BOTRYOTINIA AND BOTRYTIS SPECIES:

taxonomy physiology and pathogenicity

Monograph No. 15
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BOTRYOTINIA AND BOTRYTIS SPECIES:
taxonomy, physiology, and pathogenicity

A guide to the literature

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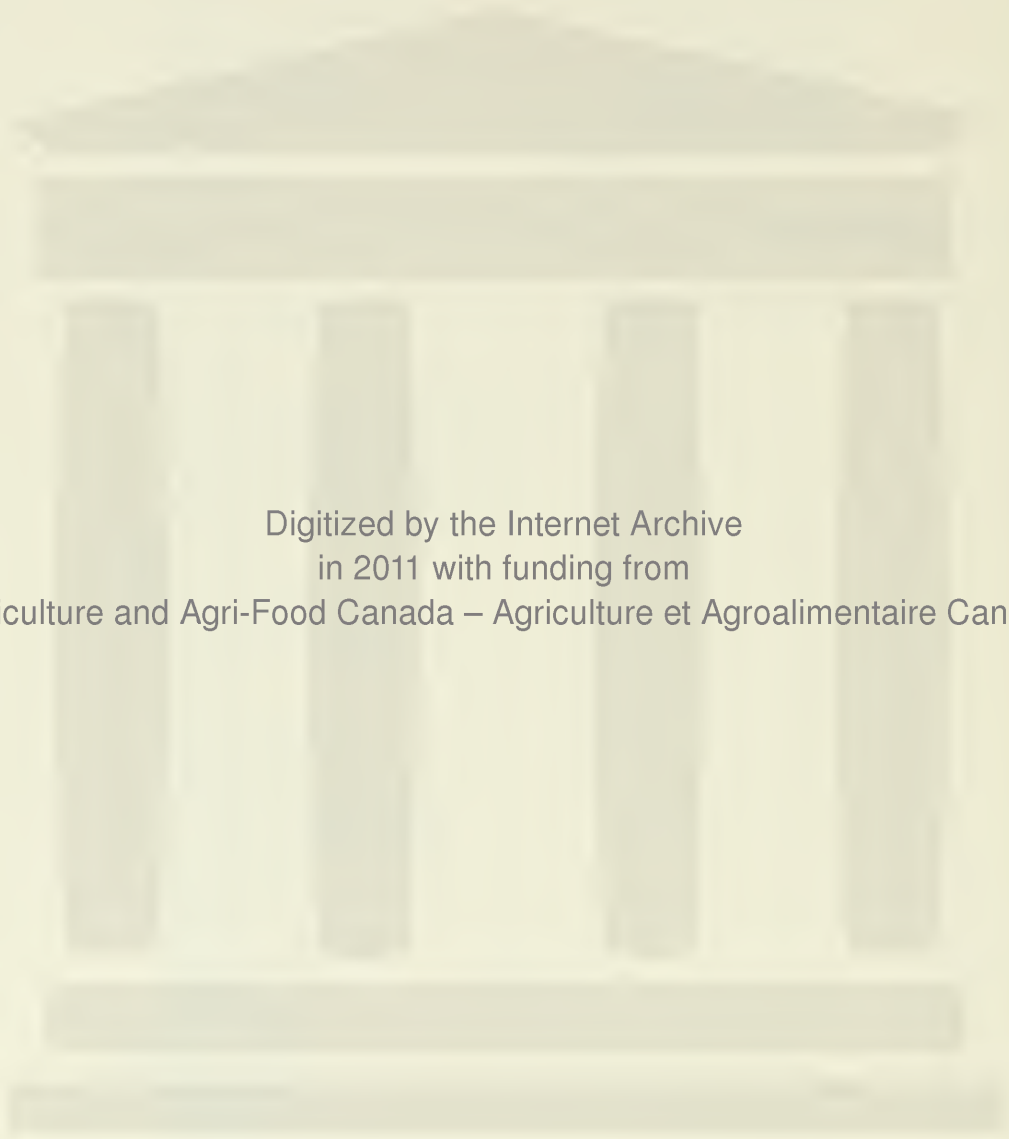

Preface

The literature on the taxonomy and biology of *Botrytis* spp., the diseases they cause, and their control is vast and I have covered only a small part of it here. I have selected for annotation what I consider to be the more informative papers that give leads into one or more of several fields. Others, no less important but not discussed here, are listed in an appendix in such a way as to link them with a computer-filed bibliography on the genus (Jarvis and Topham: Bull. Br. Mycol. Soc. 8: 37. 1974). The appendix also includes papers inadvertently omitted from this review and those that appeared after the text had been completed in December 1974.

The ever-changing spectrum of fungicide usage has discouraged me from compiling a list of all the fungicides ever used against *Botrytis* spp. and the results of their trials; instead, I have concentrated on the principles underlying control measures of all sorts, and simply listed a few reviews giving leads to detailed papers that should be consulted, together with *Review of Plant Pathology* and the American Phytopathological Society's annual *Results of Fungicide and Nematicide Tests.*

I am indebted to Professor John Webster and the late Professor William Brown, who introduced me to the rich field of *Botrytis* biology, to the many mycologists and plant pathologists throughout the world, especially those of the European *Botrytis* group, with whom I have discussed the genus, and to the many people in Scotland and Canada who have assisted me in the production of this review.

PART 1 INTRODUCTION

Botryotinia and *Botrytis* species are among the most ubiquitous and catholic plant pathogens and saprophytes. They are particularly important on:

- grape (*Vitis vinifera* L.) and other *Vitis* spp. (Bouard, Bulit, Lafon, and Roussel 1970)
- small fruits (strawberries, raspberries, blueberries, cranberries, gooseberries, and currants)
- vegetables (lettuce, tomatoes, cucumbers, peas, beans, and peppers)
- bulbous monocotyledons (onions and other *Allium* spp. and ornamental members of the Liliaceae, Amaryllidaceae, and Iridaceae)
- forest tree seedlings
- glasshouse crops (tomatoes, cucumbers, and ornamental crops) (McClellan 1964; Cramer 1967)

In the U.K. Moore (1959) lists 13 species of *Botrytis* in addition to *B. cinerea* on 5 cereal hosts, 4 root and fodder crops, 6 pulse and forage crops, 15 vegetable crops, 14 fruit crops, 6 tree species, 58 ornamental hosts, as well as on potato, hops, and flax.

Botrytis spp., and especially *B. cinerea,* are important pathogens of stored and transported fruits, vegetables, ornamental crops, and nursery stock (Harvey and Pentzer 1960; Haas and Wennemuth 1962; Smith 1962; Eckert and Sommer 1967; Lutz and Hardenburg 1968; Redit 1969; and Coursey and Booth 1972). Probably most rots that occur in stored products begin in the field and escape detection because many of these infections are latent (q.v.). They may develop only when special postharvest conditions of host physiology and the storage environment disturb the equilibrium between the quiescent fungus and its host. Their control depends as much on preharvest as on postharvest measures (Smith 1962; Jarvis 1965; and Eckert and Sommer 1967).

Botrytis cinerea sensu lato and perhaps also sensu stricto has a very wide host range; MacFarlane (1968), for example, lists 235 hosts from records in the *Review of Applied Mycology,* Anderson (1924) more than 100 hosts from Alaska including 3 genera of Pteridophytes and a species of the Bryophyte *Lunularia,* Baker (1946) 36 hosts, mostly ornamental crops from California, Heald & Dana (1924) 20 hosts from Washington, Dingley (1969) 69 hosts from New Zealand, and Conners (1967) lists 163 hosts in Alaska, Canada, and Greenland from the Canadian Plant Disease Survey.

Species of *Botryotinia* with a conidial state of the *Botrytis cinerea* type also include specialized parasites such as *Botryotinia convoluta* on *Iris* spp., *B. ficariarum* on *Ficaria verna* Huds., *B. ranunculi* on *Ranunculus septentrionalis* Poir., and *B. narcissicola* on *Narcissus* spp.

Other *Botrytis* spp. also have a much more restricted host range. Of 25 species of *Botrytis* recognized by Hennebert (1963), 14 occurred on species in the Liliaceae, Amaryllidaceae, and Iridiceae, 7 on *Allium* spp., and at least 6 of them were pathogenic to *A. cepa*. *B. allii (B. aclada)* occurred on 4 *Allium* spp. On the other hand, *A. ursinum* was host to only *B. globosa,* (although this species also occurred on *A. cepa*), *A. vineale* host only to *B. porri* (also on *A. cepa, A. sativum,* and *A. ascalonicum*), and *A. triquetrum* host only to *B. sphaerosperma* (which itself occurred on no other *Allium* host, though Hennebert (1969) later found it on *Lilium regale*).

It is interesting, phylogenetically, to note that the most restricted host-specificity in the genus occurs on members of the monocotyledonous division Corolliferae and the arguably related dicotyledonous Ranunculaceae.

Geographically, *Botryotinia* and *Botrytis* spp. occur wherever their host crops are grown, ranging from cool temperate zones of Alaska (Anderson 1924), Canada and Greenland (Conners 1967), and Lithuania (Shidla 1971*a,* 1971*b*) to subtropical areas like Egypt (El-Helaly, Elarosi, Assawah, and Kilani 1962) and northern New Zealand (Dingley 1969). However, because of the distribution of economic hosts, most records are from cool-temperate and warm-temperate zones, although *B. cinerea* often occurs as a snow mold, especially in forest nurseries (Sato, Shoji, and Ota 1959). Most species occur in all continents, but *Botryotinia ranunculi* is recorded only in North America and *B. ficariarum* only in Europe; *B. calthae* (also from the Ranunculaceae) is recorded from both continents (Hennebert and Groves 1963). None of these are known in other continents.

Botrytis spp. are not usually regarded as soil inhabitants (Park 1955) but rather as ephemeral mycelia associated with decaying plant residues (Domsch and Gams 1972; Scurti, Fiussello, and Jodice 1972), probably degrading cellulose (Janke 1949; Franz and Loub 1959; Niethammer, Krehl-Nieffer, and Hitzler 1959; and Domsch 1960), pectin (Loub 1960; Nyeste 1960; and Domsch and Gams 1969), cutin (Linskens and Haage 1963), and araban (Kaji, Tagawa, and Motoyama 1965), but not xylan (Domsch and Gams 1969). *Botrytis cinerea* and a *Botrytis* sp. were readily isolated from soils by immersion tubes and screened immersion plates by Chesters and Thornton (1956). Luppi-Mosca (1960) isolated *B. cinerea* from depths of 40–60 cm in a forest soil.

Barron (1968) thought that although *B. cinerea* may be relatively common in soil, it sporulates poorly there and is underestimated by normal techniques such as dilution plates. Lockwood (1960) and Hsu and Lockwood (1971) considered it only a moderately good competitor in soil, surviving as mycelium for less than 2 wk. Lorbeer and Tichelaar (1970) devised a selective medium for the isolation of *B. allii (B. aclada)* from soils and recovered it successfully from the sandy soils of the Netherlands and the organic soils of New York.

The position of *B. cinerea* in the ecological succession of fungi on plant remains above the soil was considered by Hudson (1968).

PART 2 TAXONOMY

TAXONOMIC REVIEW

In the most recent review of Discomycete taxonomy (Korf 1973), *Botryotinia* Whetzel (1945) is placed in the order Helotiales and the family Sclerotiniaceae Whetzel (1945).

The form-genus *Botrytis* Pers. is placed by Hennebert (1973) in the Hyphomycete family Botrytidaceae Lindley and in Hughes' (1953) conidiogenetic section IB; the conidiophores are straight, are branched alternately, and they proliferate; the conidia are usually one-celled, gray to brown, globose to ovoid, and, in Barron's (1968) classification, botryoblastospores.

For many years, the diseases caused by *Botryotinia* and *Botrytis* spp. were confused with those caused by aconidial *Sclerotinia* spp., especially *S. sclerotiorum* and *S. minor,* and the confusion extended into taxonomy. Despite a clarification by Smith (1900), the confusion persisted (e.g., Zimmermann 1927) until it was largely dispelled by Whetzel (1945) and Buchwald (1949).

Sclerotiniaceae

Whetzel (1945) erected the family Sclerotiniaceae for those Discomycetes characterized as follows: apothecium arising from a definite sclerotium or stromatized portion of the substratum, stipitate, cupulate, funnel- or saucer-shaped (except in *Verpa*), usually brown; ascus inoperculate, commonly 8-spored; ascospores ellipsoidal, often flattened on one side, usually hyaline, unicellular and smooth; spermatia (microconidia) usually globose to slightly ovate; conidial forms various, in most (9 of 15) genera lacking.

Within the Sclerotiniaceae, Whetzel (1945) used the anatomy of the food-storing stroma as an important criterion of relationships among the genera. He recognized two generalized types: the sclerotial, of more or less characteristic form, and the substratal, of diffuse and indeterminate form. Some of the former are formed in aerial mycelium or within host cavities and do not replace host tissues, nor contain remnants of them. The tuberoid sclerotia of *Sclerotinia* are of this type. In the discoid sclerotia of *Ciborinia* and the mummoid sclerotia of *Ciboria,* undigested remnants of host tissues are commonly found in the medulla. Noviello (1962) also noted this in a *Botrytis* sp. of the *cinerea* type that formed sclerotia on leaves of *Ficus elastica,* and Noviello and Korf (1961) reexamined a number of genera for the occurrence within sclerotia of cotton fragments when cotton pads, soaked in a nutrient broth, were used as substrates. Five species of *Botryotinia* and three of *Botrytis* had sclerotia containing fragments of the substrate, as had

Ciborinia and *Streptotinia* spp., whereas *Sclerotinia sclerotiorum, S. trifoliorum,* and *S. asari* ined. had not, and Noviello and Korf concluded that *Botryotinia* and *Botrytis* were clearly distinct from *Sclerotinia* and closely related to *Ciborinia.* They also noted that a flexible and gelatinous matrix containing hyphae of the medulla was present in sclerotia of *Botryotinia,* but not in *Sclerotinia.*

In parentheses it is worth noting that Korf and Dumont (1972) subsequently proposed the transfer of *S. sclerotiorum,* together with *S. tuberosum,* to a new genus *Whetzelinia,* distinct from the cypericolous and juncicolous species of *Myriosclerotinia* Buchw., from *Sclerotinia* (=*Ciborinia* Whetzel), and *Botryotinia.*

In the taxonomy of the Sclerotiniaceae, diagnostic features of sterile apothecial tissue had mostly been ignored until Korf and Dumont (1968) drew attention to their value. Korf (1973) emphasized apothecial and stromatal structure in his review of the taxonomy of the Discomycetes and Tuberales.

Phylogenetic relationships based on sclerotial structure are discussed by Willetts (1972), and those based on ascus morphology by Chadefaud (1973).

Other possible phylogenetic relationships of the Sclerotiniaceae within the Helotiales, based on Nannfeldt's (1932) classification of the inoperculate Discomycetes, are discussed by Korf (1958).

The taxonomy of the family was reviewed and revised by Dumont and Korf (1971) and by Korf (1973), who gave keys to the orders and genera.

Some North American and British collections are described by Seaver (1951) and Dennis (1968), respectively.

Botryotinia

Botryotinia is distinguished from other genera in the Sclerotiniaceae by the following characters (Whetzel 1945; Korf 1973):

stroma a definite black sclerotium, planoconvexoid, characteristically flattened, loaf-shaped or hemispherical, formed just beneath the host cuticle or epidermis and firmly attached; if covered, then eventually erumpent; rind poorly developed or lacking on the (flat) attachment surface.

medulla of slender, thin-walled hyphae, loosely interwoven and embedded in a hyaline, flexible to gelatinous matrix, with no interhyphal spaces.

rind black, distinct, more or less pseudoparenchymatous or palisade-like.

microconidiophores in a sporodochium, microconidia globose on branching microconidiophores, all enclosed in a mucilaginous matrix.

conidiophores straight, of the genus *Botrytis.*

apothecia cupulate and stalked, brown, cup varying from infundibuliform to discoid, the margin sometimes reflexed in age.

ascus inoperculate, J+, clavate.

ascospores hyaline, unicellular, ellipsoidal.

appressoria characteristically digitate, formed from mycelial tips in culture on glass.

The type species of *Botryotinia* is *B. convoluta* (Drayton) Whetzel (1945); it has a *Botrytis* of the *cinerea* type as the conidial state. Whetzel also included in his new genus *Botryotinia porri* (van Beyma) Whetzel with *Botrytis porri* as the conidial state, and *Botryotinia ricini* (Godfrey) Whetzel with *Botrytis ricini* (not of the *cinerea* type, and subsequently transferred to *Amphobotrys* by Hennebert 1973), as its conidial state.

Buchwald (1949) made a comprehensive reappraisal of Whetzel's Sclerotiniaceae. He supported the use of the genus *Botryotinia* (but with *B. fuckeliana* as the type species) to contain those species with *Botrytis* conidial states and divided it into subgenera. *Eubotryotinia* subg. n. contained species in which the conidial state belonged to the subgenus *Eubotrytis* (conidia of the *Botrytis cinerea* type) and *Sphaerobotryotinia* subg. n., in which the conidia were globose. Thus, in 1949, *Eubotryotinia* contained *B. fuckeliana* (de Bary) Whetzel, *B. porri* (van Beyma) Whetzel, *B. convoluta* (Drayton) Whetzel, and *B. narcissicola* (Gregory) Buchw.; and *Sphaerobotryotinia* contained *B. polyblastis* (Gregory) Buchw. (type species), *B. ricini* (Godfrey) Buchw., and *B. sphaerosperma* (Gregory) Buchw.

Botryotinia and *Botrytis*

The connection between *Botryotinia (Sclerotinia)* spp. and *Botrytis* spp. has been the subject of some controversy, and the situations prevailing up to 1949 are reviewed by Buchwald. De Bary (1866, 1884, 1886) was convinced that *Botrytis cinerea* and *Botryotinia (Peziza) fuckeliana* were genetically connected. In 1864 he named *Peziza fuckeliana,* but without describing it, as the perfect apothecial stage of *B. cinerea* Pers. and *P. fuckeliana* was subsequently transferred to *Sclerotinia* by Fuckel (1869) and to *Botryotinia* by Whetzel (1945). For many years *P. fuckeliana* remained a nomen nudum because of the lack of type material, but Gregory (1949) described slides of mounted material from an apothecium, sclerotium, and microconidiophore made by de Bary and deposited in the British Museum (Natural History) in London and reestablished the validity of de Bary's name.

By crossing isolates of *B. cinerea* from *Vitis* sp. from the Rhine Valley (the host and locality of de Bary's collection) with isolates from apple, potato, and celery from Canada, Groves and Loveland (1953) obtained apothecia of *Botryotinia fuckeliana* that agreed with de Bary's type material on the slides in the British Museum. Thus, they established the genetic connection between *Botryotinia fuckeliana* (de Bary) Whetz. and *Botrytis cinerea* Pers.

Botrytis

The genus *Botrytis* is one of the first described genera of fungi; Micheli erected it in 1729. Persoon (1801) designated five species under the binomial system of Linneaus, validated the genus, and included one of Micheli's species, *B. cinerea,* so named by von Haller (1771), in his *Synopsis Methodica Fungorum.* By 1822, Persoon had included 27 species and by 1886 Saccardo listed 128 species. Many of these were clearly not congeneric and Whetzel (1945), Buchwald (1949), and Hennebert (1973) have redefined the genus. A comprehensive history of the nomenclature in the genus is given by Buchwald (1949) and Hennebert (1973). The genus *Botrytis* has accommodated a large number of taxa because of misidentifications, because of mistaken concepts of the genus as defined by Persoon (1822), and perhaps because of some doubt as to the correct type-species. Saccardo (1886), for example, divided *Botrytis* into 4 subgenera on the basis of conidiophore structure: *Eubotrytis* Sacc., *Polyactis* (Link) Sacc., *Phymatotrichum* (Bon.) Sacc., and *Cristulina* Sacc.; in this system *B. cinerea* was referred to *Polyactis.* Other genera confused with *Botrytis* include *Beauveria* Vuill., *Hyphelia* Fr., *Chromelosporium* Corda, and *Haplaria* Link. Buchwald (1949) emended the description of the genus, restricting it to 23 species. Many of the references in the literature before 1949 must therefore be treated with some caution.

Buchwald proposed three new subgenera: (i) the subgenus *Eubotrytis,* having two sections: the Macrosclerotiophorae (large sclerotia) containing the species *B. porri, B. allii (B. aclada), B. byssoidea, B. squamosa, B. convoluta, B. anthophila, B. trifolii, B. cinerea* sensu stricto, and *B. cinerea* sensu lato; and the section Microsclerotiophorae (small sclerotia) with the species *B. tulipae, B. elliptica, B. hyacinthi, B. galanthina, B. narcissicola, B. gladioli, B. croci, B. paeoniae,* and *B. fabae;* (ii) the subgenus *Sphaerobotrytis,* containing the globose-spored species *B. ricini, B. globosa, B. sphaerosperma,* and *B. polyblastis;* and (iii) the subgenus *Verrubotrytis,* containing the single species *B. geranii.*

The question of the type species had long remained confused. Buchwald (1949) was of the opinion that Persoon (1822) had intended *B. cinerea* to be the type species, and himself accepted that the name had also been accepted by Fries (1832) in the *Systema Mycologicum.* Hennebert (1973) evidently considered that Clements and Shear (1931) had designated it as the lectotype, although they had not discussed the matter. Groves and Loveland (1953), however, did discuss it and, apparently overlooking the lectotype of Clements and Shear, designated a specimen (on a stem of ? *Foeniculum vulgare,* Hennebert, unpublished) in the Persoon Herbarium in Leiden as the lectotype.

Hennebert (1960, 1973) made a comprehensive reappraisal of *Botrytis* and *Botrytis*-like fungi. Of about 380 taxa assigned over the years to the genus *Botrytis,* he provisionally retained 22 species within his concept of the form-genus *Botrytis* within the family Botrytidaceae Lindley. These 22 species are connected with inoperculate Discomycetes of the family Sclerotiniaceae Whetzel, in the genus *Botryotinia* Whetzel. Within the Botrytidaceae, Henne-

bert (1973) erected 3 other new genera: *Streptobtrys* n.g., connected with *Streptotinia* Whetzel; *Amphobotrys* n.g., connected again with *Botryotinia,* and containing one species, *A. ricini (Botrytis ricini* Buchw); and *Verrucobotrys* n.g., connected with *Seaverinia* Whetzel and containing one species, *V. geranii* (*Botrytis geranii* Seaver). A number of other *Botrytis*-like fungi were assigned to *Dichobotrys* n.g., connected with *Trichophaea* Boudier in the family Pyronemataceae Corda; to *Chromelosporium* Corda, connected with *Peziza* Pers. in the family Pezizaceae Fries; to *Pulchromyces* n.g. and *Phymatotrichopsis* n.g., both with no known perfect state; and to *Ostracoderma* Fries and *Glischroderma* Fuckel, form-genera in the family Glischrodermataceae Rea with no known perfect state. Hennebert published a synoptic key to the genera in the same paper, and included the following species in his form-genus *Botrytis* (only valid species have a citation here):

B. aclada Fresen., Beitr. Mycol. 1: 16. 1850 = *B. allii* Munn

B. byssoidea Walker *in* Phytopathology 15: 709. 1925, conidial state of *Botryotinia allii* (Sawada) Yamamoto *in* Sci. Rep. Hyogo Univ., Ser. Agr. Biol. 2:22. 1956

B. calthae Hennebert *in* Can. J. Bot. 41: 343. 1963, conidial state of *Botryotinia calthae* Hennebert & Elliott *in* Can. J. Bot. 41: 343. 1963

B. cinerea Pers., Syn. meth. Fung. 690. 1801 = *Haplaria grisea* Link = *Polyactis vulgaris* Link = *Phymatotrichum gemellum* Bon. = *Botrytis fuckeliana* Buchw., conidial state of *Botryotinia fuckeliana* (de Bary) Whetzel *in* Mycologia 37: 679. 1945

B. convoluta Whetzel & Drayton *in* Mycologia 25: 475. 1932, conidial state of *Botryotinia convoluta* (Drayton) Whetzel *in* Mycologia 37: 679. 1945

B. croci Cooke & Massee *in* Cooke *in* Grevillea 16: 6. 1887

B. elliptica (Berk.) Cooke *in* Gdnr's Chron. 30: 58. 1901

B. fabae Sardiña *in* Mems R. Soc. esp. Hist. nat. 15: 291. 1929

B. ficariarum Hennebert *in* Can. J. Bot. 41: 355. 1963, conidial state of *Botryotinia ficariarum* Hennebert *in* Can. J. Bot. 41: 355. 1963

B. galanthina (Berk. & Br.) Sacc. Syll. Fung. 4: 136. 1886

B. gladiolorum Timm. *in* Meded. Inst. Phytopath. Lab. BloembollOnderz. Lisse 67: 15. 1941, conidial state of *Botryotinia draytonii* (Budd. & Wakef.) Seaver *in* North Am. cup-fungi (Inop.) 62. 1951

B. globosa Raabe *in* Hedwigia 78: 71. 1938, conidial state of *Botryotinia globosa* Buchw. *in* Phytopath. Z. 20: 250. 1953

B. hyacinthi Westerd. & Beyma *in* Meded. Phytopath. Lab. W. C. Scholten 12: 15. 1928

B. narcissicola Kleb. ex Westerd. & Beyma *in* Meded. Phytopath. Lab. W. C. Scholten 12: 15. 1928, conidial state of *Botryotinia narcissicola* (Gregory) Buchw. *in* Vet.-og Landbohøjsk. Aarsskr. 1949: 137. 1949

B. paeoniae Oud. *in* Vers. gewone Verg. Afd. Natuurk. K. Ned. Akad. Wet. 1897: 455. 1897

B. pelargonii Roed *in* Blyttia 7: 77. 1949, conidial state of *Botryotinia pelargonii* Røed *in* Blyttia 7: 77. 1949

B. polyblastis Dowson *in* Trans. Br. Mycol. Soc. 13: 102. 1928, conidial state of *Botryotinia polyblastis* (Gregory) Buchw. *in* K. Vet.-og Landbohøjsk Aarsskr. 1949: 137. 1949

B. porri Buchw. *in* K. Vet.-og Landbohøjsk. Aarsskr. 1949: 137. 1949, conidial state of *Botryotinia porri* (Beyma) Whetzel *in* Mycologia 37: 680. 1945

B. ranunculi Hennebert *in* Can. J. Bot. 41: 348. 1963, conidial state of *Botryotinia ranunculi* Hennebert & Groves *in* Can. J. Bot. 41: 348. 1963

B. sphaerosperma Buchw. *in* K. Vet.-og Landbohøjsk. Aarsskr. 1949: 137. 1949, conidial state of *Botryotinia sphaerosperma* (Gregory) Buchw. *in* K. Vet.-og Landbohøjsk. Aarsskr. 1949: 137. 1949

B. squamosa Walker *in* Phytopathology, 15: 710. 1925, conidial state of *Botryotinia squamosa* Viennot-Bourgin *in* Annls Epiphyt. 4: 38. 1953

B. tulipae Lind, Danish fungi 650. 1913 = *Botrytis parasitica* Cavara, sclerotial state of *Sclerotium tulipae* Lib., = *Botrytis tulipae* (Lib.) Hopkins

Hennebert excluded these species, which are frequently encountered in early literature: *B. carnea, B. crystallina, B. dichotoma, B. epigaea, B. fulva, B. luteo-brunnea, B. spectabilis,* and *B. terrestris.*

Other species that are probably valid, although not yet revised by Hennebert, are:

B. anthophila Bond. *in* Notes of the Seed-Testing Station, St. Petersburg 1914

B. convallariae (Kleb.) Ondrej *in* Biologia (Bratisl.) 27: 23. 1972

B. spermophila, conidial state of *Botryotinia spermophila* Noble *in* Trans. Br. Mycol. Soc. 30: 48. 1948

Doubtful species are *B. anacardii, B. artocarpi, B. cana, B. canescens, B. douglasii, B. furcata, B. gladioli, B. grisea, B. infestans, B. liliorum, B. lini, B. mali, B. plebeja, B. trifolii, B. verrucosa, B. vulgaris,* and *Botryotinia theae.*

The microconidial (spermatial) state is referred to *Myrioconium* H. Sydow and the sclerotial state to *Sclerotium* Pers.

The basis for classification

Hennebert (1973) adopted Hughes' (1953) system of Hyphomycete classification based on conidiogenesis and both placed *Botrytis* in Hughes' section IB, in which the conidia are produced by budding synchronously from denticles on a well-differentiated swollen sporogenous cell, the ampulla (Klebahn 1930; Whetzel and Drayton 1932; and Hughes 1953). Barron (1968) placed it in his series Botryoblastosporae (equivalent to Hughes' section IB), which is characterized by the production of botryoblastospores.

Barron emphasized that the ampulla in the Botryoblastosporae is distinct from the similar swelling in some genera of his series Sympodulisporae; the ampulla is formed before spore production, not, for example, as the result of successive spore formation as in *Arthrobotrys* spp.

Botrytis forms part of the Torulaceae of Subramanian (1962) and the Blastosporae of Tubaki (1963). In Ellis' (1971) terminology, the conidiophores are macronematous, acroauxic, and determinate; and the formation of conidia is holoblastic and integrated and both inner and outer walls of the conidiogenous cell contribute to the formation of the conidium on a pedicel in a blowing-out process.

