D.O. Berger

Aust. J. Bot., 1988, **36**, 339–46

The Population Biology of a Smut Fungus, *Ustilago spinificis* Ludw. I. Geographic Distribution and Abundance

G. C. Kirby

School of Biological Sciences, Flinders University of South Australia, Bedford Park, S.A. 5042.

Abstract

Ustilago spinificis, a floral smut of *Spinifex hirsutus* and *S. sericeus*, was collected across southern Australia from Yanchep, W.A. on the west coast to Seaspray, Vic. on the south-eastern coast and from the North Island of New Zealand. The host plants are most abundant on beaches with extensive sand dunes and the smut is common in regions where the host is abundant. The distribution limits for the smut are set by the replacement of *S. hirsutus* by a non-host, *S. longifolius*, north of Perth on the west coast; by the absence or rarity of host plants on rocky coastlines across the Great Australian Bight and in the SE. and SW. corners of Australia; and by the limited occurrence of host plants on the east coast of Australia. *Spinifex* inflorescences were sampled on 33 beaches and on the 29 beaches where smut was found the mean frequency of smutted inflorescences was 22%. These high infection rates represent a natural epidemic of a plant disease and data on other natural populations of smut fungi are presented to show that these results are not exceptional.

Introduction

Population studies on fungi have been restricted to either genetic variation or abundance and epidemiology. Genetic studies have utilised many different kinds of variants in different taxa: morphology (e.g. *Epicoccum purpurascens,* Kilpatrick and Chilvers 1981); auxotrophy (e.g. *Ustilago violacea,* Garber *et al.* 1978); virulence genes (e.g. mildews, rusts and smuts of cereal crops); mating-type genes (e.g. *Ustilago maydis,* Puhalla 1970); and isozymes (e.g. *Neurospora intermedia*, Spieth 1975). Most studies on fungal abundance and epidemiology have involved pathogens of crop plants, but an example of a well studied fungus in natural communities is *Ustilago violacea* (Baker 1947; Lee 1981; Jennersten *et al.* 1983). Only one aspect of the population biology of the fungus is dealt with, and general principles of fungal population biology are difficult to determine because of ignorance about so much of the biology of each fungus; there is a need for studies on several aspects of a fungal population.

Some significant questions relating to the population biology of plant pathogenic fungi include: (1) how abundant is the fungus? (2) what impact does the fungus have on the population dynamics of the host population? (3) what is the geographic range of the fungus and how is this affected by biotic factors (e.g. the host population) and abiotic factors (e.g. climate)? (4) what genetic variation is there for virulence and aggressiveness in the fungal population and for resistance in the host population? and (5) how much polymorphism is there for other genes (e.g. genes producing isozymes) and how are these polymorphisms distributed geographically?

0067-1924/88/030339$02.00

Not all questions can be answered in a study on a single species. For fungi with very rapid rates of population increase under favourable environments (e.g. mildews and rusts) question (1) may not be especially useful, because in one season the fungus may be almost extinct and in the next produce a devastating epidemic. Question (4) is particularly difficult to answer because of the large amount of careful work needed with both host and parasite populations.

This and the following paper (Andrews *et al.* 1988) report a study intended to provide at least partial answers to all the above questions, except (4). *Ustilago spinificis* (Ludw.), a flower-infecting smut of *Spinifex hirsutus* Labill. and *S. sericeus* R.Br. (Craig 1984), was chosen as the most suitable smut that could be located around Adelaide, S.A. This was because: (1) the host grasses are almost invariably present on sand dunes on sandy beaches; (2) the smut was known to be abundant in host populations near Adelaide; (3) the habitat occupied by the host has been relatively little disturbed by man, except where towns and cities have been built on the sea front, and hence the population structure of host and parasite should not have been drastically altered in recent decades; (4) the smut and host are native (McAlpine 1910); (5) the hosts have a wide geographic range from the west coast of Australia to New Zealand and hence it was possible that the smut population would be geographically subdivided; (6) *U. spinificis* teliospores germinate readily and form colonies with a predominance of hyphal cells which are easily broken, facilitating the extraction of enzymes for electrophoresis (Andrews *et al.* 1988); (7) *Spinifex* is dioecious and hence there was the possibility that the smut would differentially infect the two sexes.

