from aecidia produced externally on the fruits and never considered looking inside them. Dissection of a fruit from Plowright's voucher specimen deposited in Kew herbarium revealed a mass of internal aecidia. Plowright clearly missed the opportunity to make the first report of such internal sori.

Following the original reports of Buchenau and Smith, internal sori were subsequently discovered in a number of different rust species and host tissues. Thus, Wolf (1913) described aecidia of *Puccinia angustata* Peck developing within the pith and discharging spores into a hollow cavity in the stem of the host *Lycopus virginicus*. Wolf also made reference to other internal sori, including uredinia of *P. graminis* in stems of rye. To accompany her account of internal sori in *Puccinia sorghi,* Rice (1924) tabulated previous records of their occurrence in 16 rust species from seven genera, involving all stages of the rust life cycle, and infecting a spectrum of host fruit, seed, stem and leaf tissues.

However, although they are now known to be of quite widespread occurrence in the Uredinales, contemporary literature largely ignores the phenomenon of internal sori, and no reference to their potential presence will be found in any current rust flora. This study examines the occurrence within host fruits of internal aecidia in members of the British rust flora from a survey of collections in major national herbaria.

From the collections of aecidia on Berberidaceae surveyed it is clear that when fruits become infected, internal sori almost invariably develop. It must be stressed, however, that attribution of these infections to *P. traminis* cannot be confirmed from herbarium specimens, since a range of other graminicolous rusts also produce their aecidial stages on these hosts (Wilson & Henderson, 1966). It remains to be established whether all of these rusts produce fruit infections. Plowright's experiments (1883) confirm that *P. graminis* does occur on *Mahonia* berries.

Ingram's collection (in E) of this rust includes typical mummified fruits which may eventually become completely covered in sori, producing a striking morphology (Fig. 1). Careful dissection of an infected fruit reveals a comparable proliferation of aecidia on the internal surface of the pericarp, producing a packed mass of spores around the seed (Fig. 2). These internal aecidia are able to generate long undisturbed columns of spores in the protected enclosure of the fruit (Fig. 3). It was also noted that these internal sori matured significantly in advance of the external aecidia. In some specimens only the barely perceptible presence of pycnidia on the outer surface of the fruit gave any indication of infection, yet the interior was packed with spores. This suggests the possibility that many collections of aecidia on Berberidaceae may fail to include samples of fruit simply because overt sporulation is confined to the internal surfaces. Thus the potential for overlooking some infections on *Berberis* and *Mahonia* also exists. A number of specimens examined certainly showed a greater density of aecidia on the inner pericarp surface (Fig. 4). A section from the same fragment (Fig. 5) reveals the looser more thin-walled matrix of cells in which the internal sori develop, in contrast to the thicker walled, more densely packed tissue that restrains the external aecidia. It is likely, as previously suggested by Wolf (1913), that the more prolific development of internal sori is in part a reflection of the reduced resistance to expansion of the surrounding host tissue, but it may also relate to the more nutritive nature of the inner cell layers. Also intriguing are the factors that determine the orientation of a sorus, based on the direction of differentiation of aeciospore initials from the aecidial stroma. However, the precise nature of this control remains unclear.



FIGS 1–5. Aecidia of *Puccinia graminis* on fruit of *Mahonia aquifolium*. (Bar = 0·5mm). 1, mummified fruit covered in aecidia. 2, ruptured fruit showing mass of aecidispores packed around single seed. 3, undisturbed columns of spores inside fruit; seed removed. 4, fragment of pericarp showing few sori on the external surface in contrast to the concentration of mature sori on the inner surface. 5, light microscope section of pericarp fragment (as in Fig. 4); columns of peridial cells (p) and maturing spores (s) can be seen in the external and internal sori respectively; a portion of the testa is also visible (arrow).

FIGS 6–7. Aecidia of *Phragmidium rosae-pimpinellifoliae* on swollen receptacle of *Rosa pimpinellifolia*. (Bar = 0·5mm). 6, oblique view of dissected receptacle with caeomoid aecidium on outer surface. 7, detail of receptacle showing mass of aecidiospores surrounding the seeds.

Similar internal aecidia are reported for the first time in Britain in fruits of *Ribes grossularia*, the cultivated gooseberry. The rust complex *Puccinia caricina* DC. has been resolved by Henderson (1961) into a number of host restricted varieties. *P. caricina* var. *pringsheimiana* (Kleb.) Henderson alternates from *Carex* species to produce aecidia on *R. grossularia*.

Infection is more easily detected in such translucent fruits, but they are not often represented in herbarium collections. Only Muskett's dramatic collection (in IMI) included internal aecidia, which were present throughout the contents of the berry, paralleling the appearance described by Taylor (1920) of aecidia of *Puccinia albiperidia* Arthur within the fruits of *Ribes glandulosum*. Inspection of other *Ribes* fruits in Britain may produce further examples of internal aecidia of *P. caricina* s. lat.

A number of rust infections on *Rosa* extend to the fruits. The search of herbarium specimens revealed one example of *Phragmidium rosae-pimpinellifolia* Diet. on *Rosa pimpinellifolia* in which the erumpent external caeomoid aecidium was matched by an extensive development of internal sori producing a dense mass of spores around the seeds (Figs 6, 7). Again, the sori on the inner surface of the swollen receptacles were more extensive and mature than their external counterparts.

These examples of internal aecidia reveal that development of the sori is favoured by enclosure within the fruit, where sustained production of spores can proceed, buffered from the vicissitudes of fluctuating temperature, desiccation and UV radiation. Although the viability and longevity of these internally produced spores cannot be tested from herbarium specimens, the accumulated mass of mature spores within the unruptured fruit constitutes a potent concentration of inoculum. However, although well protected from adverse conditions for a period, ultimate fracturing of this veritable 'time-bomb' of spores confines all spore liberation to the prevailing environmental conditions, which may be unfavourable to dispersal and reinfection. By contrast, dispersal of aecidiospores from aecidia at the external fruit surface can be sustained over a long period, increasing the probability for some spores to be disseminated during favourable conditions. The most likely agents rupturing the fruits will be birds, whose habit of gathering food to carry to a safe perch for consumption may afford the means of longer range spore dispersal, when the spore bomb is exploded at the new location.

Specimens examined and found to include internal sori:

Phragmidium rosae-pimpinellifoliae. On *Rosa pimpinellifolia*: Eire, Co. Clare, The Burren, 20 vii 1979, *P. Woods* (E).

Puccinia caricina. On *Ribes grossularia*: Northern Ireland, Co. Down, 20 vi 1956, *A. E. Muskett* (IMI 63220), England, Surrey, Knowlesley, 12 v 1933, *P. Chandler* (IMI 67322).

Puccinia graminis. On *Berberis vulgaris* (as *Aecidium berberidis*): Scotland, Aberdeen, 28 ix 1885, *G. Brebner* (BM); England, Norfolk, Gressenhall, 5 vii 1964, *C. E. Hubbard* (K). *On Mahonia aquifolium*: England, Norfolk, Kings Lynn, 1883, *C. B. Plowright* (K); Suffolk, Brandon, 27 vii 1976, *D. Ingram* (E). On *M. bealii*: Scotland, Argyll, Dunoon, v 1943, *M. Wilson* (E).

The production of internal sori in the Uredinales should be noted, not simply as a curious aberration, but as a more widespread phenomenon than previously thought, an understanding of which may shed light on the normal processes of sorus production, especially the orientation of sorus development. Furthermore, the possibility of the concealed presence within certain host tissues of massed inoculum of major plant pathogens has implications for the epidemiology of these disease agents and deserves further attention from plant pathologists.

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