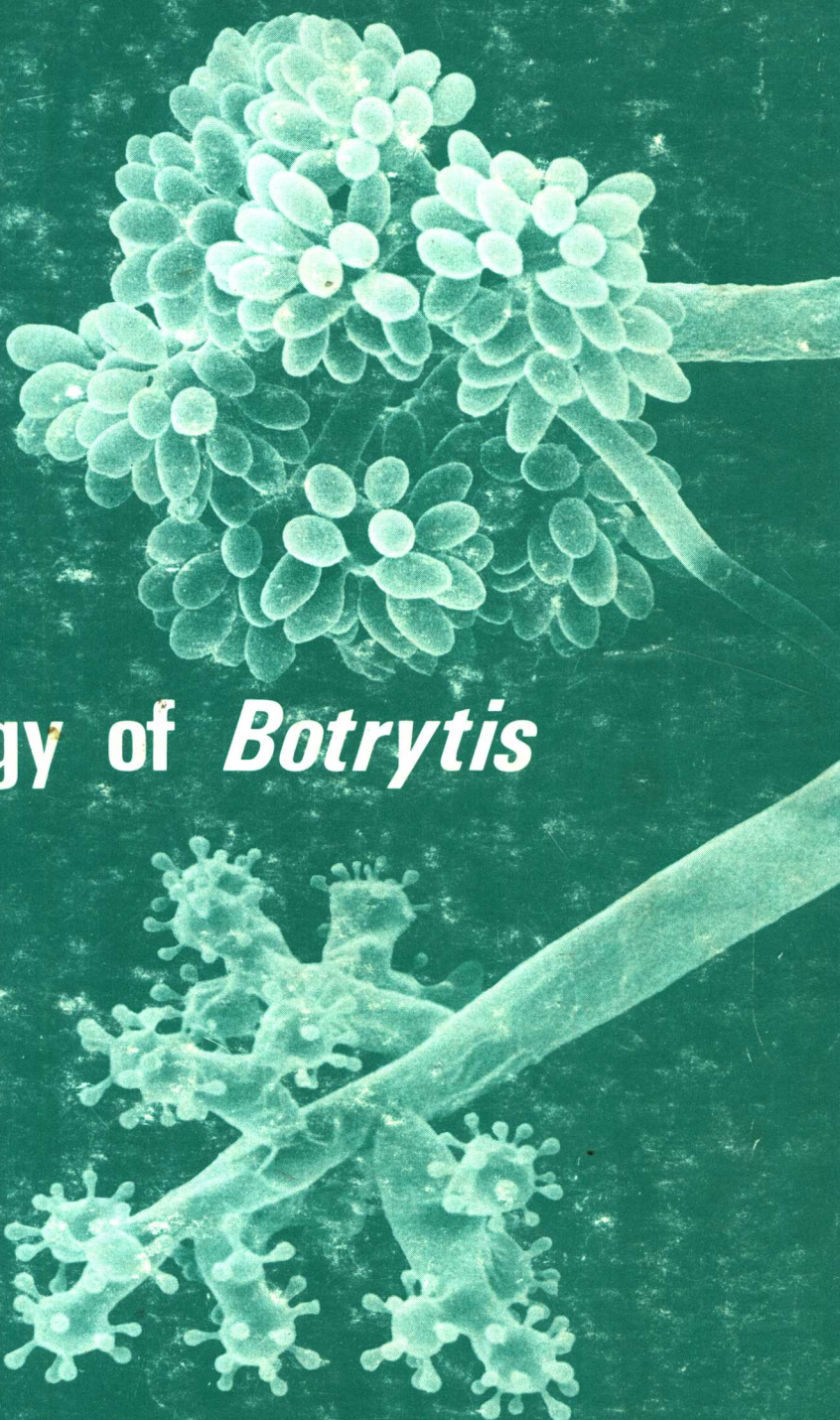




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# The Biology of *Botrytis*

edited by  
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## Preface

The decision to produce this book first arose during meetings of the European *Botrytis* group. The origins of this group date back to 1964 when a small number of *Botrytis* research workers met at East Malling Research Station. The group has grown since that time and conferences held in Scotland, Sweden, Belgium, Poland, France and the Netherlands have attracted increasing numbers of participants. From discussions held during these meetings it has become obvious that the biology of *Botrytis* now encompasses a wide range of disciplines many of which must inevitably lie outside the range of experience of the individual research worker. In addition much of the information about *Botrytis* is scattered throughout a literature which is already voluminous and which continues to expand year by year. This book attempts to summarise the present state of knowledge of a number of major aspects of the biology of this important genus in the hope that it will be useful not only to students of the genus *Botrytis* but to anyone with an interest in the biology of fungi.