After the release of the conidia, the ampulla collapses characteristically in concertina-like folds about well-marked septa, especially obvious in *B. squamosa* (Walker 1925; Viennot-Bourgin 1953), *B. globosa* (Raabe 1938; Webster and Jarvis 1951), and *B. ficariarum* (Hennebert and Groves 1963). This characteristic collapse of the ampulla is also figured in Klebahn's (1930) drawing of his *B. cinerea* f. *douglasii,* which both he and Zederbauer (1906) regarded as close to, or identical with, *B. cinerea.* After abscission a flat, rounded scar is left on the conidiogenous cell from which new conidiophores may proliferate. A slight frill is left on the conidium after its abscission.

Numerical taxonomy

The genus *Botrytis* has been subject to a numerical taxonomic study (Morgan 1971*a*, 1971*b*). Applying two biometrical methods to the *B. cinerea* complex and using 107 quantitatively expressed characters in 33 isolates, Morgan concluded that the taxon is a complex of races, identifiable mainly on cultural characters, but none of the races is sufficiently distinct to warrant a new taxon. This conclusion agrees with the general conclusions of Menzinger (1966*a*, 1966*b*), Hennebert (1971), and Vanev (1972) that cultural characters can be manipulated to some extent, and have little value in differentiating races in *B. cinerea.* However, in an analysis of 12 taxa, Morgan (1971*b*) was able to recognize two forms of *B. cinerea*; Type A was characterized by gray colonies, abundant spore production, and sparse or no sclerotia, and Type B colonies were cream or white on arabinose, raffinose, or sorbose media, with sclerotial production favored at the expense of conidia.

Of the 12 taxa, Morgan (1971*b*) was able to distinguish *B. hyacinthi* from both *B. narcissicola* and *B. tulipae*, which Brierley (1931) had suggested were conspecific; and Morgan also distinguished *B. allii (B. aclada), B. byssoidea, B. cinerea* (types A and B), *B. fabae, B. paeoniae, B. polyblastis,* and *B. squamosa.* Though Morgan produced a key that differentiates *B. anthopila* from *B. spermophila,* the two species were sufficiently closely linked in the numerical taxonomy to suggest conspecificity. The relationships between imperfect species were not altered by considering also characters of the relevant perfect stages.

Biochemical differentiation

Lilly (1963) grouped a number of fungi by their ability to utilize sorbose; *B. cinerea* utilized it, whereas *Sclerotinia (Whetzelinia) sclerotiorum* did not. Maas and Powelson (1972) found that *B. convoluta* also could not readily utilize sorbose and they suggested on this basis that *B. convoluta* had a greater phylogenetic affinity with *W. sclerotiorum* than with *B. cinerea.* Similarly, Maas and Powelson contrasted the poor utilization of lactose by *B. convoluta* with lactose utilization by *B. cinerea* (Townsend 1957) and the uniqueness of *B. convoluta* in producing a firm rather than a soft rot of *Iris* rhizomes.

Variability

Menzinger (1966*a*, 1966*b*) reviewed the taxonomy of *Botrytis* species and in 12 species and 2 isolates — one of the *B. allii (B. aclada)* type and one of the *B. cinerea* type — showed how cultural conditions could considerably modify taxonomic characters. Thus, for example, 7 species and 1 isolate were induced to form multiseptate conidia. This condition in *B. allii (B. aclada)* must cast considerable doubt on the validity of *B. septospora* from onion described by El-Helaly, Elarosi, Assawah, and Kilani (1962). Menzinger similarly considered the dimension and shape of conidia and the characters of mycelia and sclerotia to be of doubtful value in taxonomy because of variation between cultural conditions; he also found difficulty in reconciling characters of the species studied by him with their original diagnoses.

Vanev (1972) also manipulated conidial size and form and colony characters by altering the temperature and culture medium and found morphological changes to be reversible.

SEXUAL REPRODUCTION

Until 1929, the sexual process in the Sclerotiniaceae had been obscure and the genetic connection between *Botryotinia* spp. and *Botrytis* spp. had not been demonstrated (Buchwald 1949). De Bary (1884) and Brierley (1918*b*) had considered the microconidia as true spores with no sexual function, but Whetzel (1929) suggested their role as spermatia, as in the rusts. Drayton (1932, 1934) finally demonstrated this role in the sexual mechanism of *Stromatinia gladioli* of the family Sclerotiniaceae. He speculated that the gelatinous, water-soluble matrix of the microconidial sporodochia would permit the water- or animal-borne transport of microconidia to the receptive bodies on host debris and so achieve 'spermatization', the process leading to the formation of apothecia.

As a result of Drayton's work, the sexual status of *Botryotinia* species was determined. Groves and Drayton (1939) obtained apothecia from isolates of *Botrytis* of the *cinerea* type by adding microconidia to sclerotia or

to sterilized soil placed over sclerotia, but they did not attempt to equate the apothecial state with *Botryotinia fuckeliana* because of the then uncertain identity of de Bary's *Peziza fuckeliana.* Groves and Loveland (1953) investigated the situation again and found that single ascospore cultures are self-sterile and show the bipolar type of mating behavior of *Stromatinia gladioli* (Drayton 1934). Successful crosses were made between 9 single ascospore isolates from apple, potato, and celery in Canada, and also between these and 2 isolates of *Botrytis cinerea* from grapevine in Switzerland, the site of de Bary's original collection. In all cases, apothecia were morphologically similar to de Bary's *Peziza fuckeliana* and single ascospores gave rise to typical fructifications of *Botrytis cinerea.* The connection between *Botryotinia fuckeliana* and Botrytis *cinerea* was thus established. Sidorova (1972), however, failed to obtain apothecia of *Botryotinia fuckeliana* from isolates collected in different parts of the USSR.

Drayton (1937) obtained the perfect stage of *Botrytis convoluta* by spermatization; Buchwald (1953) and Webster (1954) that of *B. globosa;* Elliott (1964) that of *B. porri;* Bergquist and Lorbeer (1968, 1972) that of *B. squamosa;* Drayton and Groves (1952) that of *Botrytis narcissicola* (designated *Stromatinia narcissi*); and Hennebert and Groves (1963) those of *B. ranunculi* and *B. ficariarum.* According to Hennebert (unpublished), *B. globosa* and *B. porri* are homothallic, *B. ranunculi* is hermaphroditic and self-fertile, and *B. ficariarum* is probably heterothallic.

Bergquist and Lorbeer (1972) showed that compatibility in *B. squamosa* is controlled by a single locus with two alleles. Wild types were hermaphroditic, self-sterile, and cross-fertile, and interspecific crosses between *B. squamosa* and *B. fuckeliana* were unsuccessful.

Apothecial and ascus formation in *Botryotinia fuckeliana* was described by Kharbush (1927). In the young hymenium, somewhat elongated binucleate cells arise from the anastomosis of the tips of hyphae and are cut off by a wall. Each of the two nuclei of each cell of this ascogenous hypha has a distinct membrane, nucleolus, and chromatin; at this stage, the cell elongates among the paraphyses and swells. When the young ascus has attained the length of the paraphyses, the nuclei fuse and almost immediately meiosis begins; Kharbush saw 2 chromosomes at each pole in anaphase. According to Kharbush two mitotic divisions then result in 8 nuclei, around which the cytoplasm is differentiated into biguttulate ascospores. The nucleus of each ascospore usually undergoes further division and the spores are thus binucleate. Istvanffi (1905) found ascospores to be usually 1-nucleate, however, and only occasional large spores were 2- or 3-nucleate.

Kharbush found no ascogenous hyphae such as occur in *Stromatinia gladioli* (Drayton 1934). The dicaryon phase is very brief and limited to the period of cell fusion as the asci are initiated.

Microconidia in the Sclerotiniaceae are typically uninucleate, as are the terminal and subterminal cells of the phialide (Berthet 1964).

Cytology in the Discomycetes was reviewed by Bellemère (1969).

PART 3 FORM AND FUNCTION

ANATOMY AND MORPHOLOGY

Mycelium

The morphology and anatomy of the thallus of *Botrytis* spp., described by Istvanffi (1905) and Beavérie and Guilliermond (1903), are undistinguished and typical of the Ascomycetes. Some caution is required in reading the second paper as it includes one sterile form, known as 'toile', which was later shown to have probably been a species of *Rhizoctonia (Corticum vagum* var. *ambiguum)* (Baldacci 1937; Baldacci and Cabrini 1939). Anastomoses between hyphae have often been noted and their significance is discussed in "Cytology" in PART 3.

The pattern of hyphal growth and branching, regular for the Ascomycetes, was described by Smith (1924). Extension occurs at the hyphal apex and, from spore germination, the growth rate increases with time until a constant rate is reached. Branches arise some distance behind the apex. As in other septate fungi, aggregations of vesicles, "spitzenkörper", occur just behind the hyphal apex in *B. cinerea* (McClure, Park, and Robinson 1968). These bodies appear to be formed posteriorly and migrate to the apex of the hypha, where they fuse with the plasma membrane and liberate their contents as part of the growth process of the cell wall. They are stained with cationic dyes such as methyl green.

'Microbodies' in hyphae of *B. cinerea* were described by Maxwell, Maxwell, Hoch, and Armentrout (1973). Septa are frequent and are perforated by a simple pore. Intrahyphal hyphae may be seen frequently traversing old, empty hyphal cells (Istvanffi 1905) through this pore; the intrahyphal hyphae may bear microconidiophores (Brierley 1918).

In culture on defined media, the thallus of some species of *Botrytis* is sufficiently distinct to be of assistance in identification (Hennebert 1971): *Botrytis anthophila* and *Botryotinia spermophila* usually produce a slow-growing, immersed, and arborescent mycelium; *B. porri* has a gray radiate mycelium; *B. calthae* has a brownish prostrate colony; *B. ficariarum* has a creamy-white colony. Because all species can be induced to sporulate by manipulating the cultural conditions, taxonomy, even of the so-called sterile forms, does not depend on mycelial characters.

Conidiophores and conidia

The conidiophores of all species of *Botrytis,* except *B. spermophila* and *B. anthophila,* are tall, stout, dark-colored, and irregularly or dichotomously

branched. The conidiophores of some species — for example, *Botrytis cinerea* and *B. ficariarum* — have a globose basal cell (Massenot 1958; Hennebert 1973). Near the apex of each conidiophore are produced a number of short, dark, septate sporogenous branches, each with a terminal ampulla on which conidia develop synchronously on short, fine denticles. At intervals along the conidiophore, botryose clusters of conidia are often formed from short side branches that bear sporogenous cells, giving the appearance of nodal areas of sporulation. The conidia are hyaline or pigmented, ellipsoid-obovoid-globoid, usually continuous, and sometimes 1–3 septate (Ellis 1971; Hennebert 1973). The conidia are smooth, although Massenot (1958) showed verrucose conidia in dry mounts of *B. tulipae.* Conidia germinate in nutrient solutions, but less readily in water, to form (usually) 1–5 germ tubes.

Mason (1933, 1937) proposed the term radulaspores, originally for the spores borne directly on the ascospores of *Nectria coryli,* and applied it to the synchronously produced conidia of *B. cinerea.* Because the radulaspores of *N. coryli* are homologues of phialospores, the name cannot be applied to the conidia of *B. cinerea* (Hughes 1953). McCallan (1958) described the conidium of *B. cinerea* as a prolate spheroid and, in relation to fungicide studies, he calculated its volume from its dimensions (11.7 × 9.3 μm; 6–15 × 1–12 μm) to be 556 μm^3, with a density factor of 1.1.

In all species, but conspicuously in *B. squamosa* and *B. globosa* (Walker 1925; Raabe 1938; and Webster and Jarvis 1951), the terminal branches of the conidiophore collapse in accordion-like folds on spore release. Klebahn (1930) portrayed this, without comment, in *B. douglasii (B. cinerea).*

In the context of susceptibility to fungicides, Fisher and Richmond (1969), Fisher, Holloway, and Richmond (1972), and Richmond and Somers (1972) investigated the nature of the hydrophobic surface of conidia of *Botrytis fabae.* They found lipids on the surface with component fatty acids predominantly straight-chain, $C_{23:0}$ and $C_{23:1}$, but surface hydrocarbons were almost entirely *n*-alkanes, C_{20}, C_{21}, and C_{22}. Most species of *Botrytis* have hydrophobic conidia, although their surface structure has not been investigated.

Microconidia

The hydrophilic microconidia, which occur in all species, are phialospores. Because they differ only slightly between species, they are of no taxonomic value. Phialides may occur on any part of the thallus, sometimes within old, empty hyphal cells, or directly from germinating macroconidia (Istvanffi 1905; Beavérie and Guilliermond 1903; Brierley 1918*b*; Hino 1929; Drayton 1932, 1937; Groves and Drayton 1939; Arnaud and Berthelet 1936; Berthet 1964; and Sidorova 1972). Phialides are more usually formed, however, in what Whetzel (1945) termed spermodochia: fasciculate or tuberculate aggregations of branched spermatiophores, usually arising from single hyphal cells

and borne freely on the aerial mycelium. The spermodochia usually comprise one or two series of globose metulae, bi- or tri-furcate; the terminal metula is somewhat shorter and more slender, bearing up to about 5 phialides (Hennebert and Groves 1963; Hennebert 1973). The phialides have collarettes (Brierley 1918*b*; Arnaud and Barthelet 1936; and Berthet 1964). The whole structure is white in mass and the globose microconidia (spermidia of Whetzel 1945; spermatia of Hennebert 1973) are hyaline, unicellular, 2–3 μm, and have a conspicuous lipid droplet. They are developed in chains and embedded in mucilage.

Brierley (1918*b*) found that microconidial production was primarily a function of thallus age; relative humidity, light, temperature, and nutrition had little effect.

De Bary (1884) and Brierley (1918*b*) thought that microconidia functioned as true spores; indeed, Brierley claimed to have germinated them in water and in a nutrient broth to give a normal mycelium, although Istvanffi (1905) and Hino (1929) found them very difficult to germinate in vitro. Now, their sole function is believed to be one of spermatization; see "Sexual Reproduction" in PART 2.

Chlamydospores

Price (1911) and Brierley (1918*b*) described chlamydospore-like bodies in cultures of *Botrytis cinerea.* They are thick-walled, larger than macroconidia (35–71 μm, mostly 60–70 μm in diameter) near the surface of the stroma, and are produced on separate hyphae that project from the surface of the sclerotium. They are usually terminal but sometimes intercalary. No germination was observed. Park (1954) obtained chlamydospores of *B. cinerea* in drops of distilled water and soil solutions when spore concentrations were high. They have a distinct double wall and dense contents. Ramazanova (1958*b*) described chlamydospores and gemmae as well as sclerotia in *B. anthophila.*

Oidia

Istvanffi (1905) and Brierley (1918*b*) described globose oidia of *B. cinerea* formed by the fragmentation of hyphae in distilled water. These oidia were similar to the chlamydospores obtained by Park (1954).

Haustoria

Only in one host–parasite combination are haustoria known — that of the clover anther mold, *B. anthophila* (Silow 1933).

Appressoria

Appressoria, essentially infection structures, are formed by the dichotomous branching of germ tube and hyphal tips, apparently in response to a contact stimulus (Istvanffi 1905; Pfaff 1925; and Blackman and Welsford 1916). Their function is more fully described in "Infection" in PART 4.

Organs of attachment

When, for example, a grape berry is attacked by a mycelium established in its neighbor, well-developed organs of attachment are formed between the two (Istvanffi 1905). Initially, the organs of attachment resemble sclerotial initials and appressoria, formed by dichotomous branching of hyphae, but later they develop as more or less parallel series of dichotomously branching hyphae, with 1 or more series of branches. Eventually they form a fairly massive structure 1–2 mm in length. The tips of the hyphae, pressing against the cuticle of the healthy berry, swell somewhat, like appressoria, and penetration occurs.

Sclerotia

All species of *Botrytis* form sclerotia firmly attached to the substratum and their morphology is of some assistance in taxonomy. Although sclerotia of *Botryotinia porri* are large, 10–40 mm in diameter, and those of *Botrytis tulipae* and *B. galanthina* are less than 1 mm, it is doubtful whether species can be confidently divided into Microsclerotiophorae and Macrosclerotiophorae, with the dividing line at 2 mm, as proposed by Buchwald (1949). Sclerotia of *Botryotinia convoluta* are characteristically large and cerebriform, those of *B. ficariarum* are flat and clearly marginated, and those of *B. calthae* are brown and diffuse (Hennebert and Groves 1963). Sclerotia of the last two species are also anatomically distinct; those of *B. calthae* have a much more compact internal structure.

In culture, some species produce their sclerotia in characteristic patterns: *B. tulipae, B. hyacinthi, B. galanthina,* and *B. paeoniae* have equidistant sclerotia; *B. porri* produces sclerotia at the margin only. But because the arrangement of sclerotia can be manipulated to some extent by cultural conditions, this criterion is unsatisfactory.

The structure of the sclerotium has been described several times (de Bary 1884; Beauvérie and Guilliermond 1903; Istvanffi 1905; Reidemeister 1909; Townsend 1952, 1957; Townsend and Willetts 1954; Hennebert and Groves 1963; Willetts 1969, 1972; and Nonaka and Kaku 1973). Hyphal tips branch repeatedly and dichotomously; the branches have many septa and may also fuse to form the characteristic structure, which is at first hyaline but later turns brown or black because of deposition of melanic pigments in the outer rind (Brierley 1920; Willetts 1969).

In *Botrytis allii (B. aclada)* the sclerotium has a rind 6–8 cells thick, rounded, and thick-walled; a narrow cortex 3–4 cells thick, thin-walled and pseudoparenchymatous, with dense contents of stored materials; and a large central medulla of filamentous hyphae loosely arranged in a gelatinous matrix. The sclerotium of *B. cinerea* is similar but with a thinner rind and a thicker cortex (Townsend and Willetts 1954). The outer surface of the sclerotium of *B. cinerea* is composed of closely arranged, thick-walled hyphae with outward-projecting tips. A film covering most of the surface appears to be an accumulation of dried pigment (Willetts 1969).

Istvanffi (1905) distinguished 4 types of sclerotial development in *B. cinerea:* (i) from single sclerotial initials ('pelottes'); (ii) from a felted layer of closely packed, roughly parallel hyphae, beneath and raising the host cuticle; (iii) the same, containing a layer of pelottes; and (iv) from a layer of felted hyphae containing a random arrangement of pelottes. He also described small, conical pseudosclerotia in thickened hyphae, which later develop directly into conidiophores. Loosely arranged, thickened hyphae, lying beneath the cuticle in a single layer, comprised another resting structure. In the field, sclerotia germinate in one of three ways (Istvanffi 1905): (i) conidiophores arising within the medulla push singly through the rind; (ii) conidiophores arise in a tuft from a small stromatic cushion formed at the surface of the sclerotium; and (iii) after a resting period of 2–6 mo, the rind cracks open at any point to reveal the elongating stipe of an apothecium, and sometimes 2–6 apothecia arise from one sclerotium.

During germination, the sclerotial cells empty except those around the base of the conidiophores, or stipe; the hyphae collapse and the intercellular spaces become filled with air.

The ability of sclerotia to produce apothecia decreases with time; after 9–12 mo they are able to produce only sterile apothecia, but the conditions affecting whether or not sclerotia germinate, and how they germinate, have not been determined. In culture and after surface-sterilization, sclerotia give rise to vegetative mycelium. Sclerotia of *B. tulipae* were believed to germinate in this way in soil (Beaumont, Dillon Weston, and Wallace 1936), but Coley-Smith and Javed (1972) observed this only in sclerotia very close to tulip bulbs.

The most frequent mode of germination is conidiophore production. When mature, the sclerotia of *B. cinerea* can germinate over a wide range of temperatures (3–27°C) to form a succession of conidiophores for as long as 2 mo, and in the field they germinate mostly in the spring and autumn (Vanev 1966; Kublitskaya and Ryabtseva 1970). At 5°C, after exposure to near-ultraviolet light, sclerotia of *B. convoluta* gave rise to up to 6 crops of conidiophores until 75% of their original dry weight was expended (Jackson and Patrick 1969; Jackson 1972). Resporulation was dependent on re-exposure to ultraviolet light at 25°C but not at 5°C and it was suppressed by the continued presence of old conidia but not by that of old conidiophores alone. Sclerotia of *B. fabae* also give several crops of conidia (Yu 1945), but those of *B. tulipae* decay soon after the production of conidiophores in the winter and early spring (Coley-Smith and Javed 1972).

Some sclerotia of *B. cinerea,* however, do not give rise to conidiophores but in late summer germinate to form apothecia, which are viable for 20–30 days at 3°C, but only for 3 days at 23°C (Istvanffi 1905; Kublitskaya and Ryabtseva 1970).

Apothecia

During apothecial formation in *Botryotinia fuckeliana,* the generative hyphae grow through the cortex of the sclerotium (Istvanffi 1905; Kharbush 1927). A columnar structure, the stipe, forms and when it is about 4–5 mm long a hard cap develops, which differentiates into the apothecial disc. Sometimes the base of the stipe is invested in rhizoidal hyphae (Hennebert and Groves 1963). The apothecium is cupulate, stalked, and usually some shade of brown; the cup is infundibuliform to discoid and sometimes has a reflexed margin in age.

The anatomy of the apothecium has been described several times (see PART 2, "Taxonomy"), particularly well in the case of *Botryotinia calthae, B. ficariarium,* and *B. ranunculi* (Hennebert and Groves 1963). The apothecium comprises (Korf 1958, 1973) the hymenium, a palisade layer of asci with paraphyses of about the same length as asci; the hypothecium (subhymenium of some authors), a tightly arranged mass of hyphae below the hymenium; and the excipulum, which envelops the hypothecium and the margin of the hymenium. The excipulum is divided into two parts: the ectal excipulum forms the outer layers of the tissue, including the margin of the apothecium; and the medullary excipulum forms the layer between the ectal excipulum and the hypothecium. The terminology of the various tissue types is defined by Korf (1958, 1973).

The asci are unitunicate, inoperculate, and long clavate; the tip of each ascus is thickened with an apical pore-plug giving a positive blue reaction with iodine (J+).

The ascospores, 8 per ascus, are uniseriate, hyaline, unicellular, smooth, and obovoid-ellipsoid, sometimes asymetrically so (Istvanffi 1905). Sometimes more than 8 spores may be in the ascus and they may germinate there (Hennebert and Groves 1963). The paraphyses may be branched and, at the tip, clavate.

In a medium such as grape juice, the ascospores may germinate directly to form a conidiophore of the *Botrytis* type (Istvanffi 1905), but usually a mycelium is formed and eventually sclerotia and conidiophores (Kharbush 1927).

Ultrastructure

The ultrastructure of conidia of *Botrytis cinerea,* which was examined by Hawker and Hendy (1963), Buckley, Sjaholm, and Sommer (1965, 1966),

and Gull and Trinci (1971), seems similar to that of many other fungi. Dormant conidia of *Botrytis cinerea* have a 2-layered wall: a thin electron-dense outer layer and a thicker inner layer. The cytoplasm is typically multinucleate and contains numerous rodlike mitochondria. Short strands of endoplasmic reticulum appear to originate from the cytoplasmic membrane lining the cell wall; they are continuous with the mitochondrial and nuclear membranes and storage bodies, which suggests that they are involved in organelle development. At germination, some of the mitochondria appear cup-shaped and lobed; the strands of endoplasmic reticulum are much longer, more numerous, and often close to nuclei. The nuclei appear to divide early in germination. When the conidium germinates, 3 new layers appear between the original wall and the cytoplasm. The inner two of these are continuous round the cytoplasm; the third is formed only near the point of germ tube emergence and is continuous with the germ tube wall. The original wall thickness would be expected to decrease as it stretches during spore swelling at germination, but the formation of new layers increases wall thickness from about 260 nm to 340 nm.

The outer cell wall ruptures as the germ tube emerges. The contents of the conidium, leaving behind large vacuoles, flow into the germ tube, whose wall is elastic and invested by a mucilaginous sheath. An apical corpuscle appears in the germ tube and a cross wall is laid down near the base.

The wall of the dormant conidium of *B. fabae* is unornamented and consists of microfibrils in a granular matrix in 2 distinct but similar layers; branched invaginations of the plasmalemma are a distinctive feature (Richmond and Pring 1971*a*). On germination, the ramifications are reduced as the conidia swell and they disappear after the germ tube is formed. Three different types of particles are present on the inner surface of the plasmalemma and the mitochondria have dense spherical inclusions, not previously known in fungi, which disappear when germination begins, as do glycogen particles.

The endoplasmic reticulum, which appears as short strands associated with the cell wall in the dormant conidium, increases on germination and multiple strands surround the nuclei. Vesicles pass through the plasmalemma to form simple vesicular lomasomes and, by a similar process, complex tubular lomasomes form in young hyphae. Prevacuoles become vacuoles and an apical corpuscle appears in the germ tube. No Golgi apparatus is known. The fungicide benomyl interferes with ultrastructure and development of the cell wall in *B. fabae* (Richmond and Pring 1971*b*); the germ tube is swollen and distorted and much branched.

The structure of the hyphal wall of *Botrytis narcissicola* was investigated by Jones, Farmer, Bacon, and Wilson (1972). X-ray powder data indicated the presence of chitin and the infrared spectrum indicated that of β-(1–3) glucan; hydrolysates included glucose and mannose. A glucan constituent, sclerotan, was found in *B. cinerea* and *B. tulipae* as well as in *B. narcissicola*. Electron microscopy showed microfibrils on the inner surface of the hyphal wall and on the septum, which is perforated by a central pore bounded by a thick rim.

The ultrastructure of hyphae of *B. fabae* invading tissues of *Vicia faba* and the ultrastructure of the invaded tissue were described by Abu-Zinada, Cobb, and Boulter (1973). Growth of the fungus was restricted (see PART 4, "Quiescent Infections"). The only difference between hyphae outside and inside the host was the somewhat less dense cytoplasm of the invading hyphae. Numerous lomasome-like structures were formed at the junction between the fungus and host; Abu-Zinada et al. suggested that these might be the sites of hydrolytic, cell-wall-disrupting enzymes. Incubating the fungal mycelium in an extract of infected leaves resulted in considerable disorganization of fungal ultrastructure; thus these enzymes perhaps form the basis of the lesion-restricting mechanism.

CYTOLOGY

The vegetative cells and asexual conidia of *Botrytis* species may be heterokaryotic, and the hyphal cells, with a few exceptions, are multinucleate (Menzinger 1965, 1966*a*, 1966*b*). As many as 120 nuclei per cell have been recorded in an isolate of *B. cinerea,* whereas uninucleate hyphal cells were found in *B. allii (B. aclada), B. cinerea, B. convoluta,* and *B. narcissicola.* Between these extremes, Menzinger (1965) found an average of 2 to nearly 50 nuclei in hyphal cells and up to 20 nuclei in single-celled and multi-celled conidia, although there was no correlation between the number of nuclei per cell and conidium size. Welsford (1916) had earlier noted the tendency of nuclei in rapidly growing hyphae of *B. cinerea* to be associated in pairs, termed conjugate nuclei. The tendency was less obvious in hyphae growing in water and in *Vicia faba* leaves, and Welsford thought that nuclear divisions in well-nourished hyphae were so rapid that the nuclei did not have time to separate widely before undergoing mitosis again. Menzinger (1965) found nuclei of all shapes, the shape apparently depending on the rate of cell growth.

Menzinger (1965) found that the number of nuclei varied from cell to cell in the same thallus; nuclei were most numerous in the sporogenous ampullae and terminal cells of the hyphae, but markedly less numerous in subterminal cells. The heterokaryotic condition was maintained by the transfer of nuclei across hyphal anastomoses, just as Köhler (1930) and Hansen and Smith (1932, 1935) had found, and Menzinger also observed the passage of nuclei from cell to cell through the septal pore.

Heterokaryosis was intensively studied by Hansen and Smith (1932*a*, 1932*b*, 1934, 1935) and Hansen (1938) as a source of variability in *Botrytis* spp. Köhler (1930) had earlier observed contact between hyphae of *B. allii (B. aclada)* and *B. narcissicola*, but it is doubtful that transfer of nuclei occurred. Hansen and Smith (1932*a*, 1932*b*) obtained 47 isolates of the *B. cinerea* type, from each of which subcultures were repeatedly made by single-conidium transfers. After many such transfers, there was a wide range of morphologically distinct strains in culture. Some strains remained similar

to the parent strain throughout subculturing and were termed homotypes. Other strains continued to produce homotypes and further inconstant heterotypes. Anastomoses were common; hyphal cells and conidia were multinucleate, the number of nuclei ranging from 6 to 18 per cell in one homotype and from 3 to 9 in another. Hansen and Smith (1932*b*) considered that such cells could act as heterokaryotic propagules.

Hansen and Smith (1934, 1935) also noted occasional anastomoses in co-culture between the hyphae of two distinct species, *B. allii (B. aclada)* and *B. ricini*. The fungi were first passed through several subcultures to obtain uniformity and then spores from them were mixed to give 20 co-cultures: 6 *B. allii* type, 9 *B. ricini* type, and 5 different types, intermediate between *B. allii* and *B. ricini,* though more resembling *B. ricini*. From 1 of these 5 intermediate types, 20 subcultures were made, all of which were unlike *B. allii* and *B. ricini*. Hansen and Smith considered that they had established new homogenic forms that were stable and distinct enough to be regarded as new varieties or even as new species. They suggested that the production of aberrant homotypes resulted from gene changes in *B. ricini* brought about by the association of nuclei of *B. allii* in interspecific anastomoses, rather than from the combination of homogenic nuclei.