There were three disadvantages to the choice of the *U. spinificis*. Firstly, the host is a large perennial grass and the large size of plants prevents extensive studies on virulence/avirulence polymorphisms in the smut population and resistance/susceptibility polymorphisms in the host population. Secondly, the host reproduces clonally by means of long runners that spread across the sand, and many clumps over a wide area may all be the same genet (Harper 1977). The smut is systemic and sometimes a group of clumps of the same sex, all bearing smut-infected flowers, was spread over more than 20 m of sandhill, as though all the clumps originated from a single infected plant. Thirdly, nothing is known about the mode of infection of *Spinifex* by *U. spinificis*. Fischer and Holton (1957) described four infection pathways for smut fungi, and one of these (local infection) is unlikely here because host plants usually appear systemically infected. Any of the remaining three pathways (the embryo, seedling or shoot) are potentially possible.

In a revision of the *Spinifex* taxa in southern Australia, Craig (1984) recognised three taxa: *S. sericeus* R.Br. on the eastern side of the Great Australian Bight, *S. hirsutus* Labill. on the western side and *S.* × *alterniflorus* Nees around Perth where *S. hirsutus* and *S. longifolius* R.Br. (a northern Australian species) overlap in their distribution (it may be a hybrid between them). In the field work for this study no distinction between *S. hirsutus* and *S. sericeus* was noticed, and plants thought to be *S. longifolius* but might have been *S.* × *alterniflorus* will be referred to as *S. longifolius*-like.

Materials and Methods

The sex ratio and smutting rate of each *Spinifex* population were assessed by walking along the foredune (if there was a dune system) randomly picking inflorescences after definite intervals. No sampling was done in the central or inland section of large dune systems. This ensured that all samples came from comparable habitats on different beaches where the dune systems varied in width from a few metres to over a kilometre. Since smutted and non-smutted flowers can often be discriminated several paces away, each picked flower was selected at a distance before smutting was detected. In the first

season (Dec. 1977) the emphasis was on sampling genets and flowers were selected from what appeared to be distinctly different clumps. In dense populations the clumps all coalesced, and in these cases the next flower was chosen after either the sex of flowers changed or about 14 m had elapsed. This procedure had the disadvantage that flowers were less intensively sampled in areas where the host was most abundant and most intensively sampled in areas where *Spinifex* occurred as a series of scattered clumps. In later seasons sampling was more frequent, with the next flower being selected about 8 m from the last. This method gave a lower sampling intensity in areas where the host was less abundant, as clumps were often spaced at intervals much greater than 8 m. The two different methods did not appear to affect the estimates of smutting. On most beaches, 500–1000 m were covered along the foredune during a census.

On a few small beaches with only a few clumps of *Spinifex* every clump was sampled to obtain a complete census. On other beaches when time was not available for a census smutted plants were looked for and only the presence or absence of smut was recorded.

Results

Observations of the occurrence of *Spinifex* plants and *U. spinificis* on beaches around southern Australia and New Zealand are summarised in Fig. 1. Moving from west to east, smut was not found on Lancelin or Guilderton beaches, W.A. (the most northerly sites where *S. hirsutus* was observed) or beaches further north where only *S. longifolius* grew. South of Perth the coastline was sandy and *S. hirsutus* was abundant, especially further south where *S. longifolius*-like plants were rare or absent, and the smut was easily located. No host plants were found along the coastline in the south-west corner of Western Australia: the beaches lacked sufficient sand to support *Spinifex*. Smut was present on *Spinifex* populations on large sandy beaches around Esperance on the south coast.

