INTERACTION BETWEEN *PHYTOPHTHORA CINNAMOMI* AND VICTORIAN NATIVE PLANT SPECIES GROWING IN THE WILD

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Abstract

The interactions were studied between *Phytophthora cinnamomi* and 158 species of Victorian native plants which grow naturally in areas exposed to the pathogen. *Phytophthora cinnamomi* invaded the roots of all species examined, and the interactions ranged between field resistance and highly susceptible. Symptom expression varied with environmental conditions, but not always with phylogenetic relationship. A table was compiled from the results using the system of classification adopted for other Australian States.

G. Weste (2002). Interaction between *Phytophthora cinnamomi* and Victorian native plant species growing in the wild. *Australasian Mycologist* 21 (2): 64–72.

Introduction

Phytophthora cinnamomi Rands is a soil-borne water mould belonging to the Oomycetes, and is not a true fungus. It is dispersed by biflagellate zoospores, and thick-walled chlamydospores. Sexual reproduction is by oogamy, but is rare, and two mating types are required (Zentmyer 1980). *Phytophthora cinnamomi* is a pathogen that lives in the roots, collar or more rarely stems of susceptible plants, causing root necrosis, dieback of shoots and frequently death of the whole plant (Weste & Taylor 1971). The most dramatic expression is that of jarrah dieback in Western Australia.

Plant reaction to this pathogen varies with the species infected. *Phytophthora cinnamomi* penetrates all young roots, but in field resistant plants such as most sedges the necrotic root is rapidly replaced by a new root which grows from immediately behind the infection (Phillips & Weste 1984). In highly susceptible species, such as the horny cone bush, *Isopogon ceratophyllus*, there is good evidence that the pathogen acts hormonally to inhibit water transport within the root, and the plant dies from drought in a subsequent period of water stress (Cahill *et al.* 1986, Dawson & Weste 1983). Because of the importance of environmental conditions in disease expression glasshouse and laboratory experiments do not reflect susceptibility in the wild. Recently Podger (1999) published a comprehensive list of West Australian, New Zealand, Queensland and Tasmanian species of native plant growing naturally in the wild from which he isolated *P. cinnamomi*. He requested that others publish comprehensive and up-to-date records of native species that are susceptible to *P. cinnamomi* in the wild.

The list prepared for this paper complements that of Podger with the names of Victorian native plant species growing in the wild from the root tissue of which *P. cinnamomi* was isolated, and describes the associated symptoms and disease severity. The plant names are according to Walsh & Entwisle (1994–1999).

The aim of this paper is to record accurate information on the interactions that occurred between *P. cinnamomi* and Victorian native plant species while they were growing within the natural plant communities.

Materials and Methods

Most of the data recorded in this paper were collected during field studies which measured vegetation changes caused by *P. cinnamomi* in native plant communities in the Grampians, the Brisbane Ranges, Wilsons Promontory and Narbethong. The vegetation changes were measured biennially over a period of 10 to 30 years. Results were recorded as species present, any symptoms, deaths, and percentage cover on defined quadrats. At each measurement samples of root tissue were collected for each quadrat, from living plants with symptoms. Roots were embedded in soil which then formed part of the sample but no roots from other plants were included. The samples were baited with either lupin seedlings with radicles of 2–4cm (Chee & Newhook 1965) or with

cotyledons of *Eucalyptus sieberi* (Marks & Kassaby 1974). After two to five days the baits were plated onto antibiotic agar, and the cultures subsequently examined for growth of the pathogen. When severe disease had killed all susceptible species, root samples were collected from field resistant plants without symptoms, since these also produce infective zoospores.

In recent years endangered species from these same plant communities have been tested for susceptibility and risk in their present restricted growing region, and isolations of the pathogen from these species growing in the wild have been included in Table 1.

Table 1. Description of symptoms in relation to susceptibility ratings (modified from Podger & Brown 1989).