Hansen (1938) applied similar methods to an analysis of the dual phenomenon in *B. cinerea,* the condition in which the fungus is made up of 2 culturally different elements. He showed that a strain, stable in producing mainly mycelium in culture, mixed with a stable, predominantly sporing culture, formed cultures of intermediate character. The cultures formed varied in appearance from almost the mycelial type to almost the sporing type, and subcultures gave mycelial, sporing, and again intermediate types. Of 309 isolates of *B. cinerea,* 144 showed this dual phenomenon, which Hansen regarded as the normal condition. He regarded certain reactions, such as sectoring, reversion, and loss of ability to sporulate, as resulting from a change to the homotype condition.

Menzinger (1966*b*), also using single-conidium cultures of several species of *Botrytis,* confirmed the results of Hansen and Smith (1934, 1935) in their studies of co-cultures and showed that anastomoses often occurred between species and between isolates of the same species. However, only once was a morphologically distinct and stable intermediate type obtained; it was from a co-culture of two isolates of *B. cinerea* from *Gloxinia.*

Lauber (1971) obtained a number of strains from single-conidium selections of *B. cinerea* over six subcultures; they were differentiated by several physiological characters such as growth on nutrient agars and in soil, tolerance for actidione, and production of citric acid. He concluded that his original five wild isolates were genetically heterogeneous and heterokaryotic.

VARIANTS

It has long been recognized that *Botrytis* spp. in culture can be divided into 3 types — mycelial, sporulating, and sclerotial — although the division is often not clear. This division has led to considerable taxonomic confusion (Killian 1926) because later work has demonstrated the fallibility of using cultural characteristics as taxonomic criteria.

Only one case is known of a clearly distinct morphological race: an isolate of *B. cinerea* from *Crassula perforata,* apparently lacking a phenolic oxidase system, had white sclerotia, but was otherwise of typical form and equally as pathogenic as normal black-sclerotial isolates (Brierley 1920).

Most other workers have found morphological characters in culture to vary with environmental and nutritional conditions; for example, Vanev (1972) and Shidla (1972*a*, 1972*b*) found that conidia in *B. cinerea, B. paeoniae, B. tulipae,* and *B. gladiolorum* differed in size between a given host and culture, and differed again in size when re-isolated from artificially infected hosts. Some other workers, perhaps because they worked with relatively few isolates, have persisted in recognizing distinct morphological races. Thus, Berkeley (1924) found 4 morphologically distinct races of *B. cinerea* isolated respectively from geranium, squash, sunflower, and hemp; and Jorgensen and Weber (1929) found another on raspberry, which did not sporulate in culture. Abdel-Salem (1934) isolated 2 forms of *B. cinerea* from lettuce, which formed in culture predominantly either sclerotia or conidia. Those that formed conidia could be further divided on the basis of conidial shape and size: type A conidia were obovoid-oblong, measuring 11.1 × 7.25 μm and type B were more round, 9.7 × 8.0 μm. Similarly, Gupta (1960) found morphological, cultural, and physiological differences between isolates from *Dolichos lablab* and *Tagetes patula;* conidia from *D. lablab* were numerous, subglobose, and 7–10 × 6–9 μm and the sclerotia were large, hard, and black, whereas the conidia from *T. patula* measured 9–12 × 7–9 μm and the sclerotia were smaller, soft, and dark gray. Gupta also found physiological differences, principally in their production of pectinases. Nyeste (1960) found similar differences in polygalacturonase activity among isolates of *B. cinerea.*

Another form, apparently of *B. cinerea,* occurred on kenaf, *Hibiscus cannabinus,* in Peru and Florida (Perez and Summers 1963). This form was considered to differ from *B. cinerea* and *B. hortensis* previously reported on *H. esculentus.*

Saponaro (1953) concluded that isolates of *B. cinerea* from grapevine in different parts of Italy could be divided by conidial size in vitro into 7 morphological races; Pesante (1947), Kublitskaya and Ryabtseva (1969), Kublitskaya and Rubitskaya (1969), and Gorlenko and Manturovskaya (1971) came to a similar conclusion. Courtillot, Lamarque, Juffin, and Rapilly (1973) also found differences in the morphology of conidia, microconidia, and scle-

rotia, and in conidial germination and temperature relations among isolates of *B. cinerea* from different regions of France.

Nonaka and Morita (1967) recognized 8 sclerotial types among 80 isolates of *B. cinerea* from 56 host species, but 80% of them changed their type with temperature. The isolates had different temperature optima for growth; 79% of them grew best at 20°C, 6% at 15°C, and 15% at 25°C; most sporulated best at 10°C, and all were pathogenic to azalea petals and broad-bean leaves.

Heald and Sprague (1926), Morquer (1933), and Peyronel (1934) obtained isolates of *B. cinerea* that consistently produced a red pigment in agar.

Variability in *Botrytis anthophila* was noted by Ramazanova (1958*a*); isolates from 5 regions of the USSR showed morphological, cultural, and pathogenic differences. An isolate from Leningrad area was the most pathogenic to clover, and one from Bashkir the least. A variant that grew well on a potassium-deficient medium was more pathogenic than the isolate from which it was originally derived, and, moreover, retained its cultural characters on reisolation. Buderacka-Niechwiejczyk (1970) also recognized different forms of *B. anthophila* in culture.

When more isolates are studied or when cultural conditions are varied, it becomes evident that morphological forms are less easily distinguished. For example, Paul (1929) found that sclerotial formation by *B. cinerea* in culture was encouraged by lowering the temperature of incubation to 12°C, and by incubating in the dark or in high relative humidity. In richer media, sclerotial formation in the dark tended to occur at the edge of the petri dish, but because darkness was achieved by wrapping dishes in black paper, the effects of impeded gas and water vapor exchange cannot be excluded. On the other hand, sporulation was encouraged in illuminated cultures, at a temperature of 27°C, and at lower relative humidities. Despite being able to manipulate morphological characters in this way, Paul nevertheless recognized 3 types: mycelial, sclerotial, and sporulating. There were no distinct differences in conidial size among these types, but the sporulating races were generally slower-growing. The mycelial isolates were the most actively parasitic, as is to be expected if considered in the light of inoculum potential (q.v.), and the sclerotial isolates the least pathogenic. All types achieved the penetration of formalized gelatine membranes equally well, and Paul was unable to attribute differences in pathogenicity to differences in pectinase production.

Marked and consistent differences in pathogenicity between isolates of *B. cinerea* on stored cabbage were obtained by Yoder and Whalen (1973). Eleven isolates could be divided into 5 groups differing significantly in the rate at which they degraded wounded and unwounded tissue.

Barnes (1930, 1931) induced variation in *B. cinerea* by exposing conidia to sublethal heat before sowing on agar. Of 520 cultures from treated conidia, 424 failed to germinate, 20 grew indistinguishably from the check, 64 showed slight variation in growth, and 12 showed marked morphological variation.

Of the 12 with marked morphological variation, 4 were stable over 2 years: 1 produced many sclerotia and few conidia, 2 formed white mycelial colonies, and 1 was characterized by the production of microconidia that germinated readily; one subculture of the last variant produced some white sclerotia (cf Brierley 1920). The remaining 8 of the morphological variants slowly reverted to original type, including one with pink sclerotia, which perhaps represented an incomplete state in melanin pigmentation.

Owen, Walker, and Stahmann (1950) investigated the variability in onion neck-rot fungi. Wild-type isolates of *Botrytis allii (B. aclada)* and of *B. byssoidea,* sometimes suspected of being conspecific, caused similar symptoms, although *B. allii* sporulated more profusely. An atypical isolate of *B. allii,* obtained once from the wild, was induced to form morphologically distinct types in culture by treatment with the mutagen methyl-*bis* (β-chloroethyl) amine, but none resembled *B. byssoidea.* Similarly, wild-type forms of *B. allii* were induced to form mycelial types, but they soon reverted to the original type on subculturing. Owen et al. considered that they had failed to demonstrate that *B. allii* and *B. byssoidea* were conspecific, and concluded that these fungi, often confused on onion, were indeed separate species.

Bergquist and Lorbeer (1973) induced morphological mutants in *Botryotinia squamosa* by treating ascospores with N-methyl-N-nitro-N-nitrosoguanidine. Each form apparently carried several mutant genes that controlled production and pigmentation of sclerotia, formation of appressorial fans, compactness of colony growth, growth rate, sporulation, and tolerance for dichloran.

Lauber (1971), starting with five wild-type isolates, obtained a number of physiologically distinct lines and showed that conidial size, although closely related to the number of nuclei per conidium, also depended on the age of the culture, pH, C:N ratios and amounts in the medium, and relative humidity. He thus substantiated Menzinger's (1966*a*, 1966*b*) conclusions.

Adaptation to fungicides

Of profound importance in plant pathology is the special case of formation of physiologic races of *Botrytis* spp. adapted to fungicides.

Roy (1947) and Reavill (1950, 1954) were apparently the first to note that *Botrytis cinerea* could tolerate the presence of the chlorinated nitrobenzene group of fungicides in the vapor phase and could produce resistant strains in culture in their presence. Fungistasis, rather than fungicidal activity by these materials, was also demonstrated by Brook and Chesters (1957). Priest and Wood (1961) further investigated tolerance and the induction of resistant strains in *B. allii* growing in the presence of the vapor phase of some chlorinated nitrobenzenes. At first growth was very slow, the hyphae were distorted, and sporulation was reduced or suppressed, but eventually more rapidly growing strains appeared that more resembled the original strain and

that had apparently normal hyphae. The most resistant strain was that induced by 2,3,4,6-TCNB, followed in effectiveness by 2,3,5,6-TCNB, 2,3,4,5-TCNB, and PCNB. The strains resistant to TCNB and PCNB were also resistant in some degree to diiodo, dibromo, and dichloronitrobenzenes, to benzene, to 2,3,5,6-tetrachlonitroaniline, and to 2,6-dichloro-4-nitroaniline (dichloran). Resistant strains retained their resistance throughout subculturing for at least 18 mo and were as pathogenic to onion as the original strain.

Esuroso, Price, and Wood (1968, 1971) further investigated the effect of cultural conditions on the germination of conidia of *B. cinerea* in the presence of PCNB (quintozene), TCNB (tecnazene), and dichloran; and they analyzed the conidial population in resistant strains. About half the spores formed by resistant strains growing in the absence of fungicide produced resistant colonies when re-exposed to them, whereas all the viable spores of the same strains continuing to grow in the presence of the fungicide produced resistant colonies, although some of the spores failed to germinate.

The growth of dichloran-tolerant strains of *B. cinerea* was unaffected by dichloran at 2 g/litre in liquid media (Lankow 1971), and on solid media their growth was stimulated 60% by 0.1 g/litre and normal germ tubes were formed. Susceptible strains were inhibited by concentrations greater than 5×10^{-5} M; conidia germinated but the germ tubes disintegrated. Crystals appeared in hyphal tips and growth ceased within 5–10 min of exposure.

Parry and Wood (1958, 1959*a*, 1959*b*) demonstrated the ability of conidia of *B. cinerea* to germinate on agar media containing 300 ppm copper as sulfate, 0.375 ppm phenylmercuric acetate, 31 ppm thiram and similar concentrations of zineb, ziram, and nabam, 125 ppm ferbam (and up to 500 ppm in one case), and 250 ppm captan. The volume, and hence depth of agar in petri dishes, was critical in the initial stages of the adaptation process and spores germinated mainly at the edge of the agar. By taking successive subculture inocula from the edge of colonies the tolerated level of the fungicides was increased, for example, to 250,000 ppm captan and to 12 ppm phenylmercuric acetate, and the tolerance was maintained through several subcultures in the absence of the fungicide. The ability of these strains to survive selection pressures in the field was not tested.

Golyshin and Abelentsev (1973) noted synergistic effects in the adaptation of *B. cinerea* to zineb, zinc salicylanilide, and their mixture.

Kovacs and Garavini (1959) found that not only did *B. cinerea* tolerate the presence of some organic fungicides, but some, for example, captan and thiram, when in low concentration in agar, stimulated germination of conidia.

A race of *B. cinerea,* tolerant of the systemic fungicide benomyl, was isolated by Bollen and Scholten (1971) from *Cyclamen* sprayed 2 wk previously with 0.0625% benomyl, a rather high rate of application. Growth of this race was inhibited in vitro by benomyl at 1000 μg/ml; another isolate from unsprayed *Cyclamen* was inhibited at 0.5 μg/ml. The benomyl-tolerant isolate was also tolerant of methyl thiophanate, furidazol, and to a lesser

extent, thiabendazole. Its tolerance for benomyl was retained through 20 weeks of repeated subculturing in the absence of benomyl.

Bollen and Scholten (1971) and Dommelen and Bollen (1973) considered that the exceptional pathogenicity of the tolerant race on *Cyclamen* might also result in part from the inhibition of benomyl-sensitive antagonists. The tolerant strain grew rather slowly, and Bollen and Scholten questioned its ability to survive in the wild in the absence of benomyl, though this was not tested. Jarvis and Hargreaves (1973), however, isolated a strain of *B. cinerea* tolerant of 1000 ppm benomyl that had been applied to strawberry plants a year previously and also found a tolerant strain on raspberries some 50 m from a benomyl-treated crop. Ehrenhardt, Eichhorn, and Thate (1973) showed that the natural population of spores of *B. cinerea* in a vineyard had a wide range of tolerance for benomyl and they considered that continued exposure of the population to this and related materials would increase the proportion of tolerant isolates. Watson and Koons (1973) and Miller and Fletcher (1974) made similar observations on *B. cinerea* in greenhouse crops, and Jordan and Richmond (1974) in strawberries.

In general, benomyl-tolerant isolates of *B. cinerea* are susceptible to normal field concentrations of other unrelated fungicides (Jarvis, unpublished), but Jarvis and Slingsby (unpublished) obtained one from *Rosa* in Canada that was somewhat tolerant of captan, copper, ferbam, dyrene, and chlorothalonil, but not of dichloran or Dikar.

GROWTH

Effects of temperature

The effect of temperature on germinating conidia of *Botrytis cinerea* has been determined by a number of workers including Schneider-Orelli (1912) and Brooks and Cooley (1917) who recorded germination at 0°C on corn meal agar within 31 days, Doran (1922) who found a maximum temperature for germination of 26°C and a minimum temperature of 7°C, Brown (1922*c*) who obtained good germination at 5°C, and Hawker (1950) and Haas and Wennemuth (1962) who germinated spores between 1°C and 10°C (80% in 40 days and 95% in 14 days at the respective temperatures).

Brooks and Cooley (1917), Brown (1922*c*), Schneider-Orelli (1912), and Adair (1971), among many others, have data on the effect of temperature on mycelial growth in *B. cinerea.* The mycelium is able to grow at low temperatures; Schneider-Orelli (1912) recorded appreciable growth at 0°C on nutrient gelatine in 35 days. The growth rate is optimum at about 20–22°C and decreases markedly above 25°C. Similar results were obtained for *B. squamosa* by Stinson, Gage, and MacNaughton (1958) and Shoemaker and Lorbeer

(1971). Shiraishi, Fukutomi, and Akai (1970*a*) found a somewhat higher optimum temperature, 24–28°C, for mycelial growth of *B. cinerea* on potato sucrose agar, with a minimum of 0°C and a maximum of 35°C.

Hennebert and Gilles (1958) distinguished 2 optimum temperatures in early growth of *B. cinerea*. Spore germination, lasting about 5 h, had an optimum of 20°C, but after about 18 h, germ tube growth became dependent on external nutrients and the optimum temperature was then 30°C.

After growth of *B. cinerea* at the optimum temperature of 22°C to the point of incipient sporulation, Jarvis (unpublished) transferred cultures to other temperatures. The optimum temperature for sporulation from this point was 15°C; sporulation fell rapidly at higher and lower temperatures in contrast with the mycelial growth rate and was very slow at both 10°C and 24°C. Brooks and Cooley (1917) found that sporulation occurred at 5°C and 10°C within 10 to 31 days of inoculation of agar plates.

From field work, Jarvis (1962*b*) deduced that sporulation in a raspberry plantation did not occur to any appreciable extent at temperatures below about 12°C but could occur overnight in suitable conditions.

Shiraishi, Fukutomi, and Akai (1970*a*) studied synchronous conidial formation in cultures of *B. cinerea* at 24°C on potato sucrose agar and on a sponge matrix. Formation occurred about 3 days after inoculation of potato sucrose agar and within 24 h after transfer of a shake-culture inoculum to the sponge matrix.

The effects of temperature on sporulation of *B. tulipae* were defined by Yamada, Kajiwara, and Ozoe (1972).

Temperatures favoring mycelial production in *B. cinerea* generally depress sclerotial production and vice versa (Townsend 1952; Vanev 1966; and Kublitskaya and Ryabtseva 1972). Morotchkovski and Vitas (1939) gave 11–13°C as the optimum temperature range for sclerotial production in *B. cinerea* but 12–22°C for sporulation and 27–28°C for appressorium formation. Kochenko (1972) gave data on sclerotia; they germinated at temperatures above 2°C and the optimum temperature for germination was between 22°C and 24°C.

Effects of relative humidity

There have been many studies on the effect of relative humidity on the germination of fungal spores. The results, however, must be viewed with extreme caution, especially in atmospheres of relative humidities greater than 90%, because the usual limits of control in this type of experiment can easily permit the temperature to fall below the dew point, so that spores come to lie in condensate (Schein 1964).

Thus, Rippel (1930*b*) found 100% germination of conidia of *B. cinerea* and a *Botrytis* sp. at 20°C, 15°C, and 5°C in 100% RH when, almost cer-

tainly, the conidia must have been lying in condensate. There was complete germination of the *Botrytis* sp. at 95% RH, 80–85% germination at 90% RH, and none at 85% RH. At 95% RH, 80% of conidia of *B. cinerea* germinated at 15°C and 5°C and all germinated at 20°C; at 90% RH, 85% of conidia germinated at 20°C, and none at lower temperatures or lower humidities. Similarly, Ilieva (1970) claimed germination of conidia of *B. cinerea* in the absence of free water.

Snow (1949) concluded that conidia of *B. cinerea* require high levels of moisture for germination (93–100% RH) and Sirry (1957*a*) found that at 21°C, conidia of *B. allii (B. aclada), B. cinerea, B. fabae, B. tulipae,* and *B. squamosa* germinated at 100% RH, but not at 95% RH.

Yarwood (1950) found that the water content of conidia of *B. cinerea* was only 17% of their fresh weight but that a high proportion was 'hygroscopic water' when the conidia were on glass and in equilibrium with the laboratory air (42–51% RH). He thought that the hygroscopic water was probably much less active physiologically than the non-hygroscopic (total less hygroscopic) water. Imbibition of water is probably a prerequisite for germination; soon after their immersion in water, conidia of *B. cinerea* swell slightly, reaching a maximum in about 3 h (Ekundayo 1965). It is interesting to note that Snow (1949) found a lag period before conidia of *B. cinerea* (from cultures 1–2 mo old) germinated if they were applied dry to dry gelatine, and then equilibrated in atmospheres of different RH. At 100% RH, the lag was 1 day; at 95% and 93% RH 2 days, and at lower humidities germination did not occur. The lag phase may be interpreted as a period during which sufficient water is being imbibed from the atmosphere, or more likely from condensate.

Most species of *Botrytis* seem to sporulate best in less than saturated atmospheres; then, the conidiophores are short and bear numerous spores that are readily dispersed (Paul 1929; Hawker 1950). In a saturated atmosphere, however, the conidiophores are long, of indeterminate growth, and bear few conidia. Hopkins' (1921) method for inducing sporulation in *B. tulipae* in petri dishes, by partially uncovering cultures overnight to promote drying, seems applicable to all species.

Apothecia are usually produced in conditions that are cool and moist, but otherwise undefined (for example in *Botryotina convoluta,* Drayton 1937 and in *B. fuckeliana,* Kochenko 1972); certainly apothecia dry out rapidly in dry atmospheres and presumably stop discharging spores, as they do in *Whetzelinia sclerotiorum* (Jarvis, unpublished).

Effects of light

Light has different effects on various growth processes according to its wavelength and plane of polarization, although all species are able to germinate and grow in the dark (Reidemeister 1909; Doran 1922).

A snow mold, a *Botrytis* of the *cinerea* type (Sato, Shoji, and Ota 1959), perhaps adapted to the environment, grew better in the dark than in the light; red light depressed the mycelial growth rate of an isolate of *B. cinerea* (Rabinovitz-Sereni 1932), as did continuous, near-ultraviolet irradiation (Tan and Epton 1973). By contrast, orange light stimulated the germination of conidia in *B. cinerea* (Chebotarev, Lanetskii, and Naberezhnykh 1968; Zemlyanukhin 1973).

The absorption of energy by *B. cinerea* irradiated by visible and ultraviolet light was investigated by Zemlyanukhin and Chebotarev (1973).

The effect of light in enhancing sporulation of *Botrytis* spp. has long been known from the work of Reidemeister (1909), Paul (1929), Rabinovitz-Sereni (1932), and Harada, Takashima, Fujita, and Terui (1972). Usually, few conidia of *B. cinerea* are formed in the dark or in red light.

Harada, Takashima, Fujita, and Terui (1972) found that a 12-h dark cycle or continuous light promoted sporulation and suppressed sclerotial formation in *B. cinerea;* no sclerotia were formed in continuous light intensities exceeding 500 lx.

Page (1956) considered that the mycelial growth of *Botrytis squamosa* was arrested by light from incandescent and fluorescent sources and that concentric rings of sclerotia formed on Czapek agar were a sequel to alternating darkness and light. Stinson, Gage, and MacNaughton (1958), however, suspected that Page's results could be interpreted in terms of temperature effects and found that *B. squamosa* could withstand exposure to a light intensity of 100 ft-c for several days and to 250 ft-c for a few hours. Bjornsson (1956, 1959) noted a similar concentric ridging of mycelial growth in cultures of *B. gladiolorum* on potato dextrose agar at 21°C.

Beck and Vaughan (1949) found that *B. cinerea* parasitizing *Saintpaulia* sporulated profusely in conditions of low light intensity and Melchers (1926) noted that bright sunlight reduced sporulation of *B. cinerea* on geranium.

Beaumont, Dillon Weston, and Wallace (1936) exposed cultures of *B. tulipae* to sunlight to induce sporulation and Leach (1961, 1962), Leach and Tulloch (1972), Schlösser (1970), and Hite (1971, 1973*a*) found that near-ultraviolet radiation induced prolific sporulation in cultures of *B. cinerea,* in common with many other fungi; ever since, exposure to light, especially near-ultraviolet light, has become a standard practice for inducing sporulation in all species. Leach's technique was to illuminate cultures in Pyrex glass containers at 76–740 μWcm^{-2} and 21°C with light of wavelength 320–380 nm.

Tan and Epton (1973) found that infrared, red, and yellow light stimulated the sporulation of *B. cinerea* only slightly and blue and green light not at all. This contrasts with the blue light stimulation of sporulation in *B. gladiolorum* (Bjornsson 1956, 1959).

The photoreception system in *B. cinerea* was found by Tan and Epton to be extremely sensitive to near-ultraviolet light; a single exposure of 1 min

at 151 μWcm^{-2} in the most sensitive phase (the culture aged 4–5 days) was sufficient to induce sporulation but continuous irradiation was inhibitory. Like Pieris (1947), Tan and Epton found that the age of the culture is critical in the light response; cultures older than 10 days become unresponsive. The receptor system of *B. cinerea* evidently can receive blue light as well as near-ultraviolet and red light but Tan and Epton could not suggest what the system might be.

Tan and Epton (1974) next showed that the inhibition of sporulation by continuous irradiation in the wavelength range 300–420 nm is temporary and that the blue component is probably responsible because the sporulation response induced by near-ultraviolet is partially reversed by blue light. This reversal is nullified by further exposure to near-ultraviolet. They postulated the existence of the near-ultraviolet and blue photoreceptor mycochrome (Honda 1969) in *B. cinerea.*

Tan (1974*a*) next showed that 12 h after the sporulation response was induced by near-ultraviolet irradiation, blue light in an exposure of 15 min at 250 μWcm^{-2} gave 20% suppression of sporulation of *B. cinerea.* There were 2 phases of maximum sensitivity to blue-light inhibition of sporulation, one 12–16 h after induction by near-ultraviolet and the other at 20–24 h. The inhibition response reached a maximum at 60% inhibition of sporulation after 6 h of blue-light irradiation. Spore formation was arrested and dedifferentiation of conidiophores to sterile hyphae began.

Tan suggested that blue light might convert the M_B form (effective for sporulation) of the hypothetical mycochrome to M_{NUV}, the form that is not effective for sporulation but is effective in the formation of sterile, erect hyphae instead of conidiophores. M_{NUV} is converted back to M_B by near-ultraviolet light and by darkness. Blue-light inhibition of sporulation is repeatedly photoreversible (Tan 1974*b*), especially by red and far-red irradiation. This reaction suggested to Tan that phytochrome or some other pigment system was involved.

Hite (1973*b*) demonstrated the presence of a sporogenic substance — coded P310 because it has an absorption peak at 310 nm (Trione and Leach 1969) — only in sporulating mycelia and sporulating sclerotia of *B. cinerea* irradiated with near-ultraviolet light. P310 was absent from nonsporulating sclerotia despite near-ultraviolet irradiation.

Requirements for sclerotial production are generally the opposite of those for sporulation; regular diurnal light inhibits sclerotial formation in *B. cinerea* (Reidemeister 1909; Paul 1929; and Vanev 1966) and in *B. squamosa* (Page 1956), but a light stimulus was reported to be necessary in *B. gladiolorum* (Bjornsson 1956, 1959). Tan and Epton (1973) found that *B. cinerea* formed sclerotia in darkness, in yellow, red and infrared light, and when irradiated for less than 30 min with near-ultraviolet light.

Both visible and ultraviolet light affected the activity of various extracellular enzymes of *B. cinerea* (Zemlyanukhin and Chebotarev 1972).

Light is essential for the full development of the ascigerous disc in apothecia of *Botryotinia ricini* (Godfrey 1923) and of *B. squamosa* (Bergquist, Horst, and Lorbeer 1972; Bergquist and Lorbeer 1968, 1972) and other species probably also have this requirement, which is common in other genera of the family.

Phototropism

Negative phototropism was first noted in the germ tubes of a *Botrytis* sp. by Robinson (1914) and confirmed in those of *B. cinerea* by Gettkandt (1954) using daylight and incandescent lamps of about 200 lx as light sources and by Jarvis (1972) using near-ultraviolet fluorescent illumination. In all cases, the majority of germ tubes were oriented in the direction of incident light on gelatine or agar plates illuminated from the side. Only short-wavelength light is effective (Bünning and Etzold 1958; Jarvis 1972). Gettkandt could find no carotenoid pigment or other possible photoreceptive pigment in the spores or germ tubes, but Banbury (1959) thought that the photoreceptor riboflavin was probably present in the tips of the germ tubes of *B. cinerea.*

Positive phototropism was noted in the stipe of the apothecium of *Botryotinia ricini* by Godfrey (1923) and of *B. fuckeliana* by Gettkandt.

Jarvis (1972) found the conidiophores of *B. cinerea* to be positively phototropic when grown on a dilute soil extract agar plate, illuminated from the side by near-ultraviolet lamps to induce sporulation (Leach 1962). By rotating the plates through 45°, 90°, etc. in the same horizontal plane, the conidiophores could be induced to change direction, so that they continued to grow towards the light. Within a limited range of Wratten filters and with the same illumination, the maximum phototropic effect was obtained with the filter transmitting light of a wavelength around 420 nm, less effect around 440 nm and the least effect around 480 nm. No phototropism was found when the light passed green, yellow, orange, or red filters.

When conidia of *B. cinerea* were illuminated from vertically above with plane-polarized light, Bünning and Etzold (1958) found that the germ tubes were oriented parallel to the plane of polarization in either direction from the spore. Only short-wavelength light of less than 500 nm was effective. By turning the agar plates through 45°, the direction of growth of the young germ tubes could be changed.

Interposing a doubly-refracting polarizer between the conidia and the first polarizer gave light differing in wavelength by 225–230 nm and polarized in directions 45° apart and resulted in germ tubes growing perpendicular to the initial direction. These results led Bünning and Etzold to postulate that a yellow photoreceptive pigment is in doubly-refracting dichroic structures, probably near the cell membrane and this hypothesis received further support from Jaffe and Etzold (1962) studying the germination of conidia of *B. cinerea* in blue light of about 470 nm. They deduced that

the photoreceptors were highly dichroic and oriented anticlinally within the inner half of the cell wall. In plane-polarized light, the germ tubes emerge from the areas of maximum light absorption.

Nothing is known of the photoreceptive mechanism in the conidiophore of *Botrytis cinerea* or in the stipe of *Botryotinia fuckeliana* or of *B. ricini.*

B. cinerea in culture was killed by radiation of 5.6 m wavelength (Metlitski and Soboleva 1936) and 8–40 m and 5.2–10 m wavelengths (Treveskoy 1937) probably as the result of high temperatures induced in the substrate.