The Great Australian Bight is bounded by cliffs and lacks sandy beaches except at isolated locations like Eucla, where there is a large sandy beach several kilometres long with sand dunes and *Spinifex* extending over 1 km inland, but despite an extensive search no smut was found. On Eyre Peninsula there are abundant sandy beaches and the smut was observed on both sides of the Peninsula, although field work has not progressed very far south on the Peninsula. The coastline on Yorke Peninsula, Fleurieu Peninsula, Kangaroo Island and the south-east of South Australia is dominated by sandy beaches with abundant *Spinifex* and smut in most locations. On the Victorian coast, field work has been sparse. Smut has been collected west and east of Melbourne. In the Ninety-Mile Beach and Lakes Entrance areas of eastern Victoria are extensive sandy beaches with sandhills that should provide good habitat for *Spinifex*, but they are dominated by *Ammophila arenaria* (L.) Link which has been introduced and densely planted to control beach erosion. *Spinifex* appeared almost excluded from some beaches by the thick growth of *A. arenaria* and *U. spinificis* was very hard to find on the scattered and small *Spinifex* clumps.

The south-east corner of Australia and southern New South Wales has a predominantly rocky coast, only sporadically broken by sandy beaches. *Spinifex* occurs but not in great abundance on nearly all of the sandy beaches in this region. *U. spinificis* was not found and has not been recorded here or further north on the east coast (J. Walker, personal communication).

On the beaches examined in New Zealand, *Spinifex* was usually common on the foredune and *U. spinificis* was always found when a search was made.

The field work summarised in Fig. 1 suggests that the distribution of *U. spinificis* is broken into at least four geographically isolated populations: west coast around Perth; south-west coast around Esperance; Eyre Peninsula to eastern Victoria and New Zealand. Tasmania has not been surveyed: *S. sericeus* occurs there but smut has not

been reported. Table 1 presents the census results from 32 beaches in Australia and one in New Zealand.

Because of clonal reproduction in *Spinifex* successive observations are not necessarily independent of each other, and so the data on sex ratio and smutting rates on each sex could not be analysed on a sample-by-sample basis. Instead, the overall sex ratio was tested by a Wilcoxon matched pairs signed ranks test on the numbers of male and female inflorescences counted in each of the 33 sites listed in Table 1. Similarly, the Wilcoxon test was applied to the proportion of smutted male and female inflorescences at each site where smutting was recorded. In both tests the null hypothesis was accepted ($P>0{\cdot}05$), showing that the sex ratio appears to be 1 : 1 in *Spinifex* and that both sexes suffer equally from smutting. Since sex had no overall effect on smutting rate, only total

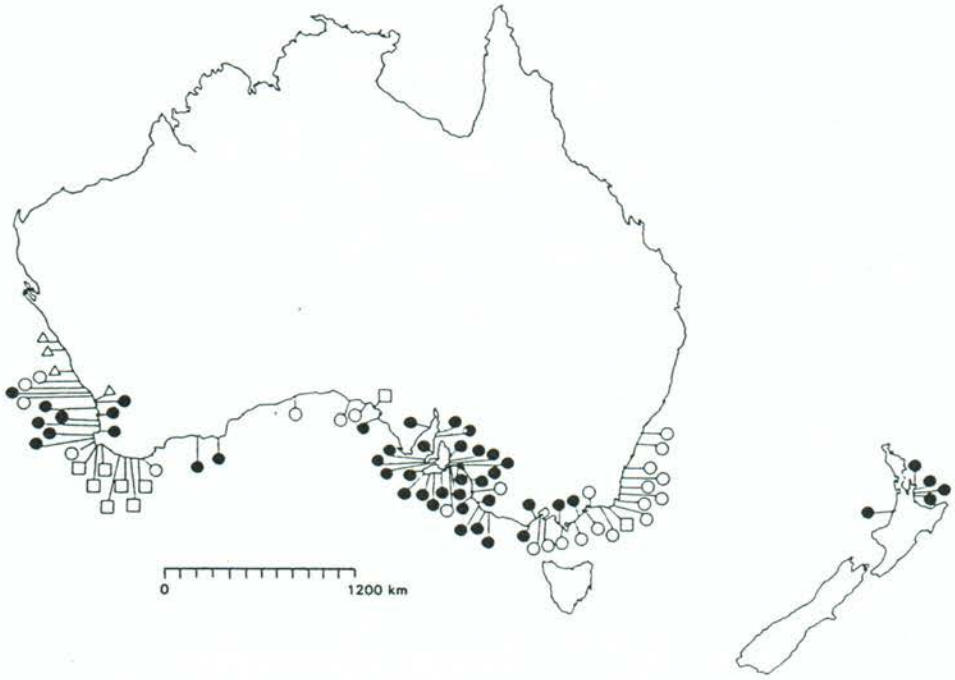

Fig. 1. Summary of field observations on the occurrence of *Ustilago spinificis*, host species (*S. hirsutus* and *S. sericeus*) and non-host *S. alterniflorus* on beaches in Australasia. △ Only *S. longifolius* present; ○ *S. hirsutus* or *S. sericeus* present but no smut observed; □ no *Spinifex* observed; ● *U. spinificis* present.