Susceptibility		**Plant Reaction**
1. field resistant	FR	Continued growth without symptoms
2. slightly susceptible	SS	Survival, chlorosis, browning of branches, recovery in cold or dry, 'fluctuating' species
3. susceptible	S	Depressed growth, chlorosis, dieback, deaths rare in one season
4. moderately susceptible	MS	Chlorosis, dieback,deaths in one or two seasons, mortalities 25–50%
5. highly susceptible	S	Chlorosis, dieback, deaths immediately with infection, mortalities >50%

Koch's postulates have been tested in two ways. The first method involved inoculation into disturbed forest soil with washed mycelium of *P. cinnamomi*. The control plots were merely disturbed (Weste 1974). The pathogen was subsequently isolated from susceptible species at some distance downhill from the inoculated site. Koch's postulates have also been tested by inoculating susceptible species grown outdoors in *Phytophthora*-free non-sterile soil with the relevant local isolate of *P. cinnamomi*. The pathogen was subsequently re-isolated from the diseased host.

Results

The symptoms associated with each native species of the understorey, shrubs and herbs, are described and classified using a system modified from Podger & Brown (1989). Table 2 lists 158 Victorian native plant species from the roots of which *P. cinnamomi* was isolated.

The interaction between trees of the overstorey, *Eucalyptus* spp. and *P. cinnamomi* varies from that described elsewhere according to the amount of inoculum present. Most eucalypts are field resistant, but others such as *E. obliqua*, *E. sieberi* and *E. baxteri* are moderately susceptible and react as follows: When the inoculum was high, that is many zoospores were being produced, and the environment was conducive, that is warm moist conditions at infection, followed by a period of water stress, leaves turned brown and the trees died suddenly with leaves attached. This sudden death of trees was observed both in the Brisbane Ranges and at Corner Inlet, Wilsons Promontory.

However, with less infection, in a more healthy environment, the death of susceptible *Eucalyptus* spp. was more commonly a three year process. In the first year the leaders shed all leaves and projected leafless and dead above the foliage. In the second year rapid growth of epicormic shoots was observed to cover the trunk, and during the third year the tree either recovered or died, but the leaders persisted gaunt and bare without recovering foliage.

Discussion

The interactions between *P. cinnamomi* and Victorian native plants are determined by the presence of the pathogen in a community of susceptible plants, but it is important to realise that the severity of disease depends not only on a high zoospore inoculum, but on a conducive environment, on the time of exposure to the inoculum, on the degree of host susceptibility and on any environmental stress experienced by the host plant. In a highly conducive environment such as the Brisbane Ranges where soils are shallow and duplex, with low organic

content and small microbial populations, plant species with susceptibility ratings between 2 and 5 will show symptoms such as dieback after rainy periods providing soil temperatures are greater than 10°C (Weste & Vithanage 1979). During subsequent periods of water stress infected susceptible plants frequently die.

In natural plant communities the ground surface is frequently uneven, with small hillocks and depressions. Surface water therefore spreads the zoospores unevenly resulting in disease escapes for shallow rooted plants. Large eucalypts are surrounded by a raised mound of dry soil on which susceptible species such as *Xanthorrhoea australis* escape zoospore infection (Weste, unpublished research). Some areas of Victoria, such as the Brisbane Ranges, have experienced a five year drought with about only one-third of the mean rainfall during spring, the period of maximum zoospore formation and release (Commonwealth Bureau of Meteorology). In this period the inoculum potential of the pathogen declined and its detection was rare. Highly susceptible species regenerated evidently from seed in the soil on some severely diseased quadrats in the Brisbane Ranges, Wilsons Promontory and at Anglesea (Weste *et al.* 1999).

The species have been listed under families (Table 2), but susceptibility is often not phylogenetically related, and varies even within a genus. The family Proteaceae and the genera *Banksia* and *Grevillea* contain both susceptible and field resistant species. Susceptibility occurs within ferns, gymnosperms, Monocotyledons and Dicotyledons. There are some physiological characteristics which affect susceptibility such as the ability to form new roots to replace those infected and necrotic. This has been demonstrated for the Monocotyledons, *Poa sieberiana*, *Lepidasperma laterale* and *Gahnia radula* (Phillips & Weste 1984). However the Monocotyledon *Xanthorrhoea australis* is highly susceptible and the grass *Themeda triandra* is moderately susceptible. Some Dicotyledons such as *Bauera sessiflora* and *Pultenaea pedunculata* grow as mats which root as the mat extends. Both are susceptible and the infected region turns chlorotic, then brown and dies, but the plant survives as a newly rooted extension of the mat ahead of infection. As the mat extends, the infection may gradually extend, and more sections die.

As a result of the varying interactions between the different species in a native plant community, infection with *P. cinnamomi* may change the vegetation from an open forest with a species rich heathtype understorey to an open sedge woodland. The information contained in this paper provides data from which to plan strategies for protection from or revegetation for a susceptible forest, woodland or heathland community at risk from *P. cinnamomi*.