Effects of pH

Webb (1921) found that conidia of *Botrytis cinerea* germinated over a very wide range of pH, from 1.6 to 6.9 on mannite and from 2.0 to 9.8 on a sugar beet decoction; the optima ranged between 3.0 and 7.0 depending on the medium. At pH 2.1, germ tubes were abnormal in appearance and below this they began to disintegrate. Vanev (1965) gave the pH range for growth of *B. cinerea* as pH 2–8 (–8.5) with an optimum around 3–5. Sclerotia are formed best at pH 4 and not at all in alkaline media (Vanev 1966).

The pH changes induced by *B. cinerea* in culture depend on the medium; Weimer and Harter (1923) found an isolate to induce a final pH of 2.5 in a Czapek solution, but an alkaline reaction in a potato decoction.

Effect of age and nutrition

The germinability of conidia of *B. cinerea* depends in part on the age of the culture (Brown 1922*c*; Singh 1940). Conidia taken from very young cultures, perhaps when immature, and those taken from old cultures, perhaps when senescent, germinated relatively slowly while those from cultures of medium age (16 days) germinated fastest. A similar relation held for the rate of germ tube growth. The addition of an extract of lentils as an exogenous source of growth substances, including biotin and thiamine, considerably enhanced the germination and germ tube growth of young conidia. Conidia contained an endogenous source of growth substances if taken from a culture grown on a medium augmented with lentil extract and germinated better than those taken from a medium not so augmented (Singh 1940). Similarly, Shiraishi, Fukutomi, and Akai (1970*a*) were able to restore the germinative ability of aged conidia of *B. cinerea* by supplying them with mono-, oligo-, or polysaccharides at concentrations of the order of 10^{-2} M, or 10^{-3} M, but not 10^{-5} M. In decreasing order of effectiveness were glucose, fructose, sucrose, maltose, lactose, dextrin, inulin, and starch.

It has long been known that the germination of conidia of *Botrytis* spp. in infection drops is enhanced by the addition of plant extracts (Brooks

1908; Brown 1916, 1922*a*; Wilcoxon and McCallan 1934; Kovacs and Szeoke 1956; Kosuge and Hewitt 1964; among many others). Hawker (1950) distinguished between the effect of nutrients on germination and those on germ tube growth. Thus, for example, conidia of *B. cinerea* germinated more slowly in 3% malt extract or undiluted turnip extract than in water or dilute extracts, though the proportion germinating was higher and eventually the germ tubes were longer in the undiluted extracts.

Kosuge and Dutra (1962) found that the conidia of an isolate of *B. cinerea* germinated very poorly in water, but well in a medium containing L-serine, D-glucose, and sodium acetate, each at 0.002 M, and buffered at pH 5.2. Oxygen uptake during germination was enhanced in the medium when serine and aspartic acids, the main components of the free amino acid pool in ungerminated conidia, were readily metabolized. When the conidia were germinated in the presence of (^{14}C) bicarbonate, the labelled carbon appeared in aspartic acid and 2 other unidentified compounds.

Chou (1972) also failed to germinate conidia of *B. cinerea* in water, in solutions of aspartic or glutamic acids, or in solutions of growth substances (gibberellic acid, indole-3-acetic acid or kinetin). Solutions of more than 100 ppm glucose, fructose, or sucrose, however, permitted germination.

Sztejnberg and Blakeman (1973*a*) showed that the supply of necessary nutrients on beetroot leaves to germinating conidia of *B. cinerea* was probably controlled by the other epiphytic microflora, especially bacteria with copious polysaccharide sheaths, an effect simulated by nutrient-leaching treatments. Borecka and Millikan (1973) demonstrated that the presence of pollen grains of many species enhances the germination of spores of *B. cinerea*.

Botrytis cinerea can be grown in solutions of high osmotic pressure; Hawkins (1916) found it grew in solutions of 4.75×10^3 kNm^{-2} and Rippel (1933*a*) germinated conidia of *B. cinerea* and of a *Botrytis* sp. in 1.0 M, 1.3 M, and 1.96 M sucrose solutions (3.50×10^3, 6.66×10^3, and 1.03×10^4 kNm^{-2} respectively). There was a direct correlation between the rate of germination and osmotic pressure.

Another important factor in spore germination is spore concentration. Brown (1922*c*) and Schütt (1971*b*) found that the optimum concentration for germination varied with the isolate of *B. cinerea*; two of three isolates had an optimum concentration of 127×10^3 spores/ml, the third 65×10^3 spores/ml.

The sporulation of *B. fabae* in culture is promoted by relatively high concentrations of inorganic salts or very high concentrations of glucose (Leach and Moore 1966). This species does not sporulate on host leaves until they are almost desiccated, and Leach and Moore interpreted these results in terms of a high osmotic pressure requirement for sporulation.

Sporulation of *B. convoluta* was generally most profuse on media which supported maximum growth (Maas and Powelson 1972) and was inhibited by sorbose, glycine, or urea and on media lacking a carbon or nitrogen source.

The germination, growth, and sporulation of the specialized *Botryotinia ricini* was found by Orellana and Thomas (1964) to be considerably enhanced by the addition of 0.4% gallic acid and 1% glucose to the medium.

Sclerotial formation is also considerably influenced by nutrition and especially by the ratio of carbon to nitrogen supplied. Townsend (1957) recognized, however, that sclerotia of *B. cinerea* and of *B. allii* are initiated, develop, and mature in three distinct stages, each with a different set of nutritional requirements. A high carbohydrate and, to a lesser extent, a high nitrogen concentration favors sclerotium initiation, but the amounts permitting initiation do not always permit full maturation as judged by full pigmentation. This last stage does not begin until mycelial growth is checked by nutrients becoming unavailable or possibly by a qualitative change in metabolism. Thus when large numbers of sclerotia are initiated, some fail to mature. The fact that manipulation of the C:N ratio determines whether sclerotia or conidia are formed suggested to Hawker (1950) that the two types of growth are induced by different metabolic sequences.

Sclerotia of *B. cinerea* develop best on rich media in high relative humidity and in the dark (Reidemeister 1909; Paul 1929; Vanev 1966; and Harada, Takashima, Fujita, and Terui 1972), requirements opposite to those for sporulation. Pieris (1947) found that sclerotial formation by *B. cinerea* was favored by a high carbon:nitrogen ratio in the nutrients supplied. Townsend (1952) and Vanev (1966) confirmed this and showed that sclerotial production increased in proportion to the amount of sucrose supplied; glucose, fructose, or maltose were suitable substitutes for sucrose. Valaskova (1963*a*) also found a rich carbohydrate supply to favor sclerotial production by *B. tulipae.*

Staling

Hawker (1950) classified *Botrytis cinerea* as a non-staling organism because it does not produce concentric zones of poor or abnormal growth in cultures that result from the local accumulation of growth-inhibiting metabolites. It is, however, sensitive to the staling products of some other organisms, for example *Fusarium* spp. (Lutz 1909; Pratt 1924*a*, 1924*b*; and Boyle 1924). Inhibitors include potassium bicarbonate, fatty acids, and thermo-labile materials.

On the other hand, Hawker (1936) showed that culture liquids staled by prolonged growth of *B. cinerea* contain inositol, which stimulates sporulation in *Melanospora (Sordaria) destruens.*

Lahoz, Ballesteros, and Gonzalez (1971) demonstrated changes in polyol concentration in autolysing cultures of *B. cinerea.*

Other species of *Botrytis,* for example *B. squamosa,* form sclerotia in concentric rings in culture (Page 1956); this formation may result from

staling, but has been interpreted in terms of light and temperature effects (Stinson, Gage, and MacNaughton 1958).

Effects of volatile metabolites

When Carlile and Sellin (1963) placed conidia of *Botrytis cinerea* on cellophane over colonies of the fungus, germination was inhibited but proceeded normally when the fungus was removed. Germination was similarly inhibited by colonies of *Aspergillus niger, Penicillium notatum,* and *Chaetomium globosum.*

Dick and Hutchinson (1966) also noted inhibition of growth and sporulation of *B. cinerea* on cellophane when placed over cultures of 19 other fungi, 8 of which decreased sporulation by more than 25%. They attributed inhibition to the effects of volatile fungal metabolites but they also found 5 fungi that stimulated *B. cinerea* and 38 others that had no effect.

In fruit and vegetable stores, *B. cinerea* was sensitive to acetaldehyde, ethyl acetate, and other volatile metabolites (Aharoni and Stadelbacher 1973; Prasad, Stadelbacher, Shaw, and Aharoni 1973).

Effects of atmospheric gases and pollutants

Although Doran (1922) noted that conidia of *Botrytis cinerea* germinated better on the surface of water drops than in the interior and interpreted this in terms of oxygen supply, Brown (1922*c*) found that conidia of *B. cinerea* were relatively insensitive to a wide range of concentrations of oxygen. Follstad (1966) noted a decrease in mycelial growth rate with decreasing oxygen supply, and complete suppression of sporulation by concentrations below 1%. Similarly, Adair (1971) found that oxygen concentrations below 1.7% decreased the radial growth rate of *B. cinerea* on agar, and that gray mold rot in stored cabbage was adequately controlled in a concentration of 1.4%.

Wells and Uota (1969) found that mycelial growth of *B. cinerea* in a liquid medium decreased linearly with decreasing oxygen concentration below 4%.

Brown (1922*c*) found that the germination of spores of *B. cinerea* was inhibited at 20–30% CO_2 when in water, but a higher concentration, above 50%, was required to inhibit germination when in dilute turnip extract. Temperature and other physiological factors were also important in determining the effect of CO_2, and Brown concluded that the retarding effects of CO_2 are greatest when the energy of growth (sic) is lowest in unfavorable conditions for germination and growth. Wells and Uota obtained 90% inhibition of germination in 16% CO_2 at 19°C and Rippel and Heilmann (1930) found considerably enhanced growth of *Botrytis* sp. from sunflower

at increasing concentrations of CO_2 up to 0.1%; thereafter growth was increased only slightly by concentrations up to 1%.

The sporulation of *B. allii (B. aclada)* was retarded in an atmosphere of 2% CO_2 and 2% O_2 (Littlefield, Wankier, Salunkhe, and McGill 1966) and though the height of the aerial mycelium was reduced, the radial growth was unaffected. In 10.5% CO_2 and 2% O_2, sporulation was inhibited and growth retarded in height and radial extension.

When the partial pressure of oxygen was reduced by Wu and Salunkhe (1972) to 102 mm of mercury (about 0.13 bar) in a gas mixture of 2.7% O_2 and 97.3% N_2, mycelial growth of *B. aclada* was reduced to about 90% of the growth in a laboratory air atmosphere (646 mm of mercury), and the sporulation rating reduced from 8 to 7. At subatmospheric air pressures, growth and sporulation were progressively delayed and reduced at 278 mm and 102 mm, but not at 471 mm of mercury.

Of pollutants, ozone is fungistatic to *B. cinerea* in concentrations as low as 0.5 ppm, although very low concentrations stimulated germination of conidia (Magdycz 1972). A successful pilot attempt to use ozone in controlling gray mold in stored strawberries was made by Spalding (1966). Aerial mycelium was almost completely absent but stromatic tissue was formed in an atmosphere containing 2 ppm. On removal from the ozone, this tissue resumed growth. Magie (1960) also used ozone to control *B. gladiolorum* in picked *Gladiolus* flowers but Manning, Feder, and Perkins (1972) failed to control *B. cinerea* on poinsettia flowers and bracts with ozone.

Ozone at 100 and 50 ppm reduced the germination of conidia of *B. allii (B. aclada)* and colonies showed abnormal growth (Hibben and Stotzky 1969). There was little effect, however, on air-dried spores or on those suspended in liquid media.

An unusual effect was noted by Magdycz and Manning (1973): *B. cinerea* protected broad beans from ozone injury.

Although the effects of sulfur dioxide as an atmospheric pollutant on *Botrytis* spp. have not been investigated, SO_2 has been widely used to control gray mold in stored grapes, raspberries, strawberries, and black currants (Harvey and Pentzer 1960; Nelson 1973; Cappellini, Stretch, and Walton 1961; and Jarvis 1967). Couey and Uota (1961) found that the effectiveness of SO_2 in inhibiting conidial germination in *B. cinerea* increased with increasing relative humidity; at 96% RH a given concentration of SO_2 was 20 times more effective than at 75% RH. Between 0°C and 30°C, the Q_{10} value was 1.5. The reduction in percent germination was directly proportional to SO_2 concentration and to exposure time.

McCallan and Weedon (1940) compared the toxicities of SO_2, HCN, H_2S, Cl_2, and ammonia to the conidia, mycelium, and sclerotia of *B. cinerea* and of some other fungi. SO_2 and Cl_2 were the most toxic, H_2S and HCN the least toxic, and ammonia was intermediate.

Autotropism

When spores of *Botrytis cinerea* germinate close together in pairs, the germ tubes tend to emerge from adjacent areas and to grow towards each other. Jaffe (1966) analyzed many such pairs of spores germinating in a thin layer of Czapek-Dox broth in air, and termed the phenomenon autotropism. The majority of germ tubes emerged on the same side of a line joining the centers of adjacent spores, a *cis* arrangement, as opposed to the *trans* arrangement where germ tubes emerged on opposite sides of the line. There was also a tendency for the second emerging germ tube to be + (growing towards its neighbor) if the first germ tube was + (a + + arrangement) and for the second germ tube to be − if the first germ tube was − (a − − arrangement). There were relatively few + − pairs. Jaffe interpreted his results to mean that there was an emission of a diffusible, unstable, locally effective, macromolecular stimulant. In an atmosphere staled by fungal growth and containing 17.5% O_2 and 4.5% CO_2, there was a striking reversal of autotropism. Only 9% of the pairs were + + compared with 92% in laboratory air, and there was a reduction in the *cis* tendency from 92% to 72%. When the laboratory air was enriched with 0.3% or 3% CO_2 there was again reversal of autotropism, and Jaffe postulated that in higher CO_2 atmospheres, spore pairs were dominated by a locally effective, but uniformly emitted inhibitor, although the stimulator continued to have some effect. Altering the pH of the system had no effect.

Robinson, Park, and Graham (1968) confirmed Jaffe's results but found that spore pairs were neutrally autotropic on agar, though still predominantly *cis*. However, on cellophane on agar, on which germ tubes were in one plane as in thin layers of broth, spore pairs were again + + and *cis*. In + − pairs, there was a strong tendency for germ tubes to curve away from each other.

Though in semi-isolated spore pairs there was a tendency for each germ tube to be in line with the major axis of its spore, it was not considered to contribute to autotropic effects. Robinson et al. found that Jaffe's postulated factors diminish markedly in effect with increasing distance between spores, and the effect was hardly demonstrated at distances greater than 50 μm.

Autotropism is reviewed by Robinson (1973).

Rheotropism

Jönsson (1883) proposed the term 'rheotropism' to apply to the directional growth of young hyphae of *B. cinerea* downstream and of old hyphae upstream when the culture medium was flowing past the thallus. Much later, Müller and Jaffe (1965) found that when spores of *B. cinerea,* sparsely sown and hence largely independent, were fixed to the wall of a laminar flow chamber and subjected to a flow of a dilute nutrient broth, most of the germ tubes grew downstream. The rate of germination fell so slowly with increasing flow rate of the medium as to suggest the localization of a growth stimulant

and Müller and Jaffe (1965) considered that this rheotropic response is mediated by convection across each cell of a diffusible stimulator emitted by the cell. They deduced that the stimulator is macromolecular and has a diffusion constant of about $10^{-7}cm^2sec^{-1}$ and a half-life of about 10 sec. Dark-grown cells were slightly less oriented by flow.

Sporulation inhibitors

A number of materials, mostly chelators and mitotic inhibitors, specifically inhibit sporulation of a number of fungi including *B. cinerea,* but copper salts and α,β-unsaturated ketones enhance spore differentiation, possibly, suggested Horsfall and Rich (1959), by reversing the action of some natural inhibitor, which could be a sulfydryl compound. Thus the inhibitory action of ethylenebenzene-2-thiol is reversed by an α, β-unsaturated ketone, pulegone, and by copper sulfate. Also inhibiting sporulation and similarly reversed is 2- (γ-trichloropropyl) benzothiazole. Horsfall and Rich (1960) also found sporulation in *B. cinerea* to be inhibited by 1,1,1,3,3,3,3-hexachloro-2-propanol incorporated into nutrient agar at 50 and 100 ppm; although clavate conidiophores were formed, they bore no conidia. Unlike trichlorobenzothiazole, hexachlor-2-propanol also bleached the black pigments of the fungus. Its 1,3-dichloro- analogue was only weakly active and the ketone tautomer was inactive, indicating that its OH^- group is the site of activity. Hexachlor-2-propanol is cheap and easy to manufacture, and Horsfall and Rich (1960) suggested that it could be added to control programs. It was added to standard captan spray programs (Jarvis 1962*e*), and some slight improvement was indeed obtained in the control of strawberry gray-mold.

Tecnazene, a fungicide widely used in lettuce cultivation for the control of gray mold, is believed to be effective mainly because of its antisporulant activity (Reavill 1950, 1954).

Storage

The sclerotia are commonly regarded as food storage organs for survival; those of *B. cinerea* were reported to contain 68–73% water, 2.5% nitrogen, 0.5% reducing sugars, 0.7% non-reducing sugars, and 2.7% lipid material (Townsend 1952). The lipid content may vary with the source of sclerotia; those of *B. tulipae* collected from the host by Sumner and Colotelo (1970) had 3.3% by dry weight, and those from culture had 2.9%. Further, the component fatty acids, mainly palmitic, oleic, linoleic, and α-linolenic acids, tended to be more unsaturated in sclerotia from the wild. Haskins, Tulloch, and Micetich (1963) found the mycelium of an isolate of *B. cinerea* to have an oil content of 2.6% and a fatty acid composition mainly of palmitic, oleic, linoleic, and α-linolenic acids, the last amounting to 9.4% of the fatty acid fraction, compared with 41.7% reported from another isolate of *B. cinerea* (Shaw 1965) and with less than 5% in sclerotia of

B. tulipae (Sumner and Colotelo 1970). Shaw considered that the presence of γ-linolenic acid differentiated Phycomycetes from all other fungi, and that the inter-isolate differences in α-linolenic acid may be associated with taxonomic differences in the genus *Botrytis*.

METABOLISM

All *Botrytis* species are relatively easy to grow in culture on a wide range of synthetic and natural media, and all are aerobes.

Selective media

Netzer and Dishon (1967), Lorbeer and Tichelaar (1970), Ellerbrook and Lorbeer (1972) and Barkai-Golan (1973) devised a few selective media, mostly ones that exploit interspecific differences in fungicide tolerance.

Carbohydrates

The metabolism of carbohydrates by *B. cinerea* has received most attention in the field of enology (q.v.). In general, *B. cinerea* is able to utilize most sugars but an isolate of *B. cinerea* used by Fraser (1934) was unable to utilize pentoses, mannose or lactose and it failed to grow on raffinose.

Stadler (1954) found that *B. cinerea* grew poorly on *l*-rhamnose and inulin but it was able to utilize some glycosides, namely, in order of descending utilization, amygdalin, aesculin, arbutin, salicin, digitalin, and saponin.

Smirnov, Kostik, Todirazh, Mazur, and Mogilenko (1972) found that *B. cinerea* could utilize maltose, starch, and several related substances. *Botrytis convoluta* utilized, with decreasing ability, maltose, glucose, starch, galactose, and fructose, but not lactose or sorbose (Maas and Powelson 1972).

The ability of *Botrytis* species, with the possible exception of *B. convoluta* (Maas and Powelson 1972), to degrade cell-wall materials is of profound importance in pathogenesis; and the activity of pectinases, cellulases and cutin-esterase in this respect is discussed elsewhere. The in vitro production of pectinases has been studied in detail, notably by Brown and his students over a number of years (Brown, 1915, 1917, 1934, 1936, 1955) and others, including Davison and Willaman (1927), Vasudeva (1930*a*), Gäumann and Nef (1947), Ashour (1948), Jermyn and Tomkins (1950), Damle (1951), Jarvis (1953), Winstead and Walker (1954), Wood (1960), Deverall and Wood (1961*a*, 1961*b*), Thomas and Orellana (1963*b*), Hancock, Miller, and Lorbeer (1964), Kaji, Tagawa, and Yamashita (1966), Sherwood (1966),

Tani and Nanba (1969), Smirnov (1972), Urbanek and Zalewska (1973), Verhoeff (1973), Verhoeff and Warren (1972), and Shishelova and Fedorova (1974).

The enzymes include pectin methylesterase, polygalacturonase, and pectin- and polygalacturonate-methyl-*trans*-eliminase, and are reported from *B. cinerea, B. allii (B. aclada), B. squamosa, B. fabae,* and *B. ricini;* each species probably produces some or all of the enzymes, both exogenously and endogenously, because all species except perhaps *B. convoluta* attack cell walls in characteristic soft rots. In general, pectinases are readily produced on simple media containing a carbohydrate, a nitrogen source, and simple salts. Gäumann and Böhni (1947) found that polygalacturonase was a constitutive enzyme of *B. cinerea,* whereas, as Zalewska, Rochowska, and Urbanek (1970) also demonstrated, pectin methylesterase was adaptive and its activity in culture filtrates largely depended on the presence of pectin.

Verhoeff and Warren (1972) detected pectin methylesterase and endo- and exopolygalacturonase activity in media containing germinating spores of *B. cinerea,* and, at some temperatures, endopolygalacturonase activity before germination. Some endo- and exopolygalacturonase activity was detected in water used to wash the spores. Verhoeff and Warren thought that all the enzymes were adaptive.

The role of pectinases in pathogenesis is more fully discussed in PART 4, "Pathogenesis". There is no doubt however that these enzymes also play a considerable role in the saprophytic degradation of plant tissues above and below the ground (Peltier 1912); see PART 1, "Introduction".

Pectic materials of all types and of all degrees of methylation are readily utilized as carbon sources.

Cellulose is also utilized by *B. cinerea* (Lyr and Novak 1962; Köhlmeyer 1956; Hancock, Millar, and Lorbeer 1964; Lapsker, Trofimenko, and Al'man 1973), by *B. allii (B. aclada)* and *B. squamosa* (Hancock et al. 1964) and by a *Botrytis* sp. in soil (Felsz-Karnicka 1936). In Köhlmeyer's study, 4 isolates of *B. cinerea* from different host genera produced different amounts of cellulase. On cellulose hydrate discs, the isolates caused grooves but no penetration of a membrane 0.04 mm thick, although each was able to degrade natural cellulose from sunflower and elder pith. Deverall and Wood (1961*b*) and Verhoeff and Warren (1972) also detected cellulase activity by *B. cinerea.* Cellulase is probably important to the saprophytic rather than to the parasitic activity of *Botrytis* species.

Other enzymes from *B. cinerea* capable of degrading cell-wall materials have been investigated in vitro; they include hemicellulase, xylanase, and mannanase (van Parijs 1961; and Lyr and Novak 1962), and arabanases were reported from *B. allii (B. aclada), B. tulipae,* and *B. fabae* by Fuchs, Jobsen, and Wouts (1965).

In *B. cinerea,* Ampuero (1966) found an inverse relation between sugar utilization and mycelial growth inhibition by nystatin and phleomycin. This

relationship may be connected with the effect of griseofulvin on the proper construction of the cell wall of *B. cinerea* (Gottlieb and Huber 1965) and of *B. allii (B. aclada)* (Evans and White 1967). Similar distortions were noted in germ tubes of *B. cinerea* treated with benomyl (Richmond and Pring 1971*b*). Barathova, Betina, and Nemec (1969) found that 29 of 31 antibiotics they examined inhibited the growth of *B. cinerea* and of these, 20 induced abnormalities of hyphal growth. Betina, Micekova, and Nemec (1972), Betina, Micekova, and Daniela (1973), and Fassatiova (1972) observed similar effects of cytochalasins on *B. cinerea.* A mixture of sclareol and 13-epi-sclareol (diterpenes from the leaf surface of *Nicotiana glutinosa)* did not inhibit germination of *B. fabae,* but affected radial growth by their griseofulvin-like effect on hyphal branching (Bailey, Vincent, and Burden 1974). Another antibiotic, roseofungin, had a similar effect (Nikitina and Kazakova 1972).

The utilization of carbohydrates by *B. cinerea,* particularly in higher concentrations, has been extensively investigated by Kamoen (1964, 1966) and carbohydrate metabolism in relation to the production of oxalic acid (of controversial role in pathogenesis; q.v.) by Jamart and Kamoen (1972) and Gentile (1954). Gentile proposed a Krebs-cycle system: glucose → gluconic acid → phosphogluconate → pentose phosphate → triose phosphate → pyruvate → malate → oxalate, the last stage by direct oxidation.

In an attempt to utilize enzymes from *B. cinerea* in the commercial production of sweet wines (see PART 4, "Enology"), de Jong, King and Boyle (1968) examined some of the other enzymes involved in carbohydrate metabolism. Glucose-6-phosphate NADP dehydrogenase was active and an NADH-sensitive phenol oxidase was implicated in a decolorizing action on the wine.

The calorific value of the cell contents of hyphae of *B. cinerea* in culture on potato dextrose agar was found by de Soyza (1973) to be about 3.5 kcal/g ash-free wt.

Nitrogen

B. cinerea was among a number of fungi reported by Nilova, Egorova, Rashevskaya, and Kozhevnikova (1964) to fix atmospheric nitrogen. Protein accumulated both in the mycelium and in the medium, and fixation was stimulated by ammonium salts. Morton and Broadbent (1955) demonstrated the formation of extracellular nitrogen compounds by *B. allii (B. aclada)* in a medium containing ammonium sulfate. The new material was mostly peptide that the fungus was unable to utilize, although on hydrolysis it yielded 14 amino acids that were utilized.

The growth of *B. cinerea* was significantly correlated with nitrogen level when grown in nitrate- and phosphate-containing media (Dowding and Royle 1972). Although nitrate assimilation was almost always complete, that of

phosphate was not, especially in low-nitrate media. After nitrogen incorporation into mycelia, only 10% was available for incorporation into conidia, but 40% of the phosphate was available.

All species of *Botrytis* can utilize a wide range of nitrogenous materials, from nitrites and nitrates to hydrolysates of casein and similar materials, although there are differences between species. Thus, for example, Hacskaylo, Lilly, and Barnett (1954) and Maas and Powelson (1972) found *B. cinerea* and *B. convoluta* to respond poorly and well, respectively, to ammonium nitrogen as compared with nitrate nitrogen. Stadler (1954) found asparagine to be the best, and potassium nitrate the poorest, source of nitrogen for *B. cinerea* and there were interactions between acid and nitrogen.

Of recurring interest in physiological work has been the effect of the carbon:nitrogen ratio. It affects pectinase production (see above) and the type of growth, sclerotial production, sporulation, etc. (Pieris 1947; Hawker 1950; Townsend 1952, 1957; Valaskova 1963*a*; Kamoen 1964, 1966; for example); such changes are usually the result of shifts in pH of systems.

Amino acids and proteins

The uptake and accumulation of amino acids by *B. fabae* was studied by Jones (1963); L- and D-isomers both accumulated, the former more rapidly. The uptake mechanism was dependent on unsubstituted $-NH_2$ and $-COOH$ and was inhibited by uncouplers of oxidative phosphorylation.

Some synthetic analogues of amino acids, purine and pyrimidine markedly depressed the growth rate and enzyme production in cultures of *B. cinerea* (Urbanek and Zalewska 1973).

Zemlyanukhin and Chebotarev (1971) found that light had a marked effect on amino acid metabolism; free lysine, serine, alanine, tryptophane, valine, methionine, and leucine all increased in the mycelium of *B. cinerea* exposed to red, yellow, or violet light, but glutamic acid decreased. Exposure to ultraviolet light increased the accumulation of all amino acids at least fourfold, and that of tryptophan about 40-fold. Zemlyanukhin, Chebotarev, and Tsiomenko (1971) found that ultraviolet light at 36 $mWcm^{-2}$ in a 30-min exposure destroyed protein, but amino- and C_3 acids accumulated in the mycelium and in the medium.

The cytostat 1,6-dibromo-D-mannitol was shown by Szabo, Holly, Horvath, and Pozsar (1972) to effect an increase in protein nitrogen in the mycelium of *B. cinerea,* sometimes by as much as 20%, possibly by DNA induction.

Lyr and Novak (1962) reported amylase and proteinase activity in cultures of *B. cinerea* and Ovcarov (1938) reported an endogenous de-urease in *B. cinerea,* which split off urea from protein, in this case, gelatine, and this

enzyme was considered to be of considerable importance in nitrogen metabolism. Smirnov, Kostik, Todirash, Mazur, and Mel'nik (1972) and Astapovich, Babitskaya, Hrel, and Vidzischchuk (1972) detected peptolytic enzymes in *B. cinerea*. Tseng and Lee (1969) reported the production of a proteolytic enzyme by *B. cinerea* in vitro that was active over the pH range 5–8.5, with its optimum at the higher value. Trofimenko and Shcherbakov (1973) found a strain of *B. cinerea* that synthesized an acid proteinase.

Aliphatic compounds

B. cinerea was shown by Kosuge and Dutra (1962, 1963) to fix carbon dioxide during germination. ^{14}C appeared mostly in amino and other organic acids when supplied in the medium as $Na_2{}^{14}CO_3$.