counts and smutting percentages are given in Table 1. For all except two sites (12 and 33) the *Spinifex* host species can be deduced from Craig (1984). The proportion of smutted inflorescences does not differ between the *S. hirsutus* sites without the competing *S. longifolius*-like plants and the *S. sericeus* sites (ignoring sites 24 and 26 which are small host populations free of disease) by Mann-Whitney U test. Hence the smut appears equally virulent on both host species, although this test is weakened by the few *S. hirsutus* sites sampled. The abundance of smut on *S. hirsutus* is significantly lower on populations competing with *S. longifolius*-like plants by Mann-Whitney U test. Four samples are given in Table 1 where no smutting was recorded, although nearby sites were smutted. The frequency distribution of smutting percentages for non-zero samples is skewed so that the median is only 15% whereas the weighted arithmetic mean is 22%.

Discussion

The wide range of smutting percentages in Table 1 resembles the published data for *Ustilago violacea* populations on *Silene album* (Baker 1947), *S. dioica* (Lee 1981) and *Viscaria vulgaris* (Jennersten *et al.* 1983). Some sites were without smuts and others had a very high frequency of smutting. Casual observations on other smut fungi (see Table 2) suggest that such wide variation in smutting frequencies between sites is often a characteristic of smut populations. With *U. violacea* an important factor is the stability of a stand of host plants: because this smut is not seed-transmitted, a new stand

Table 1. Counts of smutted and unsmutted flowers of *Spinifex*

Host species based on a distribution map by Craig (1984). *S. longifolius*-like plants were also present on sites 1–5 and 7

Site	Date	Lat. (° 'S.)	Long. (° 'E.)	No. counted	Percentage smutting	Host species
1 Guilderton, W.A.	17.xi.81	31 21	115 30	25	0	*S. hirsutus*
2 Yanchep Beach, W.A.	16.xi.81	31 33	115 38	64	6	*S. hirsutus*
3 Quinns Beach, W.A.	16.xi.81	31 41	115 42	16	0	*S. hirsutus*
4 Warnbro Beach, W.A.	16.xi.81	32 20	115 44	62	7	*S. hirsutus*
5 Dawesville Beach, W.A.	16.xi.81	32 38	115 37	60	20	*S. hirsutus*
6 Preston Beach, W.A.	16.xi.81	32 53	115 39	66	5	*S. hirsutus*
7 Biningup Beach, W.A.	16.xi.81	33 9	115 41	36	8	*S. hirsutus*
8 Busselton Beach, W.A.	15.xi.81	33 39	115 20	24	38	*S. hirsutus*
9 Quindalup, W.A.	15.xi.81	33 38	115 7	32	31	*S. hirsutus*
10 Yallingup, W.A.	15.xi.81	33 39	115 1	15	33	*S. hirsutus*
11 Esperance, W.A.	15.xi.81	33 52	121 54	66	9	*S. hirsutus*
12 Streaky Bay, S.A.	11.xi.81	32 48	134 7	63	16	
13 Pondalowie Bay, S.A.	10.xii.77	35 17	136 52	99	14	*S. sericeus*
14 Marion Bay, S.A.	10.xii.77	35 14	136 58	93	7	*S. sericeus*
15 Edithburgh, S.A.	8.xii.77	35 6	137 44	77	21	*S. sericeus*
16 West Bay Beach, S.A.	16.xi.78	35 53	136 32	56	27	*S. sericeus*
17 Sandy River, S.A.	16.xi.78	35 58	136 38	51	23	*S. sericeus*
18 South West River, S.A.	17.xi.78	36 1	136 51	57	13	*S. sericeus*
19 Vivonne Bay, S.A.	17.xi.78	35 54	137 11	39	8	*S. sericeus*
20 American River, S.A.	20.xi.78	35 48	137 49	53	38	*S. sericeus*
21 Noarlunga, S.A.	21.xii.78	35 10	138 28	55	38	*S. sericeus*
22 Moana, S.A.	21.xii.78	35 12	138 28	66	45	*S. sericeus*
23 Myponga Beach, S.A.	7.xii.78	35 22	138 23	21	62	*S. sericeus*
24 Normanville, S.A.	9.xii.78	35 26	138 19	52	33	*S. sericeus*
25 Fishery Beach, S.A.	9.xii.78	35 28	138 6	28	0	*S. sericeus*
26 Waitpinga Beach, S.A.	9.xii.78	35 38	138 30	59	10	*S. sericeus*
27 Cape Jaffa, S.A.	14.xii.77	36 57	139 51	44	0	*S. sericeus*
28 Robe, S.A.	15.xii.77	37 10	139 45	81	42	*S. sericeus*
29 Beachport, S.A.	15.xii.77	37 29	140 00	102	10	*S. sericeus*
30 Southend, S.A.	16.xii.77	37 34	140 7	83	10	*S. sericeus*
31 Pt Macdonnell, S.A.	16.xii.77	38 3	140 42	67	87	*S. sericeus*
32 Brown Bay, S.A.	16.xii.77	38 2	140 50	69	3	*S. sericeus*
33 Raglan, N.Z.	23.xii.81	37 48	174 54	27	7	