Table 2. Victorian native plant species which have yielded *Phytophthora cinnamomi* from root tissue collected from plants growing in the wild.

* denotes species for which Koch's Postulates have been tested. Date refers to date of publication. Susceptibility ratings: FR field resistant, SS slightly susceptible, S susceptible, MR moderately susceptible and HR highly susceptible.

Plant Family & Species	Plant Community	Region	Reference	Suscept Rating	Deaths
Sellaginaceae					
Selaginella uliginosa	open woodland	Grampians	Kennedy & Weste (1986)	S	no
Gleicheniaceae					
Gleichenia dicarpa	open woodland	Grampians	Kennedy & Weste (1986)	S	no
Lindsaeaceae					
Lindsaea linearis	open forest	Grampians	Kennedy & Weste (1986)	MS	rarely
Cupressaceae					
Callitris rhomboidea	open woodland	Grampians	Kennedy & Weste (1986)	MS	yes
Cyperaceae					
Lepidosperma laterale *	open woodland	Grampians	Phillips & Weste (1984)	FR	no
L. semiteres	open forest	Brisbane Ranges	Weste *et al.* (1973)	FR	no
L. tortuosum	open woodland	Grampians	Kennedy & Weste (1986)	FR	no
Gahnia radula *	open forest	Brisbane Ranges	Weste & Taylor (1971)	FR	no

G. sieberiana *	open forest	Grampians	Hinch & Weste (1979)	FR	no
Isolepis marginata	open woodland	Grampians	Kennedy & Weste (1986)	FR	no
Schoenus apogon	open woodland	Grampians	Kennedy & Weste (1986)	FR	no
L. filiforme	open woodland	Brisbane Ranges	Weste (1974)	FR	no
Restionaceae					
Hypolaena fastigiata	open woodland	Grampians	Kennedy & Weste (1977)	FR	no
Lepidobolus drapetocoleus	open woodland	Grampians	Kennedy & Weste (1977)	FR	no
Leptocarpus brownii	open woodland	Grampians	Kennedy & Weste (1977)	FR	no
Juncaceae					
Juncus bufonius *	open forest	Brisbane Ranges	Weste & Cahill (1982)	FR	no
Poaceae					
Poa sieberiana *	open forest	Grampians	Phillips & Weste (1984)	FR	no
Themeda triandra *	open woodland	Grampians	Kennedy & Weste (1977)	MS	rarely
Phormaceae					
Dianella revoluta	open forest	Grampians	Kennedy & Weste (1986)	SS	no
Liliaceae					
Laxmannia orientalis	open woodland	Grampians	Kennedy & Weste (1986)	SS	no
Borya mirabilis	heathland	Grampians	Reiter & Weste (unpublished data)	S	yes
Xanthorrhoeaceae					
Xanthorrhoea australis *	open woodland	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
X. minor *	heathland	Grampians	Hinch & Weste (1979)	S	yes
X. resinifera *	open woodland	East Gippsland	Weste & Cahill (1982)	S	yes
Lomandra filiformis	open woodland	Grampians	Kennedy & Weste (1977)	SS	no
L. longifolia	open woodland	Grampians	Kennedy & Weste (1986)	SS	no
Fagaceae					
Nothofagus cunninghamii *	rain forest	Warburton	Weste (1975)	S	yes
Casuarinaceae					
Allocasuarina paludosa	open woodland	Wilsons Prom.	Weste & Law (1973)	SS	no
A. muellerana *	open woodland	Grampians	Hinch & Weste (1979)	SS	no
A. pusilla	open woodland	Grampians	Kennedy & Weste (1977)	SS	no
Dilleniaceae					
Hibbertia riparia	open forest	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
H. fasciculata var *prostrata*	open forest	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
H. virgata	open forest	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
H. humifusa subsp. *humifusa*	open woodland	Grampians	Hewett *et al.* (submitted)	S	yes
H. cistiflora	open forest	Grampians	Kennedy & Weste (1986)	HS	yes
Epacridaceae					
Acrotriche serrulata	open forest	Brisbane Ranges	Weste & Taylor (1971)	S	yes
Astroloma conostephioides	open woodland	Grampians	Kennedy & Weste (1977)	HS	yes