Species of *Botrytis* are able to form citric acid in a wort agar containing calcium carbonate and to deposit calcium citrate (van Beyma 1930; Schreyer 1931; Behr 1968, 1969). Pollettini (1961) demonstrated the enhanced growth of *B. cinerea* in Raulin's solution with 2.5% and 11% lactic acid both in normal and oxygen-depleted atmospheres.

B. cinerea is able to utilize citric and oxalic acids very poorly (Stalder 1954) and pyruvic, acetic, and proprionic acids not at all. It is able to utilize malic and tartaric acids (see Part 4, *"Enology"*). Novák and Vörös-Felkai (1958) found that *B. cinerea* utilized several aliphatic acids (lactic, citric, tartaric, succinic, fumaric, malonic, and ascorbic), as well as sodium lactate, sodium acetate, and ethanol, but it could not utilize formic, proprionic, oxalic, or acetic acids, nor sodium oxalate. With the exception of malonic acid, the data supported the hypothesis of a Krebs cycle, but Novák (1958) was able to reconcile this apparent departure. He found that malonate is decarboxylated to acetate and oxidized to succinic and oxalic acids. At a concentration of 0.005 M or less, malonic acid stimulated oxygen consumption and there was no succinodehydrogenase activity, so that sugars were probably directly oxidized.

Gluconic acid is not synthesized from sucrose by *B. cinerea* (Schreyer 1931).

Of probable significance in predisposition to infection (q.v.) is the ability of a *Botrytis* sp., reported as *B. spectabilis* (Ilag and Curtis 1968), to form ethylene from simple media. A culture produced 0.25 ppm in 24 h, a concentration known to predispose certain tissues to attack by *B. cinerea*.

Botrytis cinerea has been reported to oxidize straight-chain primary alcohols (except methanol), aromatic alcohols, and unsaturated primary alcohols to yield the corresponding aldehydes and an equal molar quantity of H_2O_2 (Fukuda and Brannon 1971). The introduction of a polar group into the alcohols completely inhibited oxidation.

Vitamins

According to Lilly and Barnett (1949) and Gough and Lilly (1956) *B. cinerea* apparently needs no exogenous source of vitamins; they found that it grew as fast in a simple medium as in one augmented with thiamine, biotin, inositol, or pyridoxine. On the other hand, Singh (1940) had found that conidial germination was enhanced by the addition of a lentil extract that contained thiamine, biotin, and perhaps other growth factors, and Olivier, Akhavan, and Bondoux (1972) found that *B. cinerea* grew better in the presence of biotin, together with DL-trytophan and glycine.

Trace elements

Of minor elements, Metz (1930) considered zinc to be essential for the growth of a *Botrytis* sp. and, to a lesser extent, copper and iron; all were necessary for normal coloration. Young and Bennett (1922) found no marked effect of zinc in the nutrition of *B. cinerea,* but Valaskova (1963*a*) found it to limit growth without affecting sporulation or sclerotial formation in *B. tulipae.* Molybdenum in trace amounts enhanced the growth of *B. cinerea* (Castiglione and Landi 1948), but calcium had little effect on *B. allii* (Young and Bennett 1922). Trace elements in approximately the concentrations found in grape juice stimulated the formation of sclerotia by *B. cinerea* (Vanev 1966); the trace elements were iron, zinc, boron, calcium, potassium, copper, phosphorus, manganese, and molybdenum.

Cultures of *B. gladiolorum* did not grow or color normally in the absence of magnesium and zinc (Marshall 1955), and sporulation was depressed in the absence of iron.

Sulfur can be utilized by *B. cinerea* in the form of sulfate, persulfate, sulfite, or sulfhydryl (Armstrong 1921). *B. cinerea* is, however, very sensitive to sulfur dioxide (Couey and Uota 1961) acting as sulfurous acid. Sodium fluoride significantly suppressed the growth of *B. cinerea* at 5×10^{-3} M but at lower concentrations (e.g., 10^{-4} M and 10^{-5} M), growth was stimulated. Sporulation was abundant at the lower concentrations; even at 5×10^{-3} M there were a few conidiophores, but fewer at 10^{-2} M. Sclerotia were highly variable in number, but their viability was unimpaired at concentrations below 5×10^{-2} M (Treshow 1965).

Alkaloids

Botrytis cinerea tolerates and utilizes 2% caffeine and quinine (Ravaz and Gouirand 1896); 2% tannin, 2% amygdalin, 1% brucin, and 1% strychnine (though not of 20% quinine or thein, Büsgen 1918); 2.5% nicotine and 1% aconitin (but some inhibition by 2% atropine sulfate and slight inhibition by 4% quinine sulfate, Nobécourt 1921); and 2% atropine sulfate,

4% quinine sulfate, and 2.5% nicotine (Fischer and Gäumann 1929). Blumer and Gondek (1946) studied the action of oxyquinolins on *B. cinerea*. The alkaloids tomatin and solanin were found by Kern (1952) to have LD_{50} values of 2×10^{-4} M for germinating conidia of *B. allii (B. aclada)*.

Pigment production

Several workers, for example, Sprague and Heald (1926), Morquer (1933), Peyronel (1934), and Ellerbrook and Lorbeer (1972), have noted that some isolates of *B. cinerea* produce a red pigment in culture, but its identity and mode of production are not known.

Hydrolytic enzymes

The intracellular localization of some hydrolytic enzymes has been studied by Pitt and Walker (1967) and Pitt (1968, 1969). In cytoplasmic particles, Pitt found a latent acid phosphatase, carboxylic esterase, acid deoxyribonuclease, β-galactosidase, and some suggestion of aryl sulfatase and peroxisomes. He found no β-D-glucuronidase.

Tseng and Bateman (1968) and Tseng, Lee, and Chang (1970) found that *B. cinerea* produced an extracellular phosphatidase in culture that released palmitic acid, linoleic acid, and glycerylphosphorylcholine from soybean lecithin. This phosphatidase was also detected in parasitized onion.

Pollettini (1962) investigated alkaline phosphatase activity in *B. cinerea* in relation to exposure to X-rays. Check cultures had a steadily decreasing enzyme activity; irradiated cultures had enhanced activity up to the 5th day and thereafter activity decreased and was undetectable by the 8th day.

Hislop (1957) investigated the effect of some fungicides on enzymes of *B. cinerea*. Copper sulfate depressed catalase and increased cytochrome-C-oxidase activity; 0.05% stimulated peroxidase activity threefold but 0.1% depressed activity by 95%; captan enhanced catalase and cytochrome-C-oxidase but depressed peroxidase activity; *o*-phenylphenol increased cytochrome-C-oxidase and alkaline phosphatase, and depressed catalase and peroxidase activity; lime sulfur depressed all enzyme activity.

Polyphenols

Dubernet and Ribéreau-Gayon (1973) concluded that the polyphenol oxidase of *Botrytis cinerea* is a laccase, which degrades the anthocyanins of grape berries as well as tannins (leucoanthocyanins) and several other phenolic substances such as pyrocatechol, phloroglucinol, *p*-cresol, gallic acid, DOPA, vanillic acid, caffeic acid, ferulic acid, chlorogenic acid, and *d*-catechin.

This activity contrasts with the tyrosinase activity of the grape berry (see PART 4, "Enology").

Scurti, Fiussello, and Jodice (1972) considered that *B. cinerea* could utilize lignin, lignosulfonate, and humic and fulvic acids in litter decomposition.

Botrytis allii (B. aclada) produces a complex phenolic compound, botrallin, probably by the oxidative conversion of a substituted resorcinol ring into catechol or pyrogallol derivatives (Kameda, Aoki, Namiki, and Overeem 1974).

Test organisms

Botrytis species are common test organisms for a wide variety of fungicides, pesticides, growth substances, antibiotics, etc. In general, in vitro and in vivo tests give similar indications, although there are anomalous results, which may, in part, be interpreted in terms of altered host-susceptibility (q.v.). Brook (1957) found general agreement between the two types of test, except in the case of copper; conidia of *B. cinerea* germinated on heavy deposits of copper on glass or cellulose nitrate surfaces in the absence of free water, but not in aqueous suspension. Copper compounds were ineffective in controlling the fungus on tomato plants, though LD_{50} values were lower than those of nearly all other materials tested.

Chancogne and Fruchard (1965), Chancogne and Lefumeux (1967), and Lafon and Boniface (1971) found fungicides to act differently against conidia and mycelium of *B. cinerea.*

B. cinerea is able to induce antibody formation in rabbits, and Preece and Cooper (1969) prepared a specific test reagent for the fungus from rabbit γ-globulin labelled with fluorescein isothiocyanate. The fungus could also be stained if treated with antiserum conjugated with a dye and then stained with a commercial goat antiglobulin conjugated with fluorescein isothiocyanate.

SURVIVAL

Although sclerotia are regarded as the fungal structures best adapted to withstand adverse conditions, surprisingly few detailed studies on their survival have been made within the genus *Botrytis* (Willetts 1971).

Townsend (1952) found that sclerotia of *B. cinerea* were killed within 3 days when held at 80°C; the LD_{50} time at 66°C was 9 days and only 10% were viable after 13 days and none after 18 days. Survival was a little better at 54°C, while at 4°C, 100% survived for 81 days and 50% for 103 days;

all were dead after 123 days. At 20–25°C, sclerotia were still viable after 5 mo. The loss in viability, particularly at high temperatures, did not seem to be the result of desiccation. In soil with a 35% moisture content, no sclerotia survived for more than 1 mo, but survival was better in dryer soil; all survived in soil of 17% and 8% moisture content for more than 8 mo. Submersion in water for 30 wk did not impair viability. Similar results were obtained by Kochenko (1972).

Little is known of the survival of *Botrytis* spp. in field soil. Jeffries and Hemming (1953) found soil water to be fungistatic to *B. allii (B. aclada)* and Park (1955) and Lockwood (1960) noted that conidia of *B. cinerea* disappeared quickly when put into soil and the fungus did not colonize pieces of plant material below the surface. However, the fungus survived 4 wk on previously colonized pieces of clover stem and 2 wk on grass. Hsu and Lockwood (1971) considered *B. cinerea* to be only a moderate competitor in soil. Fungistasis of *B. cinerea* by *Trichoderma koningi* in soil is probably pH-dependent (Schüepp and Frei 1969). Park (1954) obtained chlamydospores of *B. cinerea* in soil solutions but their survival in soils seems not to have been evaluated.

Although the main structures adapted to survival in *Botrytis* spp. are the sclerotia and occasionally the chlamydospores (q.v.), conidia are also able to survive in normal field conditions quite well (Ilieva 1970; Vyskarko and Vaselashki 1973), although van der Spek (1960) found that the viability of conidia of *B. cinerea* decreased with age and Doran (1922) noted that young conidia germinate over a wider range of adverse conditions than older ones. Last (1960*a*) found the same viability in conidia of *B. fabae*. Hennebert and Gilles (1958) found that the decline in viability of conidia at a relative humidity of 60–70% and 15–20°C is accelerated by direct insolation. After a 3-day exposure, including one 3-h insolation period, only 3–5% of conidia germinated, and none were viable at the end of 10 days. Air-dry conidia, 95% of which were viable, were exposed in the shade; after 1 day 20% were still viable, after 3 days 11%, and after 12 days 5%.

Ultraviolet light can be rapidly fungicidal to *Botrytis* spp. (English and Gerhardt 1946; Masago 1959). Spores of a *Botrytis* sp. from apple were killed on the surface of agar by a 1-min exposure to an ultraviolet light source 15 cm away (Fulton and Coblentz 1929). Savulescu and Tudosescu (1968) found *B. cinerea* to be one of the most sensitive fungi they tested, although a single exposure of 15–30 min stimulated mycelial growth. Exposures of longer than 2 h decreased viability, as was also found by Chebotarev, Lanetskii, and Nabarezhnyk (1968). Ultraviolet light also reduced the ability of *B. fabae* to initiate colonies on agar (Buxton, Last, and Nour 1957), but damage to the conidia was partially reversed by subsequent exposure to daylight. The reason for this is unknown.

When conidia of *B. cinerea* were allowed to germinate, dried for 8–12 h, remoistened, redried, and allowed to grow on, 60–90% of them survived (Good and Zathureczky 1967). The proportion surviving decreased only

slightly with increasing germ tube length. Losses from the second drying were only slightly higher than from the first.

On living tomato leaves, conidia of *B. cinerea* remained viable for 3 mo and for 10–16 mo when the leaves were stored dry in the laboratory (Ilieva 1970).

Jarvis (unpublished) kept conidia of *B. cinerea* submerged in water of depths ranging from 9 to 36 mm and at temperatures between 10°C and 30°C. When the conidia were removed from the water 2 days after submersion, 10–40% germinated; when removed after 11 days, 1–10% germinated. Fewer germinated after submersion at 10°C and 30°C than at 15°C or 20°C, and a much higher proportion of conidia germinated when they were recovered in clumps. Occasional conidia germinated after submersion for 25 days. The depth of water, in which the conidia sank to the bottom, had no effect on survival.

Conidia of *B. tulipae* were found by Beaumont, Dillon Weston, and Wallace (1936) to be viable for 1–50 days and some for 6 mo when stored dry in the laboratory. They thought sclerotia would be viable for at least 2 yr.

Maas (1969) found that survival of conidia and sclerotia of *B. convoluta* was favored by low temperatures; storage at −70°C only slightly impaired germinability of conidia after 257 days and of sclerotia after 366 days. Exposure to 30°C, however, rapidly decreased the viability of conidia, and sclerotia held at 30°C for a year lost 65% of their germinability. Sclerotia held in moist, non-sterile soil at temperatures higher than 15°C rapidly lost their germinability, probably, it was suggested, because of antagonism and parasitism by other organisms.

Botrytis spp. are able to live well and parasitize plants at relatively low temperatures (see also PART 4, "Resistance"). For example, Sato, Shoji, and Ota (1959) found a *Botrytis* of the *cinerea* type causing a snow mold of conifer seedlings; viability of the pathogen was unimpaired by several days' exposure to −7°C. *B. cinerea* can be pathogenic at temperatures around 3°C, but Vanev (1965) noted that temperatures fluctuating around 0°C rapidly killed conidia. Bartetsko (1910) found that conidia of a *Botrytis* sp. were viable after immersion in a liquid medium at −14°C for 2 h. Young mycelium survived better if it was frozen in a 5% glucose solution than in a 1% solution, and Purvis and Barnett (1952) successfully preserved conidia of *B. cinerea* in a frozen aqueous suspension for 2 yr.

Van den Berg and Lentz (1968) found that the mycelium of *B. cinerea* can survive under the usual conditions of storage for vegetables. In the absence of nutrients, the mycelium survived at 0°C more than 12 mo in a saturated atmosphere, and 2–12 mo in a relative humidity of 85%; at 20°C the mycelium survived 5–12 mo, and less than 1–5 mo in the respective relative humidities. When the mycelium was supplied with nutrients, no growth occurred in relative humidities below 93% and the mycelium survived less than 1 month. Conidia at 0°C survived 3–6 mo in 99% RH and 2–6 mo

at 85%; at 20°C conidia survived less than 1–3 mo and less than 1 mo at the respective RH.

Bulit, Bugaret, and Verdu (1973) failed to detect *B. cinerea* in the buds of the grapevine after winter in the field in Bordeaux.

In a high temperature study, O'Brien (1902) found that 5- and 10-min exposures to 50°C resulted in 65% and 2% germination of conidia of *B. cinerea* respectively; and exposure to 53°C was lethal.

In a study of soil pasteurization, Zumstein (1935) found that for *B. cinerea* the minimum lethal high temperature, maintained for 15 min, was 55°C. Vanev (1965) found that some conidia of *B. cinerea* survived a 2-min exposure to 170°C, but Ogawa and McCain (1960) killed dry conidia on glass rods by a 1-sec exposure to live steam.

The susceptibility of *B. cinerea* to heat has been used as the basis of pasteurization treatments to control gray mold in strawberries (Smith and Worthington 1965; Couey and Follstad 1966). Fruit decay was considerably reduced by exposures of 20 or 30 min at 44°C and 98% RH or 60 min at 90% RH; lower humidities were not effective. Raspberries were less successfully treated (Worthington and Smith 1965); although decay was retarded, heat injury to the fruit was unacceptable. These treatments are unlikely to be of commercial value because of the fine degree of temperature control required.

Smith (1923*b*), exposing conidia of *B. cinerea* in water for 3 h at 37°C, found that subsequent germination on Czapek agar was delayed; after a 24-h incubation, 49.8% germinated and after 48 h, 74.4%. Shorter exposures did not result in a delay in germination, and Smith suggested that killing is a gradual process and that 'half dead' conidia may recover on prolonged incubation. Smith produced several curves showing the effects of high temperatures on conidia and introduced the concept of LD_{50} values, the exposure time when half the conidia were killed. The curve log LD_{50} time – $1/T°$ was a straight line, and the effect of temperature on the killing reaction velocity was unusually great.

Smith (1921) also made a study of the response of conidia of *B. cinerea* to phenol. A plot of the percentage of conidia surviving against exposure time gave a sigmoid curve and a plot against phenol dose gave a logarithmic curve. A higher concentration of conidia had an effect equivalent to reducing phenol concentration or to using very young conidia. Smith (1921) considered that the killing of conidia by phenol involves 2 processes, penetration and then the action of phenol on metabolic processes.

Blumer and Gondek (1946) made a similar study of the action of oxyquinolins on *B. cinerea* and McCallan and Weedon (1940) one on the action of SO_2, HCN, H_2S, $C1_2$, and ammonia.

The conidia and mycelium of *B. cinerea* are killed by gamma radiation (Terui and Harada 1964; Barkai-Golan, Temkin-Gorodeiski, and Kahan

1967). Mycelium irradiated by 80 × 10^4 rad at a rate of 10^6 rad/h was almost completely killed, but that irradiated at 2 × 10^4 rad/h was capable of renewed growth; the rate of irradiation, as well as the dose, is therefore important. Growth, sporulation, and sclerotial formation in *B. cinerea* were reduced by 5–40 × 10^4 rad. Established infections in grapes, especially old infections, were less susceptible to radiation than conidia were (Couey and Bramlage 1965). Sommer, Fortlage, Buckley, and Maxie (1972) demonstrated that conidia, mycelia, and sclerotia of *B. cinerea* had different sensitivities to gamma radiation, and Georgopoulos, Macris, and Georgiadou (1966) found that iodoacetamide at 70–100 ppm considerably enhanced the effects of very low radiation doses (4 krad) in conidia of *B. cinerea.*

Irradiation of fruits and vegetables has been tried often as a postharvest control measure, but the gamma radiation dosages, except on strawberries and radishes, are detrimental to quality (Eckert and Sommer 1967).

Metlitsky and Soboleva (1936) and Tverskoy (1937) found that irradiation at wavelengths of 5–40 m killed *B. cinerea* in culture.

DISPERSAL

All *Botrytis* spp. sporulate profusely; in most species the dry conidia are dispersed through the air in large numbers on air currents and thus these species fall into the anemochoric group of plant pathogens of Stepanov (1935). Nutrient agars in petri dishes exposed from aircraft have revealed the presence of *Botrytis* spp. in the air over the Arctic and Atlantic Oceans (Pady 1951; Bisby 1935; and Pady and Kelly 1954). At lower altitudes, conidia have been recorded in urban areas (Pady and Kapica 1956), mainly in the summer (Pawsey and Heath 1964) and autumn (Hyde and Williams 1949). Richards (1956) found them more abundant in rural areas where they comprised 2.2% of all spores trapped, but Gregory and Hirst (1957), using an automatic volumetric spore trap, found that they comprised only 0.42% of spores trapped at Rothamsted over the summer of 1952, with a peak in June of 288/m^3 of air sampled. Sreeramulu (1959), also at Rothamsted, found a diurnal periodicity with a peak of about 400/m^3 at midday. Spores began to appear in June and reached a peak between June 22 and July 2. Lacey (1962) found peaks of about 1500 conidia/m^3 and a mean concentration for a summer season of 1.2% and 1.6% of the total conidia trapped at two rural sites. Kimura and Yamamoto (1972) investigated the concentration of *B. cinerea* in the air spora in Japan, and Cejp (1947) in Czechoslovakia.

Matsuo et al. (1973) investigated the dispersal of conidia of *B. allii (B. aclada)* in onion packinghouses.

The mechanism of spore dispersal is best known in *B. cinerea,* having been first described by de Bary (1884); and Hopkins (1921) first described

the mechanism in *B. tulipae*. According to them, the mature conidiophore is a flattened, twisted ribbon; it responds to changes in the relative humidity of its environment by twisting about its long axis sufficiently violently to fling off the spores by centrifugal force, an observation which Ingold (1939) could not confirm.

Jarvis (1960*b*), using an apparatus to transfer sporulating cultures of *B. cinerea* between environments of differing relative humidity without mechanical shock or exposure of the cultures to an external environment, found that the conidiophore is as de Bary described, and though it twists about its long axis, the movement is not violent. In a profusely sporing culture, the ampullae and conidia of adjacent conidiophores are tangled together. The hygroscopic movements gently but jerkily dislodge the conidia from their fine attachment to the ampullae among which they come to lie loosely and whence, in the open laboratory or field, they may be readily dispersed on air currents or by other agencies.

Thus, Jarvis (1962*b*) distinguished two processes in spore dispersal; first the hygroscopic mechanism of spore release, followed by true dispersal by other agencies.

These two processes probably occur in other species, for example, in *B. tulipae* (Hopkins 1921), but no detailed examination has been made. Mason (1937) considered spore release in *B. cinerea* to be brought about by the withering of the sterigma connecting spore and ampulla at maturity.

Of particular speculative interest are those species (e.g., *B. squamosa* and *B. globosa*) in which the conidiophore twists in response to desiccation, its branches contract, and after spore release, the ampullae suddenly collapse in conspicuous accordion-like folds (Viennot-Bourgin 1953; Webster and Jarvis 1951; and Hennebert 1963, 1973). This rapid collapse suggests some release of internal pressure; however, no explosive discharge of conidia of the type occurring in, for example, *Pilobolus* spp. has been recorded. The conidiophore of *B. squamosa* can regain turgidity after spore release and form new spores laterally and terminally.

Mature conidiophores of *B. cinerea* contain a variety of cytoplasmic arrangements, including hollow reticulate cylinders, spiral arrangements, and structures resembling internal hyphae, which themselves may be flattened and twisted, and it may be speculated that uneven distribution of cytoplasm may account, in part, for hygroscopic movements (Jarvis, unpublished).

The positive phototropism of the conidiophore (q.v.; Jarvis 1972) is likely of significance in spore dispersal, although its role in the field has not been assessed.

Spore liberation by *Botrytis cinerea* from necrotic leaves of *Chrysanthemum morifolium* and *Allium cepa* was investigated in controlled environments by McCoy and Dimock (1971). At 20°C, spore release was conditioned by the presence of free moisture in the substrate, by the degree of atmospheric turbulence, and by mean wind velocity, although the effect of

the last was secondary because release did not occur in the absence of free moisture. Over 98% of conidia trapped were released in 2 daily periods of 5 h each. McCoy and Dimock suggested that the liberation of conidia depends on free water in the substrate and that the effect of wind is primarily on dispersal. Stepanov (1935) considered that the minimum wind speed necessary to disperse conidia of *B. cinerea* was about 0.36–0.50 m/s, and that conidia could even fall off under gravity. The terminal velocity was calculated to be 0.22–0.45 cm/s by Gregory and Denton (Gregory 1973). Stepanov found dispersal in convection currents. Hamilton (1957, in Gregory 1973) found that the dispersal of *Botrytis* conidia decreased significantly with increasing wind speed.

The patterns of spore dispersal of *B. cinerea* in Scottish raspberry and strawberry plantations were examined by Jarvis (1962*b*, 1962*c*) using an automatic volumetric spore trap. In raspberry plantations there is a basic diurnal pattern of two periods of prolific spore dispersal corresponding to two periods of rapidly changing relative humidity. The first, from midmorning until about noon, is typically a period of drying of dew when the relative humidity falls rapidly from about 85% to 65%; conversely, the second is an evening rise in relative humidity between the same approximate limits as dew is formed again. Thus, the field conditions reflect those of the laboratory (Jarvis 1960*b*) when spore release was achieved by both rising and falling changes in relative humidity of as little as 5%.

The stylized pattern can, of course, be considerable modified by other climatic factors. Jarvis (1962*b*) found that conidia were not generally dispersed unless the temperature of the preceding night was at least about 12°C and deduced that this was the minimum temperature for mature spore production. As many as 2×10^4 spores/m^3 of air were recorded at a height of 1 m during the morning dispersal period and the spores remaining undispersed then contributed, in suitable conditions, to the air spora of the afternoon period. The relatively small humidity changes induced by intermittent sunshine often produced moderate spore concentrations throughout the day.

More striking were the relatively high concentrations of airborne spores associated with rain showers, often in conditions otherwise unsuitable for dispersal (Lacey 1962; Jarvis 1962*b*). As had been observed in the laboratory (Jarvis 1960), the mechanical shock of raindrops falling onto conidiophores or near their substratum could cause jerky disentanglement of conidiophores and ampullae, so that spores were released to be dispersed on the shock air waves and other air currents. Perhaps changes in relative humidity in the vicinity of impacting raindrops also operate the hygroscopic mechanism. Dillon Weston and Taylor (1948) found that a single water drop falling onto a *Botrytis*-infected leaf could contaminate an area of some 2.5 m^2 with spores; if the leaf was exposed to a rain shower lasting 45 min, the contaminated area was more than 32 m^2. In one splash droplet, 156 conidia were counted.

Investigating further the role of rain in spore dispersal, Jarvis (1962*d*) found that water dropped onto a sporulating culture of *B. cinerea* in the

laboratory produced splash droplets completely coated with dry spores. These projectiles, travelling for distances up to about 1m, were remarkably stable and could be manipulated with forceps until the water within began to evaporate. The projectiles then invaginated and finally collapsed. However, if water did not evaporate quickly in the field, it is possible that spores would eventually become wet enough to enter the drop and begin germination. The role of these projectiles in epidemiology has not been investigated.

Hislop (1969) obtained infection of leaves of *Vicia faba* from rain-splashed conidia of *Botrytis fabae* and observed that they could be splashed to the underside of leaves. Beaumont, Dillon Weston, and Wallace (1936) and Price (1967) noted dispersal by rain in *B. tulipae* and Beaumont et al. further noted that this type of dispersal could also occur in greenhouses when condensate dripped from the roof. Corbaz (1972) also found rain to be important in the dispersal of spores of *B. cinerea* in the vineyard and, unlike Jarvis (1962*b*), considered disturbance of infected berries by pickers to be an important factor. In many aspects, the patterns of dispersal in a vineyard and a raspberry plantation are very similar (Jarvis 1962*b*; Bulit and Lafon 1970; Corbaz 1972; and Bulit and Verdu 1974).

In raspberries and in grapes, the sporulating sites of sclerotia of *B. cinerea* are mostly well above the ground on stems, on diseased berries, and, in raspberry, on receptacles remaining after the drupelets are picked, and so all are well-exposed to the changing environment. In strawberry plantations, however, the sporulating sites — diseased berries and colonized debris — are not so exposed; trapping at a height of 0.5 m, just above the leaf canopy, showed that very few spores become airborne in the same conditions dispersing spores in nearby raspberry plantations (Miller and Waggoner 1957; Jarvis 1962*c*). Only on days when picking occurred did appreciable spore concentrations occur in the air over the strawberry plantation, and then the concentrations were closely correlated with the numbers of affected berries beneath the canopy (Jarvis 1962*c*). The disturbance of the leaves, of necessity on dry days, changed the relative humidity around the sporulating sites, permitting dispersal. Undisturbed, sporulating sites have a microclimate that is continually near-saturated, and no hygroscopic movements occur; air currents are also minimal. By contrast, Miller and Waggoner (1957) trapped most spores in conditions of high relative humidity.

In onion crops, Lorbeer (1966) noted a diurnal periodicity of conidia of *B. squamosa;* 80% were collected between 8 a.m. and 4 p.m. He related peak concentrations to increases in temperature rather than to changes in relative humidity, and found that the same pattern of diurnal periodicity occurred in a 36-h period of relative humidity continuously at 97%.

Saprophytically based inocula of *B. cinerea* may be very important in the epidemiology of the gray mold diseases (Jarvis 1962*a*), and wind-blown and rain-splashed pieces of colonized debris are probably effective dispersal propagules as in *Whetzelinia sclerotiorum* and *Sclerotinia minor* (Natti 1971; Jarvis and Hawthorne 1972; and Hawthorne and Hartill, personal commu-

nication). Maas and Powelson (1970) also pointed out the importance of symptomless, latent infections in the survival and dispersal of *Botrytis convoluta* in rhizomes of *Iris;* other latent infections (q.v.) probably can have similar roles.

Although the conditions for maximum airborne spore dispersal can be approximately defined, at least in crops like raspberry and onion, the knowledge is of little value in forecasting epidemics. Of much more value is a knowledge of the conditions for successful infection and even then spores may play a relatively minor part, as in raspberry and strawberry (Jarvis 1962*a*).