of host plants established from seed is likely to lack smut. After some time a few plants become infected by insect-borne smut spores and the frequency of smut will rise. With *U. spinificis* nothing is known of the mechanism of infection of *Spinifex* and hence the effects of population stability and environmental factors on infection rates can only be speculated upon.

In the absence of any knowledge about possible genetic variation in host susceptibility and smut virulence, the only obvious factor affecting the presence of *U. spinificis* was the abundance of the host. The effect of host density on plant disease abundance has been reviewed by Burdon and Chilvers (1982), who pointed out that a reduction in host plant density almost always reduces disease abundance. Jennersten *et al.* (1983) showed clearly the effect of host colony size on *U. violacea* abundance: host colonies of less than 35 individuals lacked smut, and in larger colonies smut abundance correlated with colony size. With *U. spinificis* it is difficult to quantify the density of the host because of the patchiness of clumps across the sand dunes and variations in the width of the zone occupied by the host. Nonetheless, there are three factors that directly affect host abundance: firstly, the proportion of the coastline occupied by sandy beaches; secondly, the width of the sandhill zone that provides suitable habitat for *Spinifex*; and thirdly, the actual density of *Spinifex* on the sandhills.

Table 2. Counts on other *Ustilago* fungi in South Australia

Smut	Host	Locality	Total of hosts counted	Percentage smutting	Notes
U. bullata	*Bromus unioloides*	Adelaide	100	37	Randomly chosen population
U. bullata	*B. diandrus*	Tickera	485[A]	8	Randomly chosen
		Wallaroo	718[A]	4	Randomly chosen
			406[A]	22	Smutting obvious
			365[A]	18	Smutting obvious
U. bullata	*Brachypodium distachyon*	Adelaide	152[A]	19	Smut known to be present
		Flinders Univ.	146[A]	15	Smut known to be present
		Flinders Univ.	140[A]	24	Smut known to be present
		Flinders Univ.	43[A]	2	Smut known to be present
U. cynodontis	*Cynodon dactylon*	Flinders Univ.	117[B]	4	Smut known to be present
			54[B]	52	Smut known to be present
U. comburens	*Danthonia* spp.	Burra	59	32	Smut seen to be abundant
		Burra	63	2	Randomly chosen

[A]Total numbers of inflorescences were counted in 1 m^2 or 0·1 m^2 quadrats because the plants were brittle and shattered as they were harvested.
[B]Based on inflorescences sampled at 1 m intervals on transects.