A. humifusum	heathland	Brisbane Ranges	Weste & Taylor (1971)	S	yes
Brachyloma daphnoides	open forest	Grampians	Kennedy & Weste (1986)	S	yes
B. ciliatum	open woodland	Grampians	Kennedy & Weste (1986)	S	yes
B. depressum	open woodland	Grampians	Weste (in press)	MS	yes
Epacris impressa *	heathland	Brisbane Ranges	Weste & Taylor (1971)	MS	yes
Leucopogon australis	wet heath	Wilsons Prom.	Weste & Law (1973)	HS	yes
L. ericoides	open forest	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
L. glacialis	open forest	Grampians	Weste (1978)	HS	yes
L. virgatus	open forest	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
Lissanthe strigosa	open woodland	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
Monotoca scoparia	open woodland	Brisbane Ranges	Weste (1978)	HS	yes
Sprengelia incarnata	wet heath	Wilsons Prom.	Weste & Law (1973)	HS	yes
Styphelia adscendens	heathland	Grampians	Weste (1978)	HS	yes
Cunoniaceae					
Bauera sessiflora *	wet heath	Grampians	Hewett *et al.* (submitted)	HS	yes
Mimosaceae					
Acacia acinacea	open woodland	Brisbane Ranges	Weste & Taylor (1971)	S	yes
A. mitchelli	open woodland	Grampians	Kennedy & Weste (1977)	MS	yes
A. mearnsii	open forest	Narbethong	Hinch & Weste (1979)	SS	no
A. melanoxylon *	open forest	Narbethong	Weste (1980)	SS	no
A. mucronata	open forest	Grampians	Kennedy & Weste (1986)	MS	yes
A. myrtifolia	open forest	Brisbane Ranges	Weste & Taylor (1971)	MS	yes
A. oxycedrus	open woodland	Grampians	Kennedy & Weste (1977)	MS	yes
A. suaveolens	heathland	Wilsons Prom.	Weste & Law (1973)	S	yes
A. uligifolia	open woodland	Brisbane Ranges	Weste & Taylor (1971)	S	yes
A. verticillata	open forest	Narbethong	Weste (1980)	SS	no
Papilionaceae					
Aotus ericoides	open woodland	Wilsons Prom.	Weste & Law (1973)	HS	yes
Bossiaea cinerea	open woodland	Wilsons Prom.	Weste & Law (1973)	HS	yes
B. prostrata	open forest	Grampians	Kennedy & Weste (1986)	HS	yes
Daviesia brevifolia	open woodland	Grampians	Kennedy & Weste (1977)	HS	yes
D. leptophylla	open forest	Narbethong	Weste (1980)	HS	yes
Dillwynia glaberrima	open forest	Wilsons Prom.	Weste *et al.* (1973)	HS	yes
D. cinerascens	open woodland	Wilsons Prom.	Weste & Law (1973)	HS	yes
Gompholobium ecostatum	open woodland	Grampians	Kennedy & Weste (1977)	MS	yes
Hovea linearis	open woodland	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
Kennedya prostrata	heathland	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
Platylobium obtusangulum	open forest	Brisbane Ranges	Weste & Taylor (1971)	MS	yes
P. formosum	open forest	Narbethong	Weste (1980)	S	rarely
P. graveolens	open forest	Brisbane Ranges	Peters & Weste (1997)	HS	yes
P. gunnii	open forest	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
P. mollis	open woodland	Wilsons Prom.	Weste & Law (1973)	HS	yes