Many species of *Botrytis* are seed-borne, especially in the sense that sclerotia are mixed with seed, although some, for example, *B. tulipae,* are carried as mycelium within the seed (Capelletti 1931). Noble and Richardson (1968) list (with bibliography) the following: *Botryotinia ricini, B. theae, B. porri, B. squamosa, Botrytis allii, B. anthophila, B. byssoidea, B. fabae, Botrytis* sp. (including *B. parasitica* = *B. tulipae*) on 3 hosts, and *B. cinerea* on 44 hosts. Dispersal may thus take place with seed dispersal, including that of commerce and by other agents that disperse seeds (for example, birds and rodents).

In the specialized species *B. anthophila* (sporulating on the anthers of clover), bees and other insects probably disperse the sticky spores (Silow 1933). Bees also dispersed the spores of *B. cinerea* in a strawberry plantation (Kovacs 1969). Of two pests of tomato glasshouses, *Drosophila melanogaster* was found only rarely to carry the spores of *B. cinerea* (Butler and Bracker 1963), but *Aleyrodes vaporariorum* did carry those of a *Botrytis* sp. (Dickson 1920). Ondrej (1973) found that in Czechoslovakia spores of *B. fabae* were carried by the thrips *Acyrthosiphon onobrychis* but not by *Aphis fabae* or Thysanoptera, and that flower infestation by *B. fabae* could be reduced by insecticides. Spores of *B. gladiolorum* were found to be dispersed by a mite, *Pediculopsis* sp. that was apparently an obligate symbiont of the fungus (Harrison 1952).

The mechanisms of ascospore discharge and dispersal in *Botryotinia* spp. are largely unknown. There is explosive discharge from apothecia of *B. ricini* (Godfrey 1923), which is apparently similar to the puffing phenomenon in *Whetzelinia (Sclerotinia) sclerotiorum* (Dickson and Fisher 1923; Buller 1934) and probably triggered by a hygroscopic response. Frequently the 8 spores are dispersed together. The stipe, and possibly the asci, of *B. ricini* (Godfrey 1923) and of *B. fuckeliana* (Gettkandt 1954) show positive phototropism that may be of phytopathologic significance.

PART 4 PATHOLOGY

HOST SPECIFICITY

Some *Botrytis* species, previously believed to be host specific and hence often given the host name in the specific epithet, are now known to have a somewhat wider host range. Thus, *Botrytis tulipae* occurs not only on *Tulipa,* but also on *Lilium regale* (Hennebert 1971); *B. gladiolorum* is probably pathogenic to *Crocus versicolor;* and *Botrytis elliptica,* formerly recorded only on *Lilium* spp., also occurs on *Colchicum autumnale, Gladiolus* spp., *Erythronium grandiflorum* var. *pallidum, Polyanthus tuberosa* (MacLean 1948; MacLean and Shaw 1949; and Ark and MacLean 1951), *Stephanotis floribunda,* and, by inoculation, *Cyclamen indicum* (Tompkins and Hansen 1950).

In general, fairly close host-specificity occurs in *Botrytis* spp. on the corolliferous monocotyledons and the Ranunculaceae (Hennebert 1963; Hennebert and Groves 1963; Hellmers 1943; Moore 1954; Yamamoto, Oyasu, and Iwasaki 1956; Kovachevski 1958; and Nieuwhof and Meer 1970). For example, *Botrytis* spp. occurring on *Allium* spp. (Hennebert 1963) are:

A. ascalonicum	*B. aclada (B. allii), B. cinerea,* (*B. porri* by inoculation)
A. cepa	*B. aclada, B. byssoidea, B. cinerea, B. squamosa,* (*B. globosa, B. porri* by inoculation)
A. fistulosum	*B. aclada, B. byssoidea*
A. porrum	*B. aclada, B. byssoidea, B. cinerea, B. porri*
A. sativum	*B. aclada, B. byssoidea, B. porri*
A. schoenoprasum	*B. aclada, B. byssoidea*
A. triquetum	*B. sphaerosperma*
A. ursinum	*B. globosa*
A. vineale	*B. porri*

Thus, close host-specificity occurs only in *B. sphaerosperma* and possibly *B. globosa* in the wild, and outside the 2 groups mentioned above, host specificity is probably exclusive only in *B. spermophila, B. anthophila,* and *B. pelargonii.*

Though bearing a host name, *B. fabae* is not host specific; it occurs not only on *Vicia faba,* its first described host (Sardiña 1929), but also on *V. cracca, V. sativa, Lens culinaris, Pisum sativum, P. sativum* var. *arvense,* and *Phaseolus vulgaris,* though all in the Leguminosae (Sardiña 1931; Yu 1945). *B. fabae* is often confused with *B. cinerea* on beans (Wilson 1937; Ogilvie and Munro 1947); of 168 isolates from *V. faba* grown in various parts of the

USSR, 152 were ascribed to *B. fabae* and 16 to *B. cinerea* by Vasin and Gorlenko (1966*a*, 1966*b*). They found *B. fabae* to be variable in culture, with conidial size sometimes approaching that of *B. cinerea,* and they recorded *B. fabae* as a form of *B. cinerea* adapted to bean, but now sufficiently distinct to warrant species rank. Sundheim (1973) clearly distinguished them in Norway, as did Ondrej (1973) in Czechoslovakia and Shidla (1973) in Lithuania.

Sometimes, supposed host-specificity has been reflected in the erection of a *forma specialis* within a species, usually with confusion (Westerdijk 1927). For example, Hodosy (1964) erected *B. cinerea* f.sp. *convallariae,* which however more resembled *B. tulipae,* although Klebahn (1930) had accepted *B. convallariae* as a good species, as did Hennebert (1971). Klebahn (1930) erected four *formae speciales* within *B. cinerea* distinguished by spore size rather than by the results of pathogenicity tests: f.sp. *primulae* from *Primula* (with conidia measuring 10.5 × 6.3 μm), f.sp. *prunitrilobae* (9.2 × 5 μm), f.sp. *syringae* from *Syringa vulgaris* (12.6 × 8.3 μm), and f.sp. *vitis* from *Vitis vinifera* (12.6 × 6.8 μm). Klebahn also distinguished *B. parasitica* and *B. douglasii* on biological grounds, but referred both to *B. cinerea* on morphological grounds. Van Beyma (1930) added another *forma specialis* of *B. cinerea,* f.sp. *lini.* Isolated from flax seed, it was considered to differ from *B. cinerea* in certain conidial and cultural characters. Another, *B. cinerea* f.sp. *coffeae,* was described by Hendrick (1939) from coffee fruits. He differentiated it on conidial size rather than on the results of pathogenicity tests, although he assumed it to be host specific.

In the subtropical conditions of Georgia SSR, Hazaradze and Nisnianidze (1961) believed *B. cinerea* to be an aggregate species and, on slender evidence, they recognized as host specific the *formae speciales citri-limon, citri-sinensis, citri-nobilis, diospyri,* and *aleurites.* Though all ff.sp. were pathogenic to each host, ff.sp. *diospyri* and *citri-limon* were more so than the others. In culture, demarcation lines developed between colonies of the ff.sp. There were no significant differences in spore morphology or size.

Kovachevski (1958) proved the pathogenicity of *Botryotinia porri* to garlic *(Allium sativum),* in addition to leek *(A. porrum),* in Bulgaria, but found onion *(A. cepa)* to be rarely infected. On these grounds, Kovachevski considered his fungus to be a new form, *B. porri* f.sp. *allii-sativae.*

Differences in pathogenicity have been reported among isolates of *Botrytis cinerea* from lemon by Klotz, Calavan, and Zentmeyer (1946) and from grapevine by Fischer and Gäumann (1929), Pesante (1947), Kublitskaya and Ryabtseva (1969), and Kublitskaya, Ryabtseva and Vorob'eva (1970). Fischer and Gäumann (1929) noted greater pathogenicity in an isolate predominantly forming mycelium in culture, but such an isolate may have greater inoculum potential in pathogenicity tests, so this report must be viewed with caution. A more pertinent observation is that of Kublitbskaya and Ryabtseva (1969) who found differential pathogenicity among isolates of *B. cinerea* to be directly correlated with the production of polygalacturonase.

Talieva (1958*b*) noted that species of *Botrytis* with a high degree of host specificity (e.g., *B. aclada* and *B. anthophila*) responded sharply in growth to autolysates from their hosts, whereas the polyphagous *B. cinerea* responded equally to autolysates from all hosts. Neither type responded to growth factors, referred to as 'bacterial vitamins'.

An interesting and unusual case of pathogenic specialization in *B. cinerea* was noted by MacNeill (1953). A strain obtained from lettuce in the Bradford Marsh area of Ontario, Canada, was extremely pathogenic to the roots and caused deep furrows in them. The roots became coppery-green and eventually rotted completely. The strain rarely appeared on the foliage and then only after the plant collapsed.

By contrast, Schnellhardt and Heald (1936) concluded that there was no host specificity among isolates of a *Botrytis* of the *cinerea* type isolated from apple, pear, pea, geranium, and *Gloxinia* and inoculated into apple fruits; and Peyer (1963) found no evidence of pathogenic races in isolates of *B. cinerea* from the stems and berries of grape; and Morotchkovski and Vitas (1939) found isolates of *B. cinerea* from sugar beet, soil, *Pelargonium,* rose, lemon, *Primula,* and *Chrysanthemum* to be equally pathogenic to stored sugar beet.

INFECTION

Infection from conidia

The physical processes involved in host penetration by germ tubes of *Botrytis cinerea* have long been known. Ward (1888) described the infection of lily by germ tubes of a *Botrytis* sp. and Nordhausen (1899) investigated infection by *B. cinerea.* The process is best known, however, from the work of Brown and his colleagues, reviewed by Brown (1934, 1936, 1948, 1955) and, more recently, from the electron-microscope studies of Bessis (1972), Abu-Zinada, Cobb, and Boulter (1973), and McKeen (1974).

Penetration of an intact host cuticle is purely mechanical according to Blackman and Welsford (1916) and Brown and Harvey (1927). The conidium, lying on the cuticle in a drop of water or nutrient solution, soon becomes attached to the substratum by means of an adhesive mucilaginous sheath investing the germ tube. Often penetration occurs directly from the distal end of the germ tube, but sometimes a typical digitate appressorium forms first, also invested by a mucilaginous sheath. In the area of contact between the germ tube tip, or appressorium, and the host cuticle, a small peg outgrowth penetrates the cuticle over a very small area (0.2 μm in diameter; McKeen 1974), evidently by exerting mechanical pressure, because a small depression can often be seen below it. The *tüpfel* (pits), observed by Pfaff (1925) on appressoria of *B. cinerea,* have apparently not been reported since

and their function is unknown; perhaps they are artifacts and Pfaff misinterpreted infection pegs.

McKeen (1974), reexamining the infection of leaves of *Vicia faba* by *B. cinerea,* differed from Brown and his colleagues; McKeen thought that the cuticle was dissolved enzymatically rather than pierced by mechanical pressure because the hole in the cuticle appeared to be sharp and clean without curled edges. Furthermore, McKeen could not see an indentation of the cuticle or epidermal wall during penetration, and he queried the early reports of penetration of undegradable materials such as gold film.

Some support for McKeen's view is provided by Linskens and Haage (1963) who found that an isolate of *B. cinerea* could degrade potato leaf cutin and *Gasteria* leaf cutin. Shishiyama, Araki and Akai (1970) also reported a cutin-esterase from *B. cinerea,* which, they suggested, could reduce the mechanical strength of the cuticle and so aid penetration. In the latter case, the enzyme was prepared from homogenates of mycelium growing in a medium containing tomato cutin as the sole carbon source. The enzyme hydrolyzed the minor fatty acids linked to the basic structure of cutin, but the major component, dihydroxyeicosanoic acid, did not appear in the hydrolysate. A preparation of tomato cutin had visibly, though slightly, degraded in structure after prolonged incubation with the enzyme (30 days at 28°C). Because the enzyme was not shown to be secreted in the infection drop and because of its apparent slowness of action, Shishiyama et al. thought that the enzyme played a very small part, if any, in infection, although it may play some part in saprophytic nutrition (Linskens and Haage 1963). Verhoeff (personal communication, 1973), however, obtained evidence from the infection of tomato fruit by *B. cinerea* that fungal cutinase probably plays a larger part in the penetration process than the results of Shishiyama et al. (1970) would suggest.

After the bean-leaf cuticle was penetrated, McKeen found that the epidermal wall began to degrade and to split into two or more layers. The cuticle was pushed upwards, sometimes clear of the underlying and rapidly swelling epidermal wall. He detected esterase activity within the germ tube tip at the time of penetration and suggested esterases could aid in plasticizing the fungal wall and in dissolving the host cuticle. The small volume in which esterase activity could be detected histochemically could account for the failure of earlier workers to detect it by other means; also, activity soon disappears, within 23 h. At the time of penetration the infection peg is covered only by the fungal plasmalemma through which cutinase could pass readily.

Abu-Zinada et al. (1973), working with *B. fabae* and *V. faba,* also concluded that penetration is probably accomplished by hydrolysis of the host cell-wall by fungal enzymes, although this stage is preceded by an attachment stage, with frequent invagination of the wall subsequently penetrated. There was no appressorium in the infection studied by Abu-Zinada et al.

Louis (1963) agreed with Brown et al. on the penetration of bean leaves *(V. faba)* and tomato fruit. She showed that penetrations from a single germ-

tube of *B. cinerea* could induce a necrotic reaction in the neighboring host-cells in bean and tomato, but not in petals of *Cyclamen* and geranium or in leaves of *Fuchsia.* This behavior appeared to be related to cuticle thickness; the hosts with a thin cuticle had no necrotic reaction and were invaded by many germ tubes that formed confluent infections, whereas in bean and tomato, hosts with a thicker cuticle, the infections remained discrete.

Often (for example, on almond petals, Ogawa and English 1960) the appressorium is formed at the junction of adjacent epidermal cells; when penetration is complete, the hypha widens beneath the cuticle and penetrates the remainder of the wall.

In *Lilium* sp. (an edible lily), infection by germ tubes of *Botrytis elliptica* occurs directly through the leaf cuticle without the aid of wounding and spreads more rapidly on the lower than the upper surface because of the thicker cuticle and the absence of stomata on the upper surface (Ikata and Hitomi 1933).

As well as penetrating the cuticle directly, germ tubes of *B. cinerea* are also able to penetrate stomata of bean *(Vicia faba)* and *Dahlia* leaves (Louis 1963), apple lenticels (Horne 1932, 1933; Colhoun 1962) and all types of cracks and insect punctures in grape berries (for example, du Plessis 1937; Nelson 1951*a*; Stalder 1953*b*; Henner 1964; Bessis 1972; and Tonchev 1972), and in many other damaged tissues, such as those of tuberous rooted *Begonia* stems cracked by excessive nitrogen applications (Tompkins 1950) (see PART 4, *"Resistance"* and *"Predisposition"*). Germ tubes of *B. gladiolorum* penetrate stomata of leaves of *Gladiolus* when stomatal droplets are exuded in cool, moist conditions (Bald 1952).

Using a scanning electron microscope, Bessis (1972) found that germ tubes of *B. cinerea* congregated above peristomatal tissues on grape berries, where there were minute cracks and fragments of disintegrated tissue. There was also a mucilaginous deposit in this region, apparently secreted by the host rather than the fungus. Penetration occurred in the peristomatal region but only rarely through the stoma itself. In effect, the fungus seemed to behave as a saprophyte on the surface of the peristomatal area before penetrating beyond the cuticle.

The stimulus for penetration was studied by Brown and Harvey (1927). Prior to this work, there had been considerable controversy about the factors affecting the direction of germ-tube growth, and a number of possibilities were considered and rejected by Brown and Harvey and in the reviews by Brown (1934, 1936). Positive chemotropism was first postulated by Miyoshi (1894, 1895) but Fulton (1906) failed to confirm Miyoshi's results and suggested that germ tubes grow away from their own staling products in the infection drop. Graves (1916) found that some, but not all, plant extracts had a positive chemotropic effect on germ tubes, more so than sucrose, but he also supported Fulton's view. Miyoshi (1895), Lind (1898), and Brown and Harvey all found that penetration of non-plant membranes, such as paraffin wax and gold leaf, could occur in the absence of any apparent chemotropic stimulus, and Brown

and Harvey confirmed this with epidermal strips from *Allium cepa* bulb scales and leaves of *Eucharis mastersi* and *E. amazonica,* none having stomata. Penetration was achieved both in strips still with damaged cells attached to them, and in washed strips from which possible chemotropically stimulating cell contents had been removed. Penetration of washed strips occurred equally well in either direction.

Brown and Harvey (1927) found that germ tubes of *B. cinerea* could not penetrate the cuticle of intact *Eucharis* leaves when the tissue below was fully turgid but penetration did occur in leaves in which the cells were plasmolyzed by sucrose solutions, or killed. Similar results were obtained with leaves of *Hedera helix, Nerium oleander,* and *Prunus laurocerasus.* Brown and Harvey could not explain their results in terms of a chemotropic stimulus to penetration, nor in terms of a chemical or enzymic action on the cuticle; they could only explain them in mechanical terms and concluded that the only stimulus for penetration is contact.

Robinson (1914) found that germ tubes of a *Botrytis* sp. were negatively phototropic, and Gettkandt (1954) and Jarvis (1972) confirmed this for *B. cinerea.* Gettkandt suggested that this behavior would confer some advantage to the parasite in the infection process, but as *B. cinerea* can infect plants in both darkness and light, phototropism would appear to play an unimportant part in infection. Borecka, Bielenin, and Rudnicki (1969), however, found light to enhance the infection of strawberry flowers from conidia of *B. cinerea.*

Infection from conidia is fully dependent on the maintenance of a water film or drop over the conidium, its germ tube and appressorium (Brown 1915, 1916; Blackman and Welsford 1916; Brown and Harvey 1927; Jarvis 1962*a*; Borecka, Bielenin, and Rudnicki 1969; and Gärtel 1970). Jarvis (1962*a*) and Gärtel (1970) showed that, although a water film is essential to germination, the further growth of mycelium is less dependent on free water. Others have claimed that infection can occur at high relative humidities in the absence of free water but these reports are suspect (Schein 1964; and see PART 3, "Growth"). However, high relative humidities maintain infection drops in the field and so enhance the likelihood of successful infection. Epidemics and severe storage rots caused by *Botrytis* spp. are invariably associated with prolonged moist conditions (e.g., Rose 1926; Lauritzen 1930; Baker 1946; Nelson 1949, 1951*a*, 1951*b*; Stalder 1953*a*; and Tonchev 1972).

Stevenson (1939) noted that lettuce cotyledons were attacked by *B. cinerea* mainly when the testa remained over them to form a damp incubation chamber.

Shoemaker and Lorbeer (1971) showed that *B. squamosa* successfully attacked onion leaves only if they were continuously wet for at least 6 h and that the number of lesions increased significantly for each 3-h interval after 6 h. Necrosis from the leaf tip downwards increased similarly. Continuously wet plants were attacked within the temperature range 9–23 °C.

Infection can take place very rapidly in many diseases caused by *Botrytis* spp. On strawberry fruits, conidia of *B. cinerea* began to germinate within 90 min of inoculation (Hennebert and Gilles 1958) and most had germinated in 3–5 h at the optimum temperature of 20°C. However, penetration did not occur until about 20 h after inoculation when the second phase of germination, germ tube growth, began (see PART 3, "Growth") with its optimum temperature of 30°C. The incubation period (sensu van der Plank 1963) was thus regulated by two temperature optima. The interval between inoculation and the appearance of the first symptom was about 2 days for ripe strawberry fruit; this interval included the pre-penetration period for spore germination, so the incubation period was about 28 h and the latent period, ended by the appearance of conidiophores and conidia, was about 24 h longer. In grapes, a latent period of 36 h was recorded by Guillon (1906*b*).

B. elliptica on *Lilium candidum* produced conidiophores within 7 h and conidia within 9 h of rosettes, containing a perennating mycelium, being placed in an environment of 18°C and 97% RH (Taylor 1934). The conidia were able to germinate within 2 h to initiate secondary infections.

It might be supposed that flowers, with their secretions from the nectary and stigma, would be readily infected, and indeed they frequently are; for example Zeller (1926) found flowers of pear to be infected by germ tubes of *B. cinerea* in the stamens, styles, sepals, and sometimes the bracts on peduncles. He observed infection of epidermal hairs and of stamen filaments. The same occurs in strawberry flowers (Jarvis and Borecka 1968); and in grapes, *B. cinerea* infects the stylar end of the flower and becomes quiescent in the necrotic stigma and style (Lehoczky 1972; McClellan 1972; McClellan and Hewitt 1973; McClellan, Hewitt, La Vine, and Kissler 1973). Nonetheless, Jung (1956) examined 1500 inoculated stigmas of 61 species and could find no case in which the fungus had penetrated the style as far as the ovary. Jarvis and Borecka (unpublished) failed to germinate conidia of *B. cinerea* in undiluted nectar from strawberry and red raspberry flowers, and no report of natural infection via the nectary is known. Petals, however, are commonly infected (Trojan 1958).

McWhorter (1939) observed infection by *B. cinerea* of the glandular trichomes on the stem of *Antirrhinum majus* at the junction of the glabrous and hirsute zones and suggested that this infection occurred because of the water retentiveness of the zone or because of some property of the trichomes. Because infection followed insecticide application, infection also might have been associated with broken trichomes.

The infection of tomato petiole stubs reported by Wilson (1963) is unique in the literature, but possibly occurs more frequently. In the glasshouse crop, the lower leaves are usually removed by breaking the petiole or cutting it close to the stem, as they wilt and become senescent. In conditions of high relative humidity, which often occur at night or in prolonged humid weather, drops of water are exuded from the cut surface and the last drop is resorbed when transpiration is resumed. If conidia of *B. cinerea* are present in

the drop, many of them become lodged in clumps against irregularities in the xylem vessels some distance from the surface. There, they may be quiescent for as long as 10–12 wk before germinating in situ. The germ tubes then penetrate between the bands of spiral thickening into the surrounding parenchyma, which is rapidly colonized (Wilson 1966).

Many cases of parasitism of *Botrytis* spp. in woody tissues likely result from this type of infection, particularly when symptoms are associated with pruning, grafting, or other wounds of, for example, grapevine (Gärtel 1964, 1965*a*), black currant (Corke 1969), gooseberry (Rake 1966), and *Ribes alpinum* (Brierley 1918*a*). In apple shoots, *B. cinerea* was occasionally associated with leaf scars (Swinburne 1973).

Systemic infection is known only in the clover anther disease *(B. anthophila).* Conidia, mixed with pollen, invade the flower via the stigma and the mycelium reaches the seed to cause systemic infection throughout the life of the plant (Silow 1933). Ramazanova (1958*b*) also introduced the fungus successfully into the growing point.

Infection from microconidia

No case is known of infection of plants from microconidia; their only role appears to be one of spermatization (see PART 2, "Sexual reproduction").

Infection from mycelium

The process of infection from mycelium is essentially the same as that from germ tubes (Istvanffi 1905), although, as Jarvis (1962*a*), Gärtel (1970), and Bessis (1972) have pointed out, the mycelium almost always has a nutrient-providing saprophytic base. The inoculum potential of mycelium is therefore much greater (sensu Garrett 1970) than that of germinating conidia, and is also less dependent on the external environment (e.g., the requirement for free water in which conidia germinate). Thus Jarvis (1962*a*) found that only about 1% of infections of ripe intact strawberry and raspberry fruits occurred from conidia germinating in a persistent drop of water on the fruit surface; all other infections occurred from mycelia in saprophytic bases of some kind.

Infection from ascospores

By analogy with the genus *Whetzelinia,* it seems very likely that ascospores of *Botryotinia* spp. can infect plant tissues, healthy, senescent and moribund, although reports of such infection are few. Godfrey (1923) achieved infection of inflorescences of *Ricinis communis* with ascospores of *B. ricini,*

Hainsworth (1949) and Sarmah (1956) found ascospores of *B. theae* to infect the petals of tea flowers, and Vanev (1965) and Kublitskaya and Ryabsteva (1970) attributed primary infection of grapevines in the spring to ascospores of *B. fuckeliana,* as Bavendamm (1936) did in the case of conifers.

INFECTIVITY

Whether or not infection is achieved from conidia depends on many environmental factors such as moisture and temperature, but infectivity also depends on certain endogenous factors contributing to the inoculum potential of the conidia, as qualified by reference to the surface area of the host to be infected (Garrett 1970).

Last, cited by Gregory (1973), estimated that only about 5% of spores of *Botrytis* sp. arriving on leaves of *Vicia faba* achieved infection; this proportion is termed 'infection efficiency'.

Last and Hamley (1956), using a local lesion technique for assessing the infectivity of conidia of *Botrytis fabae,* found that the number of lesions on half-leaflets of *Vicia faba* was directly proportional to the concentration of conidia in the infection drop. The variation in lesion numbers between plants in a single pot greatly exceeded that between half-leaflets, as did variation between leaves of old, but not young, plants.

In terms of dose-probit responses, that is, the number of spores required to produce at least one lesion on 50% of the unit areas of host tissue inoculated (the ED_{50} value), Deverall and Wood (1961*a*) found that less than 10 spores of *B. fabae* were required to give 50% successful inoculations and that 10% of single-spore inoculations were successful. Wastie (1962) found that the ED_{50} value was about 4 spores, and obtained success with 13% of his single-spore inoculations. By contrast the ED_{50} value for spores of *B. cinerea* on *Vicia faba* was about 500 and only 1 single-spore inoculation in 116 attempts was successful. Wastie thought that the somewhat larger spore of *B. fabae* could account in part for these differences, which in turn might help to explain the natural host-range of the two fungi.

If the primary lesions, each caused by penetration from a single spore of *B. fabae,* were widely spaced on the leaf, the host defence mechanism prevented their further development, but if lesions were sufficiently close together, at some critical degree of crowding, there appeared to be some synergistic effect between lesions that overcame resistance.

B. fabae is a vigorous parasite of healthy bean leaves whereas *B. cinerea* is but a weak parasite of healthy leaf tissue and requires special conditions to achieve infection, although it readily invades senescent bean tissue such as aging flowers and otherwise unhealthy tissue. The infectivity of *B. cinerea* is

thus restricted by the particular host tissue attacked and by the physiological age and health status of the host.

Schönbeck (1967*a*) noted that a low incidence of infection of *Fuchsia* styles in low relative humidities could be increased to some extent by using a higher concentration of conidia of *B. cinerea.*

Brooks (1908), Brown (1922*a*), and Deverall and Wood (1961*a*), among many others, showed that the infectivity of spores of *Botrytis cinerea* was enhanced by the supply of exogenous nutrients. Although Brown found, at least in part, that enhanced infectivity was attributable to an increase in the proportion of spores germinating, Last (1960*a*, 1960*b*) found that this cause could be excluded in explaining the enhanced infectivity of old spores of *B. fabae* on leaves of *Vicia faba.* Spores, taken from cultures 25–40 days old, germinated equally well in water on bean leaves, but spores 25 days old were only one-tenth as infective as young spores and spores 35 days old one-hundredth as infective. Their infectivity was partially restored by adding orange juice or 0.2% yeast extract to the infection drop, or, more effectively, 4.5% sucrose (the main carbohydrate component of orange juice), glucose, mannose, or maltose. Fructose and galactose were less effective and arabinose, xylose, casein hydrolysate, peptone, or nucleic acid did not increase infectivity. Abrading the leaves increased the number of lesions when spores were in water and the effect was relatively greater with older spores. Honeydew secreted by *Aphis fabae* Scop., which predisposes leaves to infection in the field, also increased infectivity, presumably because of its sucrose content. Last interpreted these results to mean that aging conidia contain endogenous reserves, adequate for germination, but not for overcoming host resistance.

Using the local lesion technique of assessment, Last and Buxton (1955) and Buxton and Last (1956) found that conidia of *B. fabae,* exposed for 8 h to daylight, caused more lesions on half-leaflets of *V. faba* than conidia kept in the dark. The effect was enhanced by keeping plants in the light after inoculation. When inoculated plants were exposed to ultraviolet light, the proportion of conidia that infected leaflets increased with the interval between inoculation and irradiation. Irradiation immediately after inoculation resulted in 3% successful inoculations, an interval of 4 h in 13%, and an interval of 8 h in 93% successful inoculations. Germination evidently resulted in an increase in resistance to irradiation and the fungus was presumed to be protected from it after penetration had occurred. Irradiated leaves had increased susceptibility, so the same inoculum resulted in more and larger lesions than those of the check leaves.

As a result of ultraviolet irradiation, the infectivity of conidia of *B. fabae* was lost more rapidly than the ability to form colonies on agar. Irradiation damage to conidia was mitigated by subsequent exposure to normal daylight, both on the host and on agar (Buxton, Last, and Nour 1957). Similarly, Last (1960*b*) found that fungicide concentrations necessary to inhibit conidial germination in a *Botrytis* sp. were not necessarily those required to inhibit infection.

PREDISPOSITION

Moribund tissue

De Bary (1886) and Brooks (1908) early noted that attacks on plants by *Botrytis cinerea* were often associated with prior colonization of dead or dying plant debris and that the fungus usually attacked senescent rather than healthy tissue. Any factor that provided these conditions, therefore, predisposed plants to infection — a generality proved many times in specific cases.