We are very grateful to the authors of the chapters in this book for the efforts which they have made to make it a success. In addition we should like to thank all our colleagues in the European *Botrytis* group for many stimulating discussions about the genus. Many of their ideas and discoveries are incorporated in the text.

J. R. COLEY-SMITH  
K. VERHOEFF  
W. R. JARVIS

## Introduction

J. R. COLEY-SMITH

The genus *Botrytis* was first erected by Micheli in 1729 and since that time it has become widely known as a group of fungi causing destructive and economically important plant diseases. This is particularly true of those forms grouped together as the form species *Botrytis cinerea*.

*Botrytis* species tend to be concentrated in the temperate areas of the world, where they occur on a variety of crop plants. Records from tropical and cold areas on the other hand are comparatively few. The types grouped under *B. cinerea* can infect an extremely wide range of host plants whereas other species are much more restricted in this respect. Important groups of plants that are attacked by *Botrytis* are field and glasshouse vegetables, small berry fruits including grapes, ornamentals, bulb and corm-producing monocotyledons and forest tree seedlings. Many other plants may be attacked but receive little attention because they are not economically significant. In addition to their importance as pathogens of growing plants, *Botrytis* species are also noteworthy as spoilage organisms causing considerable losses of plants and plant products during storage and transit. *B. cinerea* in particular is known to be able to tolerate low temperatures and is the cause of a number of cold store problems.

There are a number of ways in which diseases caused by *Botrytis* species can be controlled but satisfactory levels of control are not always easy to achieve. This difficulty frequently arises from the rapid rate at which spore germination, infection, mycelial growth and sporulation can occur in most members of the genus. Control of *B. cinerea* with certain fungicides has been made difficult because of the existence of variants of the fungus that are able to tolerate the normal levels of fungicide used. This is a particular problem with several systemic fungicides and is discussed in Chapter 10. In other cases, particularly in soft fruits, disease often develops at or near harvest time, thereby preventing the application of fungicides because of residues that are toxic or impart taints. Control with fungicides is sometimes rendered difficult because of the long period that may elapse between infection and the development of severe symptoms. During this period the fungus may exist in a so-called latent or quiescent form. This condition is well known in *B. cinerea* but has also been found in a number of other

species. In these cases the recognition of climatic and phenological conditions during which infections take place is essential for the proper timing of application of fungicides. There are a few instances where a better degree of control has been achieved by retiming fungicide applications to coincide with such infection periods (Jarvis, 1966; Borecka, 1967). The physiological and biochemical reasons underlying latency are poorly understood (Verhoeff, 1974) and this enigmatic aspect of *Botrytis* biology deserves much more attention than it is now receiving. A chapter on the subject had been tentatively planned but lack of knowledge was judged to preclude it.

Although species of *Botrytis* are justifiably best known as organisms causing destructive plant diseases there is one form of disease produced by *B. cinerea* in grape vines which is both valued and encouraged. This is the condition known as *pourriture noble* in France and *Edelfäule* in Germany. Grapes affected by this 'noble rot' are used in the production of certain high quality sweet wines. This is not always possible however because *Botrytis* can also produce a destructive disease in grapes, the *pourriture grise* or familiar grey mould. Host-parasite interactions in enology are discussed in Chapter 9.

Some idea of the importance of *Botrytis* species is apparent from the number of research papers that continue to be published about it, both in the so-called 'pure' fields, where it is a useful model organism and in the applied fields. Over fifty years ago Brierley (1921) stated that '*Botrytis cinerea* is perhaps the commonest and best known fungus and has been a centre of mycological research since the time of de Bary. Few, if any other fungi, have been studied so thoroughly by so many able investigators, or are the subject of so extensive a literature'. Since this statement was made, the number of research papers has continued to increase year by year. This can easily be seen by examining the reviews of papers and reports involving *Botrytis* and *Botryotinia* that have appeared in the *Review of Applied Mycology* and in the *Review of Plant Pathology* since 1922. Apart from a drop during the 1939-1945 World War there has been a general upward trend and papers involving *Botrytis* are at present appearing at a rate of about a hundred per year. Many of the more important of these papers are catalogued in the BOTBIB computer-filed bibliography on *Botrytis* and *Botryotinia* assembled at the Scottish Horticultural Research Institute and filed at the University of Edinburgh Computer Centre (Jarvis and Topham, 1974). However, despite this wealth of information there has been no attempt until recently to produce a comprehensive account of the biology of *Botrytis*. Jarvis (1977) has produced a guide to the literature on the taxonomy, physiology and pathogenicity of *Botryotinia* and *Botrytis*

species, and it is hoped that this, together with the present work in which a number of specialists have written chapters on important aspects of the biology of *Botrytis*, will serve students of the genus for many years to come.