The first factor probably explains the absence of smut from the south-west and south-east corners of Australia, the Great Australian Bight and the southern coast of New South Wales where rocky seashores prevail and sandy beaches are infrequent and isolated from each other. The smut fungus is disadvantaged in two ways in colonising *Spinifex* populations in these areas: firstly, dispersal of propagules to these beaches is reduced by their isolation from existing smut populations; secondly, persistence of a smut population on a small host population is reduced by the stochastic fluctuations in abundance that always haunt small populations. The absence of smut from Fishery Beach is an example of this phenomenon, because this beach is on the tip of the Fleurieu Peninsula and isolated by about 20 km of rocky coastline in either direction. The Cape Jaffa *Spinifex* population is another example, but here the *Spinifex* population is iso-

lated by the dense growth of other plants on a section of the beach. Eucla provides an example of isolation without the complication of small population size that occurs at Fishery Beach and Cape Jaffa. Here there is a very large *Spinifex* population isolated from other *Spinifex* populations by over 100 km of cliffs to the east and west.

The second factor, the width of the *Spinifex* population, is usually confounded with the first. This can be illustrated by comparing two contrasting sets of beaches. The beaches in the SW. and SE. corners of Australia are not only separated by long rocky coastlines but the bushland advances onto the few dunes that occur and restricts the *Spinifex* to a zone only 1–3 m wide. In contrast, along the South Australian coastline beside the Coorong, the sandy beach is continuous for about 200 km and the sandhills colonised by *Spinifex* occur up to 1 km inland.

The effect of the third factor, *Spinifex* density, has not been quantified in this study but density reductions by competing species can be recognised in two areas. In both cases the density of *Spinifex* clumps was noticeably less than observed in comparable beaches where the competitors were absent or not abundant. On the west coast, *S. longifolius*-like plants had the effect of diluting the density of *S. hirsutus* clumps on beaches around and north of Perth, and this was associated with a reduction in smut abundance (Table 1). On the Ninety-Mile Beach and Lakes Entrance areas, the high density of *A. arenaria* markedly reduced the expected abundance of *Spinifex* on the large sandhills and probably explains the failure to find smut on three of the four beaches examined in this area.

The effect of stochastic processes on the abundance of smut in small host populations may be exemplified by two sites that had only small *Spinifex* populations. At Myponga Beach, 62% of inflorescences were smutted whereas at Brown Bay, only 3% were smutted. Both sites were subjected to human disturbance that was probably responsible for a reduction in the abundance of *Spinifex*. In such small host populations, the frequency of smutting is expected to vary away from the expected average values much more than in larger populations.

Speculation about the amount of dispersal of smut propagules from a smutted host population to a nearby host population that is smut-free is limited by our ignorance of the infection pathway used by *U. spinificis*. If flower infection occurs (Fischer and Holton 1957) then the host seed could be the dispersal unit and both host and smut would disperse together. Otherwise, wind-blown teliospores are the dispersal unit and dispersal of smut spores will be different from seed dispersal.

The reproductive cost to the *Spinifex* population of the *U. spinificis* population can be estimated directly as the proportion of smutted inflorescences, because in almost all inflorescences closely examined all ovaries or anthers were destroyed by smut. Partially smutted inflorescences (where some undamaged ovaries or anthers were found amongst smutty florets) were seen occasionally but were not common anywhere. Since the sites sampled in this study were chosen without foreknowledge of the amount of smutting at each, they can be treated as a random sample from the whole population of *Spinifex* stands. The mean and median of 22% and 15% smutting respectively suggest that in *Spinifex* populations carrying *U. spinificis* the reproductive cost is nearly 20%. This cost is lower in many stands but rises to high values in some localities and must cause a serious reduction in seed set. Because the relative importance of seedling establishment and clonal spread are not known in this grass, the ecological significance of a reduction in seed set cannot be fully evaluated.