Thomas (1921) found that tomato plants sprayed with a suspension of conidia of *B. cinerea* remained healthy for 2 wk in a high relative humidity but lesions rapidly appeared if pieces of diseased tissue were used as the inoculum. Bewley (1923) and Wilson (1963) also observed enhanced infection of tomato stems if the fungus was first established as a saprophyte in badly pruned leaf bases, etc. Jarvis (1963) showed that if spores of *B. cinerea* were placed between an adhering petal and the intact surface of a ripe strawberry fruit, the petal became fully colonized before infection of the fruit occurred. Similarily Kamoen (1972) observed that leaf spot of *Begonia* caused by *B. cinerea* was invariably associated with a wound or a piece of plant debris.

Senescent flowers provide an excellent substrate for prior colonization, and lesions are often associated with them, either when the flowers are still attached to the peduncle or after they have fallen onto some other tissue. Such examples are provided by Melchers (1926) for geranium, by Klotz, Calavan, and Zentmeyer (1946) for citrus, by Yarwood (1948) for apricot, by Hainsworth (1949) for tea, by Beck and Vaughan (1949) for *Saintpaulia,* by Emerson (1951) for red currant, by Leach (1955) for *Vicia faba,* by Jarvis (1962*a*) and Jarvis and Borecka (1968) for strawberry and raspberry, by Ford and Haglund (1963) for pea, by Kamoen (1972) for *Begonia,* by Lehoczky (1972) for grapevine and berries, by Strider (1973) for statice, by Kikvadze (1973) for feijoa, and by Jenkins (1974) for barley.

Other tissues, becoming senescent naturally or moribund as the result of some injury or of malnutrition, are also readily invaded and act as foci for the colonization of adjoining healthy tissue. Examples of this type are provided by Brown and Montgomery (1948), by Sommer, Fortlage, Mitchell, and Maxie (1973), and by Logsdon and Branton (1972) for lettuce; and by Johnson (1931) and by Lipton and Harvey (1960) for artichoke attacked by *B. cinerea;* by Valaskova (1963*b*) for tulip leaves attacked by *B. tulipae;* and by Moore and Leach (1968) for bean leaves attacked by *B. fabae* in the aggressive phase. Lipton (1963), however, found that postharvest tipburn in lettuce did not result in a higher incidence of decay by *B. cinerea.* Domsch (1957) considered the success of infection to be limited by the nutritional reserves of the colonized substrate and by the age of the inoculum; he attributed a decline in virulence to the gradual accumulation of inhibitory substances as well as to the depletion of food reserves.

The epiphytic flora has an important influence on infection. Conidia of *B. cinerea* seem to suffer from bacteria in the competition for nutrients (Blakeman 1972; Blakeman and Fraser 1971; and Sztejnberg and Blakeman 1973*a*, 1973*b*).

There is not always predisposition (q.v.) at the host surface but infection is usually assured if moribund host tissue is present.

Frost

Temperature is obviously of importance in predisposition and different temperatures may affect differentially the growth and infective process of the parasite and the growth and defence processes of the host. Thus, Krantz (1959) found that pre-inoculation storage at low (3°C) but nonfreezing temperatures could predispose potato tubers to attack by *B. cinerea*. Tubers kept at 15°C and 24°C before inoculation remained healthy. Stored tulip bulbs were found by Doornik and Bergman (1973) to have similar differences in susceptibility to *B. tulipae* at 5°C and 20°C. By contrast, Vasudeva (1930*a*) found that maintaining apples at 30°C for 17 days before inoculation made them susceptible to *B. allii (B. aclada)*. He was unable to relate this change to changes in content of acid, sugar, or nitrogen.

Frost damage is a common predisposing factor even if the tissues are not badly damaged (Ciccarone 1959). Thus, Abdel-Salem (1934), Brown (1935), Brown and Mongomery (1948), Weimer (1943), Halber (1963), and Jarvis (1962*a*) found lettuce, lupins, Douglas fir seedlings, and strawberry and raspberry flowers to be so predisposed, particularly if the frost was unseasonable. Kerling (1952) grew pea plants in sterile conditions and found that *B. cinerea* or frost alone caused little damage to them, but both together caused rapid death.

Wounds

Any agent that causes mechanical damage to tissues may facilitate the entry of *Botrytis* spp. Abrasion of bean leaves with diatamaceous earth prior to inoculation with conidia of *B. fabae* enhanced infection, especially by old conidia of low infectivity (Buxton, Last, and Nour 1957; Last 1960*a*); abrasion by wind-blown sand particles may also predispose beans to infection in the field. Kerling (1953) noted that sandstorms predisposed peas to foot rot caused by *B. cinerea* and *Fusarium avenaceum*.

Sun injury predisposes lettuce to head rot caused by *B. cinerea* (Abdel-Salem 1934).

Mechanical damage by machinery can also predispose a host to infection by *B. cinerea,* for example, in potato haulm (Harper and Will 1968); wind damage similarly can predispose a host to infection by *B. cinerea,* for

example, in potato haulm (Grainger 1961) and in raspberry primocanes (Jarvis, unpublished).

The damage caused by snails, slugs, and insects is often followed by *B. cinerea* (Mallet 1973; Voigt 1972).

Grapes are particularly susceptible to mechanical damage; Francot, Geoffroy, and Malbrunot (1956), Branas (1960), Henner (1964), Chaboussou (1972), and Lehoczky (1972) list as agents predisposing to *B. cinerea:* wind-blown sand particles, compression between berries, sun, hail, partial severance of the grape from its pedicel by pressures within the bunch, other fungal lesions, insects, incorrect grafting leading to grape swelling and compaction, fungicides, and undue swelling in wet soils. To this list, Vanev (1962, 1965) added prior infection by *Uncinula necator* and the effect of prolonged high relative humidities on berry swelling and splitting, and Séguin, Compagnon, and Ribéreau-Gayon (1969) the depth of rooting, the effect of soil structure and the position of the water table on water uptake, and the effect of the density of foliage on transpiration.

Water status

Tonchev (1972) investigated the role of irrigation in fruit swelling and cracking, and the subsequent development of *B. cinerea*. Over a 9-yr period, he established a correlation between berry splitting, the incidence of gray mold, and weather conditions during the ripening period. In dry years, irrigation had no predisposing effect on splitting or gray mold but in wet years additional irrigation caused the berries, which then also had a weaker skin, to burst and become susceptible to gray mold. Some cultivars were more affected than others.

Nelson (1951*a*) pointed out that wounds in grapes are probably important in giving the conidia of *B. cinerea* access to exogenous nutrients and water rather than as breaches in a mechanical barrier; in a suitable environment the fungus is able to penetrate the intact cuticle anyway, but infection is facilitated by the added nutrients (Wilcoxon and McCallan 1934). In wet weather, Stalder (1953*a*) noted the appearance of very fine cracks in the cuticle that might be entry points for the fungus. Bessis (1972), by means of the scanning electron microscope, also found cracks in the peristomatal areas through which infection occurred.

The water content of tissues is important in predisposing them to infection, even if the cuticle is not ruptured. Kerling (1952) considered that the entry of *B. cinerea* into peas is facilitated not only by the increased water: air ratio in the intercellular spaces but also by interference with normal gaseous exchange; these conditions lead to increased cell permeability combined with a decreased osmotic pressure. When potato tubers not normally parasitized by *B. cinerea* had their water content increased by 8–9% by infiltration, they became susceptible (Mishra 1953). Mishra, as well as Fer-

nando and Stevenson (1952) and Jarvis (1953), suggested that this susceptibility could be explained in terms of enhanced diffusion of pectinases; the rate of enzyme diffusion was limited by the water content of the intercellular space. A similar explanation was made by Vanev (1965) for turgid grape tissue parasitized by *B. cinerea.*

Reports of increased incidence of gray mold in plants in wet, overirrigated soils (e.g., Wilson 1937; Kirby, Moore, and Wilson 1955; and Tonchev 1972) can perhaps be similarly explained, and there may also be an effect on the transition of quiescent infections (q.v.).

Tissue in wet conditions can also be damaged by guttation (Yarwood 1952; Baker, Matkin, and Davis 1954). Guttation results in the accumulation of toxic levels of salts at hydathodes and at the ends of leaf veins, with consequent tissue necrosis; these areas are then susceptible to infection by *B. cinerea.* In *Phaseolus vulgaris* there was a positive correlation between guttation and infection (Yarwood 1952).

In contrast to the general increase in susceptibility as a result of high water content, Rubin and Artsikhovskaya (1963) noted that wilting roots of sugar beet were less resistant to *B. cinerea,* and wilting was accompanied by an increase in invertase activity. Hering and Manning (1968) found that although germination of conidia of *B. fabae* decreased on wilting leaves of *Vicia faba,* it increased on leaves recovered from wilting as compared with check leaves.

Exosmosis

In general, conidia germinate better in water on host surfaces than in water on inert surfaces in the laboratory, although sometimes they do not (Brown 1922*a*; Wilcoxon and McCallan 1934; Kovacs and Szeoke 1956; Chou 1972; Blakeman 1973; Blakeman and Sztejnberg 1973; and Sztejnberg and Blakeman 1973*a*, 1973*b*). The influence of the host tissues is usually mediated by the exosmosis of solutes into the infection drop (Brown 1916, 1922*a*). Drops of water lying on various tissues increase in conductivity and in those drops containing conidia of *B. cinerea,* germination is enhanced or not, or inhibited, depending on the tissue. The rate of exosmosis is affected by the ease of surface wetting and increases rapidly as infection begins. The materials entering such drops from grapes have been examined by Kosuge and Hewitt (1964); the materials include glucose and fructose in concentrations as high as 5×10^{-4} M, which are stimulatory to conidia of *B. cinerea,* together with amino acids, which have no marked effect. Sol (1969) demonstrated the transfer of ^{14}C from leaf photosynthate to conidia of *B. fabae* via leaf exudates. Sol (1966, 1967, 1968, 1969) pretreated leaves of *Vicia faba* in various ways to increase exosmosis and hence infection by *B. fabae.* The treatments included contact with sucrose, potassium chloride, lathanum chloride, ammonium sulfate, and calcium chloride solutions or simply keeping leaves in the dark. Cell permeability was also increased by alkenyl suc-

cinic acids, and especially by decenylsuccinic acid, which induced the exosmosis of sugars and amino acids and resulted in a higher rate of spore germination and more lesions.

Kovacs and Szeoke (1956) considered that persistent rain and dew films on leaves often contained enough solutes to exert an effect on conidial germination. Aphid honeydew may likewise predispose leaves to infection because of its sugar content (Last 1960*a*; Sode 1967).

Fungi not normally parasitic on a given host may be induced to become so by adding nutrients to the infection drop; thus *B. allii (B. aclada)* and *B. cinerea* were induced to attack apple fruits by adding nitrogen salts; the addition apparently also stimulated the production of pectinases (Vasudeva 1930*a*; Chona 1932).

Yarwood (1959) noted that adding sucrose to the substrate of detached leaves of *Vicia faba* reduced the size but not the number of lesions caused by *B. fabae.*

If water into which the nematode *Anguillulina dipsaci* had secreted enzymes was used in the inoculation of onion by *B. allii (B. aclada),* infection was enhanced, as it was in the similarly predisposed infection of cabbage by *B. cinerea* (Myuge 1959).

Volatile metabolites

In addition to the effects on conidia of direct exomosis from various tissues, Brown (1922*b*) noted that germination can also be affected by volatile materials coming from tissues. Volatiles from potato tubers and onions were inhibitory to conidia of *B. cinerea,* as were those from moist filter paper often used in incubation chambers. Other tissues emitted substances that stimulated germination, and their effects could be simulated by certain esters. Schütt (1973) found that volatile materials from the leaves and shoots of various Coniferales either stimulated or retarded the germination of conidia of *B. cinerea* and, to a lesser extent, mycelial growth. The effect of volatiles from *Abies alba, Picea abies, Pinus sylvestris* and *Pseudotsuga menziesii* was more marked in the light than the dark, and more so at 20°C than 6°C. Volatiles from *Pseudostuga taxifolia* at −6°C stimulated germination, whereas at 20°C they inhibited it.

Smith, Meigh, and Parker (1964) and Nichols (1966) found that ethylene in concentrations of the order of 0.06 ppm could predispose flowers to infection by *B. cinerea* and induce further ethylene production from carnations. The removal of ethylene from the storage atmosphere by potassium permanganate, for example, not only retards ripening of chinese gooseberries *(Actinidia chinesis)* but reduces the incidence of postharvest rots (Strachan 1968).

Ozone injury was similarly found by Manning, Feder, Perkins, and Glickman (1969) and Manning, Feder, and Perkins (1970) to predispose

potato and geranium leaves to infection by *B. cinerea;* and *Chrysanthemum* flowers were predisposed by smoke and insect damage (Taylor and Muskett 1959). In parentheses and conversely, prior infection by *B. cinerea* protected *Vicia faba* against visible ozone damage (Magdycz and Manning 1973).

McWhorter (1939) noted that attacks by *B. cinerea* on *Antirrhinum majus* occurred after applications of insecticides for thrips control; the insecticide seemed to predispose trichomes to infection, possibly because of chemical or mechanical injury or because of water retention in that zone.

An interesting interaction between *B. cinerea, Uncinula necator* (powdery mildew), and fungicides on grapes was noted by Kundert (1963). Plots were sprayed or not sprayed with a sulfur-dinocap mixture to control powdery mildew; superimposed on these treatments were sprays of copper oxychloride, or of a copper-dinocap mixture, or of dinocap alone. In all plots receiving dinocap, the incidence of gray mold increased during the season, although powdery mildew was as well controlled as by the copper oxychloride alone. Grapes sprayed with copper oxychloride had thick, russetted skins and although they tended to split open, leaving an apparently ideal site for infection by *B. cinerea*, they ripened very slowly and were less often infected than grapes receiving dinocap. Dinocap controlled powdery mildew but it induced very thin skins, which split open easily, and it prolonged the ripening period during which the grapes remained very susceptible to *B. cinerea.* Grapes with uncontrolled powdery mildew remained small and fairly thick-skinned, and they failed to ripen; they remained resistant to *B. cinerea.*

Carbohydrate status

The effect of sugar content of tissues on their susceptibility to attack by *Botrytis* spp. has been examined by many workers. Horsfall and Dimond (1957) classified *Botrytis* spp. as 'high-sugar' pathogens, that is, they usually attack tissues with a high sugar content, especially of reducing sugars. Thus grapes, both cultivars and individual berries within the bunch, are predisposed to *B. cinerea* (Roemer, Fuchs, and Isenbeek 1938; Nelson 1949, 1951*a*; Branas 1960; and Chaboussou 1972). Although Cosmo, Liuni, Calo, and Giulivo (1966) could not confirm this, they did obtain a positive correlation between susceptibility and total acids and a negative correlation with pH; but these correlations also are contrary to the experience of Horne (1932, 1933) and Horne and Gregory (1928) with *B. cinerea* on apples.

Kristofferson (1921) found a correlation between the incidence of storage rot in carrots and the reducing sugar content of four cultivars.

Kamoen (1972) found that *Begonia* leaves with a high sugar content were particularly susceptible to infection by *B. cinerea* via damaged tissues and that infection could be reduced, in part, by shading to depress the rate of photosynthesis. Barash, Klisiewicz, and Kosuge (1963, 1964) found that reducing sugars leached from flowers of safflower stimulated both the germina-

tion of conidia of *B. cinerea* and the production of polygalacturonase, xylanase, cellulase, and pectin methylesterase, and similarly Orellana and Thomas (1962) related susceptibility to *B. ricini* of castor-bean capsules to levels of leachable sugars.

In contrast, Sukhorukov, Gerber, Barabanova, and Borodulina (1933) and Sukhorukov (1957) found that cabbage leaves deprived of sugars were more susceptible to *B. cinerea,* although the method used (keeping the plants in darkness) may have induced fairly drastic changes in metabolism and perhaps senescence.

A general theory about the role of carbohydrates in predisposition has been elaborated by Grainger (1956, 1962*a*, 1962*b*, 1968). He thought that the carbohydrates surplus to the host's metabolic requirements stimulated infection, because they were available to the pathogen and aided its development. He evolved the C_p:R_s ratio as a measure of this, where C_p is the total carbohydrate content of the plant and R_s the residual dry weight of the shoot. This concept seems applicable to a wide variety of host-parasite combinations; when the ratio exceeds 0.5, plants are regarded as susceptible and above 1.0 an epiphytotic may be expected. Very young seedlings have a high C_p:R_s value giving them hypersensitivity; slightly older plants have a low value and high resistance; and maturing plants have an increasing C_p:R_s ratio and increasing susceptibility. Grainger has obtained good agreement for his hypothesis from individual strawberry fruits, which are formed in succession on a cymose inflorescence and are decreasingly susceptible to *B. cinerea,* as well as from tomato — *B. cinerea, Vicia faba* — *B. cinerea* and *B. fabae,* narcissus — *B. narcissicola,* tulip — *B. tulipae,* gooseberry fruits — *B. cinerea,* and onion — *B. allii (B. aclada).*

Possibly changing metabolism in maturing tissues likewise affects the transition of quiescent and latent infections to an aggressive state (see PART 4, "Quiescent Infections").

Many fungicides, pesticides, herbicides, and growth regulators alter the metabolism of the host, thus changing its susceptibility; many such cases have been explained in terms of altered sugar status. Zinc and carbamate fungicides were noted to increase the incidence of *B. cinerea* as a tomato pathogen (Darby 1955; Cox and Hayslip 1956; Harrison 1961; and Lockhart and Forsyth 1964) and as a grape pathogen (Stellwaag-Kittler 1964; Chaboussou 1970). Lockhart and Forsyth suggested that maneb and zineb stimulate the release of nutrients to the fungus. Zineb also predisposes onion to attack by *B. allii (B. aclada)* because, van Doorn (1959) suggests, of the prolonged ripening period. Crowdy and Wain (1950) found that 2,4,6-trichloro- and pentachlorophenoxyacetic acids, pentachlorophenoxy-*iso*-butyric acid, and α-(2-naphthyl)-phenylacetic acid checked the spread of individual lesions of *B. cinerea* on *Vicia faba* but not the number of lesions, an effect ascribed by van der Kerk (1963) to alterations in carbohydrate metabolism of the host. Corke (1969) considered that some fungicides may stimulate detoxification mechanisms.

Many herbicides interfere with carbohydrate status: lettuce became highly resistant to *B. cinerea* following the application of 2,4-dichlorophenoxyacetic acid and MCPA (Wagner 1955) and *Vicia faba* became highly resistant to *B. fabae* after 2,4-D (Mostafa and Gayed 1956; Gayed and Mostafa 1962); Grummer (1963) obtained a close correlation between the incidence of *B. fabae* on beans and the dose rate of simazine, which inhibits the Hill reaction, and Orth (1967) found that chlorpropham increased the susceptibility of tulips to *B. tulipae*. Davis and Dimond (1953, 1956) discussed the similar role of growth regulators in altering disease resistance, and Smith and Corke (1966) obtained good control of *B. cinerea* on black currant with (2-chloroethyl) trimethylammonium chloride, as did Natalina and Svetov (1972*a*) on grapes. Moore and Leach (1968) used 6-benzylaminopurine to delay senescence of bean leaves and hence the onset of the aggressive development of *B. fabae*. However, senescent leaves were attacked more aggressively after this treatment, as were senescent leaves in wider plant-spacings.

Nitrogen

Chaboussou (1970) noted an increase in the incidence of *B. cinerea* on grapes treated with DDT and attributed the increase to an increased nitrogen content of the berries (see also "Fertilizers" below).

Light

Light affects the carbohydrate status of plants and also other metabolic processes of both host and pathogen. Excessive shade predisposes glasshouse tomatoes to *B. cinerea* (Bewley 1923), as does snow and mulch cover in the case of Douglas fir seedlings attacked by *Botrytis* sp. (Sato, Shoji, and Ota 1959). On the other hand, Segall and Newhall (1960) found that *B. allii* caused lesions on onion leaves only in the light and Borecka, Bielenin, and Rudnicki (1969) obtained more infection of strawberry flowers by *B. cinerea* in the light than in the dark. Kamoen (1972) noted the same for *Begonia* leaves and attributed a higher incidence of infection by *B. cinerea* to a higher sugar content of the leaves in bright light; the higher sugar content also led to a greater production of the toxin citric acid. Exposure to ultraviolet light had no effect on the incidence of *B. cinerea* in lettuce (Sirry 1957*b*) but resulted in more infection of *Vicia faba* by *B. fabae* (Buxton and Last 1956). Bazzigher (1953) found antibiotic activity against *B. cinerea* in *Phaseolus vulgaris* to be enhanced by light and decreased by darkness.

Ultraviolet irradiation of bean leaves before inoculation with conidia of *B. fabae* increased the proportion achieving infection (Buxton, Last, and Nour 1957).

Microorganisms

Predisposition may be effected by prior damage to plants by other fungi; for example, *B. cinerea* was frequent on lesions of *Puccinia asparagi* on asparagus (Ogilvie, Croxall, and Hickman 1939) and on lesions of *Puccinia antirrhini* on *Antirrhinum* sp. (Baker 1946), on lettuce attacked by *Bremia lactucae* (Smieton and Brown 1940; Louvet and Dumas 1958) and by *Pythium* sp. (Basile 1952), on sunflower heads attacked by *Whetzelinia (Sclerotinia) sclerotiorum* (Crisan 1964), on *Pelargonium zonale* attacked by *Corynebacterium fascians* (Maas Geesteranus, Koek, and Wegman 1966), on grapevine attacked by *Uncinula necator* (Boubals, Vergnes, and Bobo 1955; Branas 1968; and Vanev 1962), on grapevine following the application of non-copper fungicides for the control of *Plasmopara viticola* (Emiliani 1963; Stellwaag-Kittler 1964), and on *Saintpaulia* injured by mites (McDonough and McGray 1957). Similarly, *B. squamosa* was often associated with *Peronospora destructor* on onion (Hickman and Ashworth 1943), and *B. globosa* with aecidia of *Melamspora* sp. on *Allium ursinum* (Hennebert 1958).

Prior infection by the pea leaf roll virus has been observed to predispose bean plants to *B. cinerea* (Tinsley 1959).

Powell, Melendez and Batten (1971) found that tobacco plants, exposed to the nematode *Meloidogyne incognita* for 4 wk, were unusually susceptible to *B. cinerea.*

Pollen

The presence of pollen grains in the infection drop affects spore germination (Brown 1922*a*) and is often associated with increased infection by *B. cinerea;* such an increase has been noted on stone fruit blossoms (Ogawa and English 1960), on holly flowers (Batchelder and Orton 1962), on strawberry flowers and fruit (Jarvis and Borecka 1968; Chou and Preece 1968; and Borecka, Bielenin, and Rudnicki 1969), on *Begonia* leaves (Kamoen 1972), on grape flowers (McClellan 1972; McClellan and Hewitt 1973), and on spikelets and leaves of barley (Jenkins 1974). This effect is attributed, at least in part, to the relatively high content of abscissic acid in pollen and other floral parts (Borecka and Pieniazek 1968; Borecka et al. 1969) and possibly to the presence of bacteria in the pollen (Borecka, unpublished). In some way, pollen also enables the fungus to overcome the antibiotic effects of wyerone acid in *Vicia faba* (Mansfield and Deverall 1971). Strange, Majer, and Smith (1974) thought that choline and betaine, two major components of wheat anthers that stimulate *Fusarium avenaceum,* were not involved in the pollen effect on *B. cinerea,* but they did find that a wheat-germ extract could increase the virulence of *B. cinerea* on bean leaves.

Fertilizers

The nutritional status of plants greatly affects the incidence of *Botrytis* spp. (Krauss 1969), especially deficiencies leading to premature senescence. Examples of deficiencies that increase the incidence of disease are:

N, P, K, Mg	*B. cinerea* (Brooks 1908)
P, K	*B. fabae* on *Vicia faba* (Glasscock, Ware and Pizer 1944; Moore 1944; Furse 1949; Leach 1955)
K	*B. cinerea* on potato (Harper and Will 1968)
K	*B. cinerea* on grape (Pevov, Chepelenko, Perova and Ilyashenko 1973)
K	*B. cinerea* on peas (Wijngaarden and Ellen 1968)
K, Mg	*B. tulipae* on tulip (Valaskova 1963*b*)

Conversely, excessive nitrogen in particular may predispose in some cases:

B. cinerea on strawberry (Darrow and Waldo 1932; Vukovits 1962)

B. cinerea on stored nursery stock (Haas and Wennemuth 1962)

B. cinerea on *Chrysanthemum morifolium* (Hobbs and Waters 1964)

B. cinerea on grapevine (Delas 1972)

B. allii on onion (Vaughan 1960)

One effect of excessive nitrogen is usually an excessive vegetative growth that produces microclimates conducive to infection, and, as Delas (1972) pointed out, similar effects could be obtained by other cultural modifications. Delas considered that the predisposing effects of excessive nitrogen result less from higher nitrogen content in grape berries than from other changes in the physiology of the whole plant. By contrast, Meriaux, Libois, N'Guyen van Long, Biol, Naudin, and Collin (1972) could find no effect of higher nitrogen applications in a young vineyard on the incidence of gray mold over a 3-yr period, and only a slight increase in the nitrogen content of the berries.

Verhoeff (1968) found that increasing the level of soil nitrogen decreased the incidence of stem gray mold in tomatoes; in this case the increased nitrogen probably delayed senescence and hence the development of latent infections (q.v.).

Calcium in correct amounts usually confers some resistance (q.v.) on plants, probably partly because of its effect on the structure of cell walls. Calcium deficiency is reported to increase gray mold of beans (Deverall and Wood 1961) but Knoblauch (1958) reported an increase in the incidence of *B. allii* on shallots treated with calcium nitrate.

The incidence of the chalky-seed condition in pea seed was correlated with the incidence of attack by *B. cinerea* (Sode 1971).

In soils having a pH below 5.0, Sirry (1953, 1956, 1958) found *B. cinerea* to be more severe on lettuce and potato, *B. fabae* more severe on beans, and *B. allii* more severe on onions. Grainger (1968) found that the strawberry cultivar Templar was least severely affected by *B. cinerea* when the soil pH was 5–5.5, and the cultivar Cambridge Vigour at soil pH of 5.5–6.

The enrichment of air in a tomato glasshouse with carbon dioxide has been reported (Anon. 1967) to result in a higher incidence of *B. cinerea,* but this effect could have resulted from an unsuitable microclimate in the poorly ventilated house; the foliage was also considerably denser than in an unenriched house and may have had a higher sugar content.

Trace elements have some effect on the general health status of plants as well as perhaps on resistance mechanisms and the fungus; Timchenko (1957) found boron and copper to decrease the incidence of *B. cinerea* on sunflower and Brandenburg (1942) noted that *B. cinerea* was secondary on boron-deficiency lesions on cauliflower and kohlrabi.

PATHOGENESIS

Most species of *Botrytis,* with the possible exception of *B. convoluta* (Maas and Powelson 1972), secrete pectic enzymes and other enzymes that degrade cell walls; the host cells die, and hyphae pass through infected tissue, starting along the lines of middle lamellae (Ward 1888; Wood 1960; and Brown 1948, 1965). The net result is that having achieved entry into the host, the fungi live saprophytically on the dying and dead host tissues, almost always parenchyma, and continue to colonize tissues at the edge of the lesion. However, hyphae never parasitize healthy tissues in the sense that obligate fungi do; hyphal tips are some distance behind their excreted enzymes and toxins and so always in moribund tissue. The fungi thus continue to build up a saprophytically based inoculum potential both for continued colonization by hyphae and for sporulation. In the case of *B. cinerea,* and probably other species, the process of degradation evidently continues on the dead shoot (Hudson 1968) and in the soil with the aid of cellulases, pectinases, cutinase, and other enzymes (see PART 1, "Introduction").

Histologically, the distribution of mycelium in strawberry fruits invaded by *B. cinerea* has been described by Stevens (1916) and Powelson (1960), in grape berries by Istvanffi (1905) and Nelson (1956), and in dry and fleshy onion scales by Clark and Lorbeer (1973*a*, 1973*b*). In all of these, the hyphae penetrate mostly along the line of middle lamella but eventually the cell walls, in various stages of degradation, are penetrated, sometimes apparently mechanically. Often cells are entered at the junction of two neighboring cells. In grapes, early separation of the epidermis from the underlying tissues gives the condition 'slipskin' (Barretto 1896) and Nelson found that the

periclinal cell walls were disrupted more readily than anticlinal walls, probably because of component differences in their respective pectins. Brown (1915) had also attributed differences in the action of the macerating factor to structural differences in the cell walls.

Enzymes

A major difficulty in work on the pectinase complex has been to correlate in vitro activity of the various enzymes with their role in infection and pathogenesis. Probably only the ill-defined protopectinase or 'macerating factor' (Byrde and Fielding 1962) is of immediate pathogenic importance in host-cell separation and the remaining factors are of greater significance in the nutrition of the fungi during their saprophytic phase (Peltier 1912); see PART 1, "Introduction".