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# Contents

List of Contributors	v
Preface	vi
Introduction	vii

<b>1 Taxonomy</b>	<b>1</b>
-------------------	----------

W. R. JARVIS

1	Introduction	1
2	<i>Botryotinia</i> and <i>Botrytis</i>	2
3	The basis of classification	3
4	<i>Botrytis</i>	10
5	Numerical taxonomy	14
6	Biochemical and serological taxonomy	15
7	Host specificity	15
8	Conclusions	16
	References	17

<b>2 Variation in <i>Botrytis</i> and <i>Botryotinia</i></b>	<b>19</b>
--	-----------

J. W. LORBEER

1	Introduction	19
2	Variation and its regulation by host, nutrition and environment	20
3	Sexual systems	23
4	Heterokaryosis	29
5	Adaptation	33
	References	36

<b>3 Formation, Structure and Germination of Conidia</b>	<b>41</b>
--	-----------

H. A. S. EPTON and D. V. RICHMOND

1	Introduction	41
2	Formation of conidia	42

- 3 Structure of conidia 64
- 4 Germination of conidia 71
- 5 Conclusions 81
- References 81

#### **4 Sclerotia and other Structures in Survival 85**

J. R. COLEY-SMITH

- 1 Introduction 85
- 2 Formation of sclerotia 86
- 3 Germination of sclerotia 94
- 4 Survival of sclerotia 98
- 5 Interactions between sclerotia and microorganisms 100
- 6 Survival of conidia 103
- 7 Survival of mycelium 109
- 8 Conclusions 111
- References 112

#### **5 Behaviour of Conidia on Aerial Plant Surfaces 115**

J. P. BLAKEMAN

- 1 Introduction 115
- 2 Pattern of behaviour prior to penetration of plants 116
- 3 Occurrence as a saprophyte on plant surfaces 119
- 4 Effect of physical environment 121
- 5 Effect of chemical environment 125
- 6 Biological contamination of aerial plant surfaces 134
- 7 Physical damage to aerial plant parts 137
- 8 Antagonism 138
- 9 Conclusions 147
- References 148

#### **6 The Infection Process and Host-Pathogen Interactions 153**

K. VERHOEFF

- 1 Introduction 153
- 2 Infection by germ tubes from conidia 154
- 3 Infection by hyphae 162

- 4 Host-pathogen interactions 164
- 5 Predisposition 172
- 6 Conclusions 176
- Acknowledgement 177
- References 177

## **7 Mechanisms of Resistance to *Botrytis* 181**

J. W. MANSFIELD

- 1 Introduction 181
- 2 Interactions between *Botrytis* species and *Vicia faba* 181
- 3 Metabolism of phytoalexins by *Botrytis cinerea* 205
- 4 Interactions between *Botrytis* species and *Tulipa gesneriana* 208
- 5 Formation of physical barriers: lignification, papillae and suberization 211
- 6 General discussion 213
- Acknowledgement 216
- References 216

## **8 Epidemiology 219**

W. R. JARVIS

- 1 Introduction 219
- 2 Dispersal 222
- 3 Infection 228
- 4 The environment and infection 229
- 5 Crop phenology and epidemiology 238
- 6 Predisposition 240
- 7 Storage diseases 242
- 8 Conclusions 245
- References 245

## **9 *Botrytis cinerea* in Enology 251**

J. RIBÉREAU-GAYON, P. RIBÉREAU-GAYON  
and G. SEGUIN

- 1 Introduction 251
- 2 Parasitism of *Botrytis cinerea* on grapes 252

- 3 Chemical changes induced in the grape by *Botrytis cinerea* 260
- 4 Alcoholic fermentation in musts from *pourriture noble* grapes 266
- 5 Enzyme reactions 269
- 6 Conclusions 272
- References 272

## **10 Disease Control**

**275**

R. B. MAUDE

- 1 General aspects of disease control 275
- 2 Control of diseases of seeds and vegetatively-propagated material 276
- 3 Control of diseases of growing crops 281
- 4 Control of diseases of stored produce 287
- 5 Control of diseases by cultural methods 297
- 6 Conclusions 300
- References 301