The estimates of smut infection rates in this study can also be used to comment on the existence of epidemics of plant disease in natural populations. The view that epidemics are a characteristic of agricultural systems and not of natural ecosystems is rarely challenged because of the lack of data from natural ecosystems. For smut fungi, smutting rates above 10% would be regarded as epidemic by a farmer if they occurred in a cereal crop, and steps would be taken to reduce the disease frequency. With

U. spinificis many *Spinifex* stands are suffering epidemic levels of smutting. Such situations are not uncommon in smut populations: *U. comburens* caused up to 99% smutting on *Danthonia* (Parlane 1929); *U. violacea* can destroy more than 30% of flowers on different host species (e.g. Baker 1947; Lee 1981; Jennersten *et al.* 1983); *U. bullata* can 'devastate' stands of several host species (e.g. McAlpine 1910; Mack and Pyke 1984); *U. readeri* 'is not at all uncommon' (McAlpine 1910); *U. scolochloae* infects over half of some host stands and *U. striiformis* infects up to 30% of *Poa* stands (reviewed by Fischer and Holton 1957). Around South Australia, several smuts can be seen in epidemic abundance. In Table 2, counts from other smut species are presented in order to demonstrate that high levels of smutting can be observed in several smut populations. As noted in Table 2, several of these counts were not made at randomly selected sites but were at sites deliberately chosen because the smut was clearly abundant. Nevertheless, these observations do confirm that the high smutting levels observed on some *Spinifex* stands are not atypical of smut fungi.

Acknowledgments

Mr S. Habel assisted with field work in W.A. and Eyre Peninsula. This research was funded by the Australian Research Grants Committee and Flinders University Research Budget. The manuscript was improved by the comments and encouragement of J. J. Burdon and A. Jaroscz.

References

Andrews, R., Kirby, G. C., and Adams, M. (1988). The population biology of a smut fungus, *Ustilago spinificis* Ludw. II. Isozyme polymorphism and geographic differentiation. *Australian Journal of Botany* **36**, 347–53.

Baker, H. G. (1947). Infection of species of *Melandrium* by *Ustilago violacea* (Pers.) Fuckel and the transmission of the resultant disease. *Annals of Botany* **11**, 333–48.

Burdon, J. J., and Chilvers, G. A. (1982). Host density as a factor in plant disease ecology. *Annual Review of Phytopathology* **20**, 143–66.

Craig, G. F. (1984). Reinstatement of *Spinifex sericeus* R.Br. and hybrid status of *S. alterniflorus* Nees (Poaceae). *Nuytsia* **5**, 67–74.

Fischer, G. W., and Holton, C. S. (1957). 'Biology and Control of the Smut Fungi.' (Ronald Press: New York.)

Garber, E. D., Baird, M. L., and Weiss, L. M. (1978). Genetics of *Ustilago violacea*. II. Polymorphism of colour and nutritional requirements of sporidia from natural populations. *Botanical Gazette* **139**, 261–5.

Harper, J. L. (1977). 'Population Biology of Plants.' (Academic Press: London.)

Jennersten, O., Nilsson, S. G., and Wästljung, U. (1983). Local plant populations as ecological islands: the infection of *Viscaria vulgaris* by the fungus *Ustilago violacea*. *Oikos* **41**, 391–5.

Kilpatrick, J. A., and Chilvers, G. A. (1981). Variation in a natural population of *Epicoccum purpurascens*. *Transactions of the British Mycological Society* **77**, 497–508.

Lee, J. A. (1981). Variation in the infection of *Silene dioica* (L.) Clairv. by *Ustilago violacea* (Pers.). Fuckel in North West England. *New Phytologist* **87**, 81–9.

Mack, R. N., and Pyke, D. A. (1984). The demography of *Bromus tectorum*: the role of microclimate, grazing and disease. *Journal of Ecology* **72**, 731–48.

McAlpine, D. (1910). 'The Smuts of Australia.' (Govt Printer: Melbourne.)

Parlane, B. (1929). An epidemic occurrence of *Ustilago comburens* Ludwig on *Danthonia pilosa*. R.Br., an unrecorded host for New Zealand. *Transactions of the New Zealand Institute* **60**, 253–8.

Puhalla, J. E. (1970). Genetic studies of the b incompatibility locus of *Ustilago maydis*. *Genetical Research* **16**, 229–32.

Spieth, P. T. (1975). Population genetics of allozyme variation in *Neurospora intermedia*. *Genetics* **80**, 785–805.

Manuscript received 7 May 1987, accepted 15 January 1988