P. humilis	open forest	Brisbane Ranges	Weste & Taylor (1971)	S	rarely
P. pedunculata	open forest	Brisbane Ranges	Weste & Taylor (1971)	MS	yes
P. scabra	heathland	Wilsons Prom.	Weste (1975)	MS	yes
P. stricta	open woodland	Wilsons Prom.	Weste & Law (1973)	MS	yes
Proteaceae					
Banksia integrifolia *	open woodland	Mt Martha	Hinch & Weste (1979)	S	yes
B. marginata	heathland	Brisbane Ranges	Weste & Taylor (1971)	S	rarely
B. saxicola *	open woodland	Grampians	Hewett *et al.* (submitted)	HS	yes
B. serrata *	open woodland	Wilsons Prom.	Weste & Law (1973)	MS	yes
B. spinulosa var. *cunninghamii*	open woodland	Wilsons Prom.	Weste (1975)	HS	yes
Conospermum mitchellii	open forest	Grampians	Kennedy & Weste (1977)	H	yes
Grevillea alpina	open forest	Grampians	Kennedy & Weste (1977)	MS	yes
G. aquifolium	open forest	Grampians	Kennedy & Weste (1986)	MS	yes
G. chrysophaea *	open forest	Brisbane Ranges	Peters & Weste (1997)	HS	yes
G. confertifolia *	open woodland	Grampians	Hewett *et al.* (submitted)	MS	yes
G. steiglitziana *	open forest	Brisbane Ranges	Peters & Weste (1997)	S	yes
G. microstegia *	open forest	Grampians	Reiter & Weste (unpublished data)	S	rarely
G. parviflora	open forest	Brisbane Ranges	Weste *et al.* (1973)	S	no
G. williamsonii *	heathland	Grampians	Hewett *et al.* (submitted)	HS	yes
Hakea decurrens *	open forest	Brisbane Ranges	Weste & Taylor (1971)	S	rarely
H. nodosa *	open forest	Brisbane Ranges	Hinch & Weste (1979)	SS	no
H. ulicina *	open forest	Grampians	Kennedy & Weste (1977)	SS	no
*Isopogon ceratophyllus**	open forest	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
Persoonia juniperana	open woodland	Grampians	Kennedy & Weste (1977)	HS	yes
Thymelaceae					
Pimelia humilis	open forest	Brisbane Ranges	Weste & Taylor (1971)	MS	yes
P. linifolia	open forest	Grampians	Kennedy & Weste (1986)	S	no
Myrtaceae					
Calytrix tetragona	open forest	Grampians	Kennedy & Weste (1977)	HS	yes
C. sullivanii	open forest	Grampians	Kennedy & Weste (1977)	HS	yes
Eucalyptus aromaphloia *	open forest	Brisbane Ranges	Weste *et al.* (1973)	S	no
E. baxteri *	open forest	Brisbane Ranges	Weste *et al.* (1973)	MS	yes
E. dives	open forest	Brisbane Ranges	Weste & Taylor (1971)	S	rarely
E. macrorhyncha *	open forest	Brisbane Ranges	Weste *et al.* (1973)	MS	yes
E. melliodora	open woodland	Grampians	Weste & Kennedy (1997)	FR	no
E. obliqua *	open forest	Brisbane Ranges	Weste & Taylor (1971)	MS	yes
E. ovata *	wet heath	Brisbane Ranges	Weste *et al.* (1973)	FR	no
E. goniocalyx *	open woodland	Brisbane Ranges	Weste *et al.* (1973)	FR	no
E. pauciflora *	open woodland	Brisbane Ranges	Weste *et al.* (1973)	SS	no
E. radiata *	open forest	Brisbane Ranges	Weste *et al.* (1973)	S	rarely
E. regnans	open forest	Narbethong	Weste (1980)	MS	rarely
E. sieberi *	open forest	East Gippsland	Weste (1973)	MS	yes
E. viminalis *	open forest	Brisbane Ranges	Weste *et al.* (1973)	SS	no