## **Subject Index**

**309**

# 1

## Taxonomy

W. R. JARVIS

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1	Introduction	1
2	<i>Botryotinia</i> and <i>Botrytis</i>	2
3	The basis of classification	3
	Conidiophores and conidia	3
	Microconidia	4
	Sclerotia	6
	Apothecia	7
	Appressoria and organs of attachment	10
4	<i>Botrytis</i>	10
5	Numerical taxonomy	14
6	Biochemical and serological taxonomy	15
7	Host specificity	15
8	Conclusions	16
	References	17

### 1 Introduction

Fungi in the botanical species of *Botrytis* (the holomorphs *sensu* Hennebert and Weresub, 1977, 1979) exist in a number of anatomical form species (Hennebert, 1971). These sometimes, but not invariably, comprise the teleomorph, characterized by the production of meiotic diaspores (the sexual state and, in this case, the apothecium belonging to the form genus *Botryotinia*), together with a number of anamorphs, which are the asexual, mitotic, diasporic expressions of the fungi. In this genus, the anamorphs include the conidiophore, of the form genus *Botrytis*, the phialoconidiophore (*Myrioconium*), the sclerotium (*Sclerotium*) and perhaps other less well-defined anamorphs such as appressoria and organs of attachment, and oidia. The nomenclatural concepts and the practical problems they pose for the taxonomist are described and discussed by Hennebert and Weresub (1977, 1979), Carmichael (1979) and by a number of other taxonomists in a discussion summarized by Kendrick (1979).

The hyphomycete genus *Botrytis*, the ascomycete genera *Botryotinia* and *Sclerotinia*, and the connection between them have long confused the taxonomist and the plant pathologist alike. The confusion has arisen

largely because of a poor understanding of the type species of the genus *Botrytis*, the difficulties in obtaining the perfect state from the imperfect state in controlled conditions (see Chapter 2) and because of certain similarities in the symptoms on plants caused by *Botrytis* spp. and *Sclerotinia* spp., particularly *S. sclerotiorum* and *S. minor*. The tortuous paths of research in these fields up to 1944 are well-reviewed by Buchwald (1949).

Buchwald's review was accompanied by a comprehensive revision of the Sclerotiniaceae. He had completed his paper in 1944, and, working alone in Denmark at that time, he was unaware of the work that Whetzel was doing in the USA. Whetzel's revision of the Sclerotiniaceae was published posthumously in 1945, the section on *Botryotinia* having been completed by H. M. Fitzpatrick (Whetzel, 1945).

Modern taxonomic treatments of the Sclerotiniaceae and the discomycetes in general are given by Kimbrough (1970), Dumont and Korf (1971) and Korf (1973).

Several authors, notably Smith (1902), Whetzel (1945), Buchwald (1949) and Hennebert (1971) recognized that *Botrytis cinerea*, on the criteria of conidiophore characters, is a collective form species and Whetzel in particular would limit identifications to 'a *Botrytis* of the *cinerea* type'. In the absence of the perfect state, some anamorphs with conidiophores of the *cinerea* type, for example *B. convoluta*, *B. narcissicola* and *B. porri*, can be distinguished by other characters, in these cases by sclerotial form, and it is likely that other fungi with conidiophores of the *cinerea* type may yet prove to be separate holomorphs and connected with other *Botryotinia* teleomorphs.

Sexual reproduction and variation within holomorphs is discussed at length in Chapter 2.

## 2 *Botryotinia* and *Botrytis*

Buchwald (1949), reviewing the early controversy on the genetic connection between *Botryotinia fuckeliana* and *Botrytis cinerea*, concluded that the evidence then available favoured the view that *B. fuckeliana* had a *Botrytis* of the *cinerea* type as its conidial state but that this fungus was probably restricted to *Vitis*, the host genus of de Bary's original (1869) description of *Peziza (Botryotinia) fuckeliana*. For many years, de Bary's type material was lost and the name remained a *nomen nudum*. The problem was compounded by the failure of mycologists to obtain the perfect state in a culture initiated from a conidium of *Botrytis cinerea* from any host. Although many had obtained conidia from ascospore cultures (Buchwald, 1949; Gregory, 1949), this did not satisfactorily

resolve the problem of the perfect state of *Botrytis* species of the *cinerea* type.

As Gregory (1949) pointed out, the pure-culture techniques that were developed at the beginning of the twentieth century inhibited the necessary transfer of microconidia to receptive bodies on the sclerotia of the same or other isolates (Drayton, 1932). Then Drayton (1937) and Groves and Drayton (1939) carried out spermatization to induce apothecial formation in cultures of *Botrytis convoluta* and *B. cinerea*, respectively, a technique which brought experimental taxonomy to the genus.

Finally, two events occurred that resolved the *Botryotinia fuckeliana*—*Botrytis cinerea sensu stricto* connection. First, Gregory (1949) found an obscure account of *Peziza fuckeliana* and *Botrytis cinerea* by de Bary (Ueber Schimmel und Hefe in Virchow und Holtzendorf's *Samml. gemeinverst. wiss. Vortr. Ser. IV, Heft 87, 1-78*), which, Gregory asserted, constituted the description of *P. fuckeliana* n.sp. There is no doubt that in this paper, de Bary intended *P. fuckeliana* and its connected *B. cinerea* to refer only to the fungus on grapevine. Gregory (1949) also found sections of *P. fuckeliana* on a microscope slide in the British Museum (Natural History) together with slides containing microconidia and sections of a sclerotium. The first of these slides evidently constitutes the type specimen.

The second event (Groves and Loveland, 1953) was the mating, by means of Drayton's (1937) spermatization technique, of various isolates of *Botrytis cinerea*. They included isolates obtained in Canada from apple, potato and celery and also isolates from grapevine in the Rhine Valley, the site of de Bary's original collection. Crosses between compatible isolates all yielded apothecia morphologically indistinguishable from the type material. While Groves and Loveland considered that many isolates of *Botrytis cinerea* would prove to belong to *Botryotinia fuckeliana*, they pointed out that it does not necessarily follow that all other isolates of *Botrytis* of the *cinerea* type belong to *Botryotinia fuckeliana*. They further commented that Fitzpatrick's selection of *Botryotinia convoluta*, with a *Botrytis* of the *cinerea* type as its imperfect state, as the type species (in Whetzel, 1945), in no way altered the concept of the genus.

### 3 The basis of classification

#### CONIDIOPHORES AND CONIDIA

Conidium ontogeny provides the main basis for delimiting the form genus, or anamorph, *Botrytis* (Hughes, 1953; Barron, 1968; Ellis, 1971).

The conidiophores are macronematous, mononematous, acroauxic, more or less straight, branched alternately and mostly in the apical region, proliferating beyond the conidiogenous region, and brown, becoming paler near the apex. Some species (*B. cinerea*, *B. globosa*, *B. porri*, *B. ficariarum*, for example) have a swollen basal cell. The mature conidiophore on the host is often flattened and twisted about its axis, a form that may have significance in the conidium dispersal mechanism (see Chapter 8).

The ultimate conidiophore branches are determinate, integrated, terminal conidiogenous cells, inflated into ampullae that are clavate, cylindrical to spherical or sub-spherical, holoblastic and polyblastic and hyaline (Fig. 1). On the release of the conidia, the ampulla in some species, e.g. *B. globosa* (Webster and Jarvis, 1951), *B. squamosa* (Walker, 1925), *B. ficariarum* (Hennebert and Groves, 1963), and perhaps all species to some extent, collapses in concertina-like folds, though not apparently in response to a sudden release of pressure.

The conidia are smooth, attached to the ampulla by a fine denticle, solitary, acropleurogenous, simple, hyaline or nearly so, aseptate or occasionally 1- or 2-septate in culture, ovate or elliptical, globose to sub-globose in some species. After release, a slightly protuberant hilum, sometimes with a slight frill, may be evident on the conidium and a flat rounded scar on the ampulla (see Chapter 3, Fig. 12a). In mass, the conidia are grey-brown.

The conidia are dry and hydrophobic when released but eventually are able to enter water to begin germination (Jarvis, 1962). Germination is by one or two germ tubes, occasionally by up to five.

#### MICROCONIDIA

This anamorph is perhaps more correctly termed the spermatial state since the spores apparently have only a sexual function (Whetzel, 1945; see Chapter 2) despite a few claims that they can behave as conidia in the initiation of new thalli. The spermodochium is referable to *Myrioconium* H. Sydow. It develops from germ tubes, more mature hyphae and sclerotia, and sometimes within empty hyphal cells (Brierley, 1918). It is a compact penicillate cluster of phialides or, especially within hyphal cells, of a single phialide, sessile or shortly stalked (Fig. 2). The phialides are short, inflated towards the base, tapering at the apex, with or without a collarette. The phialoconidia

FIG. 1 (a) A young conidiophore of *Botrytis tulipae* showing the blastic origin of the conidia on the ampullae. Scale marker represents 20  $\mu$ m. (Photograph by P. Gladders.) (b) Conidia of *Botrytis cinerea*, showing the sterigma attachment to the ampulla. Scale marker represents 15  $\mu$ m