E. willisii	open woodland	Grampians	Kennedy & Weste (1986)	MS	yes
E. yarraensis *	open woodland	Brisbane Ranges	Peters & Weste (1997)	FR	no
Leptospermum continentale *	open woodland	Brisbane Ranges	Weste *et al.* (1973)	SS	no
L. myrsinoides	open woodland	Brisbane Ranges	Weste *et al.* (1973)	SS	no
Melaleuca squamea	wet heath	Wilsons Prom.	Weste (1975)	SS	no
M. squarrosa *	wet heath	Wilsons Prom.	Weste (1975)	SS	no
Thryptomeme calycina *	open woodland	Grampians	Hewett *et al.* (submitted)	MS	yes
Euphorbiaceae					
Amperea xiphoclada	open woodland	Grampians	Kennedy & Weste (1986)	SS	no
Rhamnaceae					
Cryptandra tomentosa	open woodland	Grampians	Weste (1978)	SS	no
Pommaderris feruginea	open forest	Brisbane Ranges	Weste (1978)	SS	no
Spyridium parvifolium	open forest	Brisbane Ranges	Weste & Taylor (1971)	SS	no
Tremandraceae					
Tetratheca ciliata	open forest	Brisbane Ranges	Weste & Taylor (1971)	HS	yes
T. pilosa	open forest	Grampians	Kennedy & Weste (1986)	HS	yes
Rutaceae					
Asterolasia phebalioides *	open woodland	Grampians	Hewett *et al.* (submitted)	MS	yes
Boronia nana	open forest	Grampians	Kennedy & Weste (1986)	HS	yes
Correa reflexa	open forest	Brisbane Ranges	Weste & Taylor (1971)	S	rarely
Apiaceae					
Platysace heterophylla	open forest	Grampians	Kennedy & Weste (1986)	MS	yes
Xanthosia dissecta	open forest	Grampians	Kennedy & Weste (1986)	MS	yes
Verbenaceae					
Avicennia marina subsp. *australasica* *	estuarine waters	Westernport Bay	Weste *et al.* (1982)	MS	yes
Lamiaceae					
Prostanthera decussata *	open woodland	Brisbane Ranges	Peters & Weste (1997)	HS	yes
Goodeniaceae					
Goodenia hederacea	open woodland	Grampians	Kennedy & Weste (1977)	MS	yes
G. humilis	open woodland	Grampians	Kennedy & Weste (1977)	MS	yes
G. lanata	open woodland	Grampians	Kennedy & Weste (1977)	MS	yes
Chenapodiaceae					
Rhagodia parabolica *	saline areas	Brisbane Ranges	Peters & Weste (1997)	SS	no
Asteraceae					
Argentipallium obtusifolium	open woodland	Grampians	Kennedy & Weste (1986)	MS	yes
Brachyscome uliginosa	open woodland	Grampians	Kennedy & Weste (1986)	MS	yes
Cassinia aculeata	open forest	Narbethong	Weste (1974)	SS	no
Olearia ciliata	open forest	Grampians	Kennedy & Weste (1986)	SS	no
O. pannosa subsp. *cardiophylla* *	open forest	Brisbane Ranges	Peters & Weste (1997)	MS	yes

Acknowledgements
The author thanks Drs David Ashton (University of Melbourne) and David Cahill (Deakin University) for critical readings of the manuscript, and all those listed as joint authors of the references for assistance with the field work.

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PROF. DR MEINHARD M. MOSER

Prof. Dr Meinhard M. Moser passed away on Monday 30 September 2002, after a brief illness in Innsbruck, Austria. He had a long career as a specialist in the taxonomy of larger fungi, particularly the Agaricales and was widely regarded as a world expert in the genus *Cortinarius*.

He carried out important work at the Forest Institute in Imst and later was Director of the Microbiology Institute at the University of Innsbruck, an association that continued after his retirement.

He was widely known for his encyclopaedic knowledge of European mushrooms. This was demonstrated in his **Agaricales and Gasteromycetes** in Helmut Gams Kleine Kryptogamenflora von Mitteleuropa Band II, first published in 1953, with later editions up until the 5th Edition in 1983. The 4th Edition was translated into English and published as **Key to the Agarics and Boletes** in 1983. Other works included **The Genus Phlegmacium** (1960), and, in collaboration with W. Julich, and later, others, **Colour Atlas of Basidiomycetes,** parts 1 to 19, 1985+, an ongoing collection of photographs.

The coverage of the handbook was constantly upgraded to more adequately represent the Nordic flora, the Mediterranean flora and in later years, the eastern European flora.

A long-term project was to try to untangle the true sense of the species described by Fries. For this project he spent long holidays in most summers at Femsjo, collecting in forests where Fries had also collected, with a view to building up a set of collections which really represent the species collected by Fries.

In recent years he had spent many long trips in North America, particularly collecting the genus *Cortinarius*, to help towards an answer to the question of how many of the European species of *Cortinarius* are also found in North America.

The Australian connection was also part of his life. In 1975, he published, with Egon Horak a major monograph on ***Cortinarius* and Related Genera in South America**. In this he highlighted many new species which are similar to Australian species.

I had the opportunity to spend an extended period with him in Innsbruck in 1979 to study *Cortinarius* and to learn to understand the genus in Europe. This was followed by later visits in 1986 and 1990, when this work was extended and also to work on the genus *Galerina.* In this he was very happy to share his vast knowledge. Invitations to join in collecting trips all over Europe were a particular privilege. While by nature he was quiet and retiring, he was always generous and thoughtful in caring for visiting learners. We are the beneficiaries of his careful taxonomy and we will miss his immense knowledge and experience.

Above all we are saddened by the loss of a friend.

Alec Wood