Brown (1915), Tribe (1955), and Fushtey (1957) were never able to separate the macerating and toxic activities in preparations from *B. cinerea*. By growing *B. cinerea* for varying periods in media containing different proportions of pectin and glucose, Jarvis (1953) obtained culture filtrates with differential pectinase activity and hence circumstantial evidence that the macerating activity is distinct from polygalacturonase, pectin methylesterase, and depolymerase. Further, macerating activity on potato-tuber discs was maximal at pH 2.6 and at pH 6.2, which agreed with the pH optima for the pectin viscosity-reducing enzyme depolymerase, but not with the pH optima for pectate depolymerase. Evidence from thermal inactivation also indicated the distinction between macerating activity and other pectinase activity. The relationship between maceration and pectinase activity was also examined by Kaji, Tagawa, and Yamashita (1966). They found pH optima of 3.0 and 5.0 for a culture filtrate from *B. cinerea* macerating potato tissue, and pH optima of 1.5 and 4.5 for the bark tissue of *Wikstroemia sikokiana*. A bimodal response was also found for endopolygalacturonase, at pH 3.6 and 5.4, but only one peak for exopolygalacturonase at pH 5.0 and one peak for pectin methylesterase at pH 3.5–4.5. They concluded that macerating activity was probably the result of joint action of endopolygalacturonase and pectin methylesterase.

Tani and Nanba (1969) identified 3 kinds of macerating activity among culture filtrates from 10 isolates of *B. cinerea*: one enzyme had a pH optimum at 2.7, like Jarvis' enzyme; a second had its optimum at pH 5.5 and was inactivated at low pH values; and the third degraded mitsumata inner bark but not potato tissue and was also inactivated at low pH.

Maceration of parenchyma can occur very rapidly and is probably accomplished primarily by breaking lateral linkages of divalent ions or hydrogen bridges between parallel pectic and other carbohydrate chains and possibly protein chains (Ginzburg 1961; Joslyn 1962), rather than by the action of enzymes decreasing chain length. However, no proteinase activity was detected by Porter (1966) in apple and tomato fruits infected by 2 isolates of

B. cinerea, although proteinase activity was detected in cultures of *B. cinerea* by Lyr and Novak (1962), Tseng and Lee (1969), and Astapovich, Babitskaya, Hrel, and Vidzischchuk (1972).

In *Monilinia fructigena,* also a soft-rotting fungus, maceration has been attributed to pectin methyl-*trans*-eliminase (Byrde and Fielding 1968) but the enzyme is thought to act on the substrate in the host-cell membrane or in the protoplast (Mount, Bateman, and Basham 1970).

Verhoeff and Warren (1972) found that enzyme activity varied in tomato plants parasitized by *B. cinerea*; pectin methylesterase, endo- and exopolygalacturonase activity was detected in petioles and fruit, but cellulase was detected only in those parts softened by the advancing fungus. Polygalacturonate *trans*-eliminase was found only in the softened areas of petiole stumps. Verhoeff and Warren considered that *B. cinerea* itself produced all the enzymes necessary for pathogenesis in tomato.

Toxins

The cytoplasm of cells is killed before fungal hyphae advance into dead tissues (de Bary 1886; Ward 1888; Nordhausen 1899; Brown 1915; Stevens 1916; Menon 1934; Bocharova 1940; Jefferson, Davis, Baker, and Morishita 1954; Akai, Fukutomi, Ishida, and Kunoh 1966; Tichelaar 1969; Gärtel 1970; and Jamart and Kamoen 1972), which are then digested by the fungus (Peltier 1912; Talieva and Plotnikova 1962). Smith (1902) proposed that the toxin responsible was oxalic acid, but Peltier (1912) and Brown (1934, 1936, 1965), reviewing the evidence, felt that the toxin was not oxalic acid, but was either the macerating factor or so closely linked to it as to defy separation (Tribe 1955; Fushtey 1957; Byrde and Fielding 1962; and Tseng and Mount 1974). *B. cinerea,* however, is capable of producing oxalic acid in culture (Gentile 1954; Jamart and Kamoen 1972; and Kamoen 1972), as is *B. allii* and possibly *B. globosa* (Hellmers 1943).

Kamoen (1972) and Jamart and Kamoen (1972, 1974*a*) found citric acid in culture filtrates of *B. cinerea,* sometimes with oxalic acid, and in sap expressed from *Begonia* leaves and containing conidia. Citric acid also occurred in yellow tissue of infected leaves, that is, in the zone containing hyphal tips and extending a little beyond them. Citric acid reproduced the yellowing symptom in leaves (Kamoen 1972; Kamoen and Jamart 1974*a*) and so satisfied the criteria for a vivotoxin as defined by Dimond and Waggoner (1953).

Kamoen (1972) proposed a hypothesis for pathogenesis by toxins in *Begonia* leaves. The cell walls contain a certain amount of water, depending on the plant's environment, and corresponding films of water of various thicknesses on the walls bounding intercellular spaces. The thickness of the film, which tends to be greater in the yellow zone because of increased cell permeability, largely determines the rate of enzyme and toxin movement in

advance of the hyphae (as Jarvis 1953 had also suggested for pectinases). As conditions become drier, the translucent, water-soaked appearance of the yellow zone disappears and fungal activity slows. Eventually, a dark zone appears at the edge of the green tissue and fungal development is stopped. In resumed wet conditions, this barrier can be breached in a few points, from which fungal invasion begins again.

Toxins, other than citric and oxalic acids, have frequently been invoked in many disease situations, particularly by many Russian workers in the pathogenesis of *B. cinerea* on cabbage (Rubin and Artsikhovskaya 1963). Artsikhovskaya and Rubin (1937) noted that a zone of cell death extended beyond the hyphal zone, especially in the susceptible cultivar No. 1. Ovcarov (1937) considered that thiourea accumulating in tissues parasitized by *B. cinerea* could account for yellowing of leaves and a reduction in photosynthetic activity. Gentile (1951), Sautoff (1952, 1955), and Bazzigher (1953), obtained toxins in culture filtrates of *B. cinerea.* Krasil'nikov (1952) found that honeydew became phytotoxic after *B. cinerea* had grown in it. Bran cultures of *B. cinerea* induced some browning and soft rot in tomato stems, in common with many other wilt and root-rot pathogens, which Winstead and Walker (1954) thought to result from pectin methylesterase activity.

Purkayastha (1969, 1970) obtained culture filtrates from both *B. cinerea* and *B. fabae* that caused wilt and necrosis of cut shoots of *Vicia faba,* as well as browning of the primary root and softening of the root tip and of stem segments. Wilting was accompanied by vascular plugging and browning of the vessel walls. The active principles were non-dialysable and partially thermolabile, and their activity was influenced by culture conditions. Purkayastha (1969, 1970) also detected phytotoxicity in *Botrytis*-infected bean leaves.

Kamoen and Jamart (1974*b*) found a phytotoxic polysaccharide in *Begonia* leaves attacked by *B. cinerea.*

The biochemical effects of toxins produced by *B. cinerea* in cabbage tissues have been examined extensively by Rubin and his students (Rubin and Artsikhovskaya 1963). In general the toxins, resolvable into polysaccharide and acid fractions, interfere with oxidative processes (Chetverikhova 1952; Krasil'nikov 1953; Ladygina and Rubin 1957; Ladygina 1962; Aksenova 1962, 1964; Artsikhovskaya 1946; Rubin and Aksenova 1964; and Rubin and Ladygina 1964); thus the toxins increase invertase, peroxidase, and cytochrome oxidase activities and oxidative phosphorylation in affected tissues and induce the synthesis of enzymes and other proteins (Rubin, Aksenova, and Brynza 1973; Rubin, Aksenova, and Kozhanova 1973; and Rubin, Aksenova, and Nguyen Din Guen 1971*a*, 1971*b*). The identity of components is still unknown, as is their relation to Brown's toxin.

The effects of *Botrytis* species on plant anatomy and metabolism are complex and probably vary with each host-parasite combination (Akai, Fukutomi, Ishida, and Kunoh 1966). *B. allii (B. aclada)* secretes substances in advance of the hyphae; these substances reduce nuclear size in epidermal cells of onion bulb scale leaves, and the effect decreases with distance from

the inoculum, up to 2 cm. Nuclei in contact with hyphae disintegrate. Culture filtrates also cause nuclear disintegration and reduction in DNA content (Kulfinski and Pappelis 1971*a*, 1971*b*; Kulfinski, Pappelis, and Pappelis 1973; and Somasekhara and Pappelis 1973). The toxin of *B. cinerea* also causes a reduction in nuclear size in cabbage (Aksenova 1964), especially in the susceptible cultivar No. 1.

Ilieva (1971) considered that toxins from *B. cinerea* were responsible for initiating abscission of inoculated tomato petioles.

Evidence of considerable metabolic activity in apple fruits infected by *B. cinerea* was adduced by Fischer (1950); the temperature at a distance of 0.6 cm from the point of infection was 0.06°C higher than at a distance of 2.1 cm and 0.09°C higher than at a greater distance.

Lesions caused by *Botrytis* spp. and especially by *B. cinerea* often have a water-soaked appearance and Yarwood (1966) showed that water did indeed accumulate in broad-bean tissues infected by *B. cinerea.*

Restricted lesions

Understanding the pathogenesis of *Botrytis* spp. on onion has long presented problems. Yarwood (1938) found that oval, whitish-gray lesions on living leaves and flower stalks of onion were sterile, although on dead material *B. cinerea* usually spored. The symptoms were reproduced by inoculation and when conditions for infection were good, lesions merged eventually to cause wilt and death from the leaf tip down. Yarwood considered this to be analogous to chocolate spot of beans and ghost spot of tomato, and another example of nonaggressive infection. Segall (1953) found that while onion blast or leaf spotting could be caused by various *Botrytis* spp. including *B. allii (B. aclada), B. cinerea, B. tulipae,* and *B. paeoniae* by inoculation, only *B. allii* could be found in the field in New York State, sporing on dead foliage, but not on leaf spots. Further, Segall could find no evidence that penetration had occurred through the cuticle or stomata, and Segall and Newhall (1960) could not isolate the fungus from leaf spots, nor find mycelium in the tissues. Leaf spots were formed when spores were placed on the leaf but only in the presence of light, and the spot apparently resulted from the separation of the epidermal cells from the palisade layer. Eventually the parenchyma became disorganized. Spots were also induced by a toxin in culture filtrates, in both darkness and light, and germinating spores were thought also able to secrete a toxin. This finding is in contrast to the conclusion of Brown (1915) that spore secretions by *B. cinerea* do not act if the cuticle remains intact. Perhaps the onion cuticle differs in some way from those studied by Brown (mainly petal cuticles); Scott, Hamner, Baker, and Bowler (1957, 1958) thought plasmodesmata were continuous right through the wall and cuticle of onion epidermal cells. If so, toxins could reach the cytoplasm through them; further work in this area is obviously necessary.

Hancock, Millar, and Lorbeer (1964) tried to explain the earlier observations of Hancock and Lorbeer (1963) on the pathogenesis of *B. cinerea, B. squamosa,* and *B. allii* on onion. In New York State, *B. squamosa* and *B. cinerea* were the most prevalent: the former caused elliptical lesions throughout the leaf and eventually dieback from the tips; the latter caused more superficial leaf flecks. All three fungi produced pectin methylesterase and cellulase in potato dextrose broth, detached onion leaf sections, and leaves of intact plants. *B. allii* produced a trace of polygalacturonase in broth, but more in leaves; *B. cinerea* produced a very active polygalacturonase in broth and leaves, and *B. squamosa* produced exopolygalacturonase only in detached leaves and endopolygalacturonase in broth and leaves.

A somewhat similar situation was thought to prevail in tomato ghost spot (a small necrotic spot surrounded by a light-colored halo). For many years, attempts to isolate a fungus from the spots were unsuccessful (Bewley 1923; Ainsworth, Oyler, and Read 1938; Darby 1955; Owen and Ferrer 1957; and Ferrer and Owen 1959). Ainsworth, Oyler, and Read reproduced the disease by inoculation; Owen and Ferrer were the first to demonstrate the presence of *B. cinerea* in the spots, but only Verhoeff (1970) succeeded in isolating it. Ainsworth et al. thought that the symptoms were produced by the germ tubes penetrating the cuticle of immature fruits, secreting pectinases and thus separating the epidermis from the underlying tissues; the air gap so formed produced the halo effect. Verhoeff reexamined ghost spot and found that penetration did indeed occur. No mycelium could be found in the necrotic cells, though their dense contents make observations difficult; however, the fungus could be isolated from them. He obtained typical symptoms by inoculating fruits with only a few dry conidia. With many conidia, however, scab-like lesions resulted and, under conditions of high relative humidity, large blisters were formed before the fungus spread through the parenchyma. Under conditions of low humidity, necrotic areas appeared. Verhoeff thought it possible that meristematic activity of the rapidly expanding fruit limited the growth and enzymatic activity of the fungus in normal growing conditions but failed to limit them when conditions were very humid or when many conidia were used as the inoculum. He considered ghost spot as an example of latency (q.v.).

The blistering noted by Verhoeff in tomato fruits is paralleled by that noted by Beaumont, Dillon Weston, and Wallace (1936) on tulip flowers infected by *B. tulipae* in very humid conditions.

Nelson (1949) observed a banded appearance on infected grape berries and distinguished 3 zones: the outer, light-colored zone represented separation of the epidermis from the underlying tissues (reminiscent of tomato ghost spot and onion blast); the middle zone, dark and circular, was an area of dead protoplasts; and the inner translucent zone was one of further disorganization. Gärtel (1970) also observed repetitive parallel banding of this type on grape berries but he considered that differences in temperature between day and night were responsible. During the night, the fungus grows slowly, forming stout, closely packed hyphae that show through the cuticle

as a dark zone; during the warmer days, thin, unbranched hyphae are formed that are hardly visible through the cuticle. This banding is also characteristic of lesions caused by *B. cinerea* on raspberry canes (Jarvis 1962*a*) and of those caused by *B. cinerea* on *Begonia* leaves (Jamart and Kamoen 1972), although whether these bands are caused by different types of cell degradation or by different types of fungal growth is unknown.

Kamoen (1972) suggested that the zones on *Begonia* leaves resulted from periods of fast hyphal growth and enzyme production in wetter conditions, alternating with periods of slow hyphal growth and toxin production in drier conditions.

Osmotic relations

B. cinerea can tolerate great osmotic pressures (Hawkins 1916; Weimer and Harter 1921; and Rippel 1933*a*) and Thatcher (1939, 1942) formed a hypothesis in terms of osmotic relationships between the fungus and its host (in this case celery petiole tissue) to explain the pathogenicity and nutrition of the fungus. He found that the osmotic pressure of hyphal cells of *B. cinerea* was 31.4×10^2 kNm^{-2} compared with 8.4×10^2 kNm^{-2} of celery cells. The permeability of celery cells increased at some distance from those already killed and in advance of the hyphae (probably as a result of pectinase activity on the cell walls, membranes, and protoplasm) and Thatcher considered that the osmotic pressure differential could explain the transfer of water and nutrients from the host cells to the fungus.

The enhanced parasitism of *Botrytis* spp. on older, senescent or moribund tissues, for example of tomato stems infected by *B. cinerea* (Wilson 1963), may probably be explained in terms of Thatcher's hypothesis, as may also the transition of latent infections (q.v.) in tissues of changing metabolism in which host-cell permeability and the relative osmotic pressure of host and parasite must change.

Effects on host metabolism

Diseases caused by *Botrytis* spp. are not normally wilts in the sense that those caused by *Fusarium* and *Verticillium* spp. are; however, Hursh (1928) considered that the wilt of paeony caused by *B. paeoniae* resulted from local blocking of the vessels rather than from mobile toxins, because the shoot remained normal if excised above the lesion and kept in water. Carranza (1965) ascribed the wilt symptoms caused in *Cicer arietum* by *B. cinerea* to necrosis of the xylem. Brierley (1918*a*) found that the mycelium of *B. cinerea* was confined to dead vascular elements throughout affected shoots of *Ribes alpinum*. He thought that the fungus, as it developed with the growing shoot, existed in a symbiotic condition with the host.

Brierley also noted that the host was stimulated to form galls and adventitious roots. Adventitious root formation has also been noted in the vicinity of lesions of the stems of tomato plants infected by *B. cinerea* (Jarvis, unpublished). Wilson (1963) noticed that delaminated petioles of tomato inoculated with *B. cinerea* tended to fall from the stem earlier than non-inoculated petiole stubs, and Verhoeff (1967) tried to exploit this tendency in order to rid the plant of these stubs that were potential sites of infection for the whole plant. Petiole stubs about 5 cm long abscissed in about 21 days; those inoculated at the distal end with conidia of *B. cinerea* abscissed in 8 days, often before the fungus had grown into the main stem. Ilieva (1971) thought a toxin was responsible for abscission.

Lemon pedicel infection by *B. cinerea* was also suspected of being connected with abscission (Klotz, Calavan, and Zentmeyer 1946). Infection occurred at the abscission zone; although affected flowers abscissed, Klotz et al. were unable to determine whether the flowers abscissed before infection occurred or as a result of it. Beetz (1966) attributed abscission of about 10% of grapevine buds to the presence of *B. cinerea.* Skidmore and Dickinson (1973) could not associate the presence of *B. cinerea* in the phyllophane of barley leaves with changes in the course of senescence.

An interesting effect on the physiology of *Antirrhinum majus* flowers infected by *B. cinerea* was noted by Harrison and Hopwood (1969): a genetically blocked anthocyanin was released to produce a distinctive color-ring in the corolla providing that anthocyanin production was blocked only by the *delilah* gene.

Williamson (1950) noted that infection of *Chrysanthemum* tissue by *B. cinerea* resulted in the release of ethylene and Smith, Meigh, and Parker (1964) found that carnations infected by *B. cinerea* also produced considerably more ethylene; the ethylene damaged healthy flowers and predisposed (q.v.) them to further attack by the fungus.

RESISTANCE

Mechanical resistance

Blackman and Welsford (1927) and Louis (1963) showed that the plant cuticle is penetrated mechanically by infection pegs of *Botrytis cinerea,* but in the field *Botrytis* spp. do not often seem to infect plants directly through the cuticle but rather from a saprophytically based mycelium. Jarvis (1962*a*) found that only about 1% of all infections by *B. cinerea* of strawberry and raspberry fruits could be attributed to infection achieved in the manner described by Blackman and Welsford (1927) and Louis (1963). The remainder resulted either from development of latent infections (q.v.) from the

proximal end, equivalent to a saprophytically based mycelial infection, or directly from a saprophytically based inoculum adhering to or touching the fruit. The intact cuticle of the ripe strawberry fruit was surprisingly resistant to direct infection from spores.

Ainsworth, Oyler, and Read (1938) considered the tomato fruit cuticle as a barrier to infection by *B. cinerea* in ripening fruit; the increased resistance was associated with a rather sudden change from a slightly matt surface to a glossy, darker-green surface as the fruit ripened. Of two different types of lesion, Louis (1963) attributed one, a restricted necrotic spot, to thick cuticles and the other, a non-necrotic spot and a non-necrotic spreading lesion, to thin cuticles.

Investigating the surface of raspberry canes as a barrier to fungal infection, Jennings (1962) and Knight (1962) found the incidence of *B. cinerea* to be higher in the stems of cultivars that were relatively wax-free, hairless, spiny, and pigmented, and Doornik and Bergman (1971) attributed the resistance of tulip shoots to *B. tulipae* to the presence of a sheathing, brown scale tunic leaf.

The intact grape cuticle is relatively resistant to *B. cinerea* (du Plessis 1937; Stalder 1953*b*, 1955) and infection depends largely on wounds through the cuticle such as those caused by hail, by cracking in over-wet conditions or after using the wrong fungicide, and by insect punctures (Vanderwall 1937; Francot, Geoffroy, and Malbrunot 1956; Bessis 1972). Zilai and Lefter (1969) concluded that the grape cuticle was not an important barrier but they did find that differences in fruit susceptibility of some grape cultivars could be attributed to differences in the anatomy of the hypodermis, the first 11–15 layers of cells beneath the epidermis; the thinner the layer, the greater the resistance to gray mold, because the layer is less liable to crack under stress from high water uptake by the fruit. Beukman (1963) had also found that resistant grape cultivars tended to have berries with thin cuticles, small epidermal and hypodermal cells, and a large ratio of radial to tangential wall length in the epidermis.

Wound reactions

Fruit cracking and bruising in cherries are usually followed by various fungi, including *B. cinerea* (Gerhardt, English, and Smith 1945: Ogawa, Bose, Maji, and Schreader 1972). Wet weather conditions result in cracked fruit, and unless the surface is dried out quickly, fungi soon invade the exposed parenchyma. There is no wound reaction at a storage temperature of 10°C but if the tissue around the crack dries out, infection is considerably reduced. Tompkins (1950) also found that stem cracking, resulting from excessive nitrogen applications, permitted the entry of *B. cinerea* into tuberous-rooted *Begonia*.

Wound reactions against invasion by *Botrytis* spp. seem relatively rare, probably because the fungi usually invade rapidly and kill cells in advance of hyphae. At 20°C wounded potato tubers are not normally parasitized by *B. cinerea,* although at lower temperatures, about 5°C, they are. Ramsey (1941) attributed tuber resistance at 20°C to the formation of a wound periderm, but it was inadequate if tubers were transferred to 5°C within 3 days and then inoculated.

A periderm was also noted by Bald (1953*a*, 1953*d*) in *Gladiolus* corms and its formation too was related to temperature. *B. gladioliorum* has an optimum temperature for growth in vitro of about 20°C but, because this temperature also favors periderm formation, parasitism is considerably reduced. Bald found that curing the corms at 35°C immediately after digging promoted the formation of periderm.

Bald (1953*a*) also attributed resistance in *Gladiolus* leaves to the formation of gum as well as to cuticle thickness in both leaves and corms.

The formation of gum-like material in lettuce leaves in response to infection by *B. cinerea* was reported by Abdel-Salem (1934). The formation occurred in cells with thick brown walls adjacent to a zone of healthy cells bounding infected areas. Brown and Montgomery (1948), however, could find no abscission layer formed as a defence reaction in affected lettuce leaves, but Zeller (1926) found that in pear flowers the spread of *B. cinerea* through the pedicel was checked by the normal abscission layer at its base. In contrast, strawberry and raspberry receptacles are not shed, as pear fruits are, and the fungus is able to spread from fruit to fruit along pedicels (Jarvis, unpublished).

Gärtel (1965*a*, 1965*b*) found that *B. cinerea* could be excluded by callus tissue if woody tissues of grapevine were stored at 25–30°C after grafting but the fungus was able to infect the material at 15°C because callus formation was negligible at lower temperatures. The fungus grew well at 15°C and even at 3°C it grew at 0.1 mm/h; its growth was checked at 28–30°C but it was not killed.

IMMUNITY

Beginning with Nobécourt (1928), many investigators thought that pretreating plants with various filtrates from cultures of *Botrytis cinerea* rendered the plants more resistant to subsequent inoculation with the fungus; the investigators include Carbone (1929), Carbone and Jarach (1931), Baldacci (1932), Jarach (1932), Carbone and Kalyayev (1932), Kalyayev, Kravtchenko, and Smirnova (1935), Carbone and Arata (1934), and Arata (1935). However, Baldacci (1935) and Carbone (1935) discounted the hypothesis of immunity acquired in this way and so did Butler (1936). The idea was finally quashed by Baldacci (1937) and by Baldacci and Cabrini (1939) who showed that the fungus used in much of the earlier work was not *B. cinerea,*

but a species of *Rhizoctonia (Corticium vagum* var. *ambiguum),* the causal organism of the 'toile' disease of beans.

Heale and Stringer-Calvert (1974), re-opening this type of work, treated carrot callus tissue cultures with fluid in which spores of *B. cinerea* had germinated. Four days later, Heale and Stringer-Calvert inoculated the tissue with spores; symptoms were delayed 1–7 days in comparison with those on the check tissue, and the onset of symptoms was associated with increasing levels of insoluble invertase activity in the tissue.

Chemical resistance

The cuticle, in addition to the offering possible mechanical resistance to infection, has some components that are fungistatic. Jarvis (unpublished) found that acidic fractions of the cuticular wax of *Rubus idaeus* and *R. phoenicolasus,* in comparison with other fractions, retard the growth of *B. cinerea* when incorporated into agar. Schütt (1971*a*) found that different components of conifer needle wax had different effects on the growth of *B. cinerea* but the effects differed with host species and fungal isolate, and resistance could not be interpreted in terms of chemical resistance at the cuticle. Blakeman and Sztejnberg (1973) found that germination of conidia of *B. cinerea* was inhibited by the surface wax of beetroot leaves.

Topps and Wain (1957) found that exudates washed from the leaves of some plants were inhibitory to the spores of *B. cinerea,* especially exudates from *Sambucus nigra* and *Ligustrum vulgare.* Topps and Wain suggested that exudates, concentrated on the leaf surface, could play some part in resistance.

Beneath the cuticle many plant tissues have intrinsic resistance to the growth of *Botrytis* spp. and there have been some attempts to correlate resistance with the growth of the fungi in various tissue extracts (e.g., Irvine and Fulton 1959). However, such extracts are notoriously difficult to prepare without altering their components and results must be treated with caution. Even the growth of hyphae through tissue is usually a poor measure of resistance or susceptibility because it takes into account only one factor among many and it is difficult to associate with any particular chemical or mechanism. For example, Stalder (1953*b*) considered that the resistance of berries of different grape cultivars to the growth of *B. cinerea* was not connected with the mechanical properties of the host tissue, nor with any induced reaction, but with the chemical composition of the cell sap. However, he could find no correlation between fungal growth rate and sugar, acid content, or pH.

Only a few relatively simple materials have been implicated, directly and unchanged, in resistance. Nobécourt (1927) considered leaves of *Prunus laurocerasus* to be resistant to *B. cinerea* because of the presence of benzoic aldehyde and Fijikawa and Miyazaki (1960) found astringent cultivars of persimmon, because of their higher tannin content, more resistant than sweet

cultivars. On the other hand Vanev (1965) found tannins from grapevines had no adverse effect on the germination and growth of *B. cinerea* in vitro. Polyphenols are normally considered to impart resistance in many diseases (Kosuge 1969) but Orellana and Thomas (1965) thought that the gallic acid in *Ricinus communis* could well account for the specificity of *B. ricini* to this host. The fungus grew well in 0.4% gallic acid, spores germinated better in 0.1% than in water, and sporulation was abundant on media containing between 0.01 and 0.1% gallic acid.

Sokolov, Chekhova, Eliseev, Nilov, and Shcherbanovskii (1972) found juglone to inhibit the growth of *B. cinerea* at a concentration of 2 μg/ml, and the related plumbagin and 1,4-naphthoquinone inhibited at 10 μg/ml.

Martin (1973) reported that some furanocoumarins (pimpinellin, *iso*-pimpinellin, bergapten, and sphondylin) from *Heracleum sphondylium* suppressed the mycelial growth of *B. cinerea* at about 500 ppm.

Spencer, Topps, and Wain (1957) found a material in the lower stem and upper root tissues of *Vicia faba* that inhibited the germination of spores of *B. cinerea* and of *B. fabae*. The fungistat was believed to be phenolic and reducing.

A number of fungistatic materials, known as phytoncides, have been extracted from various plants, especially from Brassicae and *Allium* spp. Marchevskaya (1955) and Vanev (1969) extracted phytoncides from *Armoracia rustica, Allium sativum, Brassica napus, Raphanus sativus,* and *Nasturtium officinale,* which were inhibitory or stimulatory to *Botrytis cinerea* in vitro, depending on their concentration.

A series of investigations by Walker and his colleagues showed that materials in colored onion cultivars imparted resistance to some fungi but others in white cultivars imparted resistance to different fungi. Walker and Lindegren (1924) found that the neck-rot organism, *B. allii (B. aclada),* could attack the fleshy scale leaves in bulbs of colored cultivars only when the colored scales were circumvented through wounds. Walker, Lindegren, and Bachmann (1925) recognized two types of inhibition, one from a thermostable toxin and the other from volatile materials; and Walker and Link (1935) considered these results in terms of a phenolic resistance mechanism. Although phenol, catechol, and salicylic acid retarded growth of *B. allii,* comparable concentrations of guaiacol, veratric acid, vanillic acid, and protocatechuic aldehyde stimulated growth. Walker and Link concluded, however, that the inhibitory compounds played no significant part in defence because of their low concentration and location in the tissues. Walker, Morell, and Foster (1937) found *B. allii* only slightly sensitive to the vapor phase of mustard oils; the allyl mustard was very toxic, but not as toxic as its glycoside, sinigrin, the form in which it usually occurs in the unwounded plant. Hatfield, Walker, and Owen (1948) found *B. allii* less sensitive to the nonvolatile than to the volatile materials of succulent scale leaves. When *B. allii* gained access to the fleshy scales, there was no correlation between resistance and the color of the outer scales, but resistance was correlated with pungency and with the

toxicity of volatile and nonvolatile substances in the fleshy scales. Walker, Owen, and Stahmann (1950) concluded that the volatile sulphides were probably responsible, and so, to a lesser extent, were the phenolic materials. Bergquist and Lorbeer (1971) found the sclerotia of *B. squamosa* more numerous on the neck of cultivars with white bulbs and those with yellow bulbs than on the neck of cultivars with bulbs of other colors.

The role of phenolic compounds has been implicated in many resistance mechanisms, for example in the resistance of grape berries to *B. cinerea* (Pliskanovskii and Zotov 1971; Pliskanovskii 1972; Zotov and Pliskanovskii 1973; and Rizvanov and Karadimcheva 1973) but their role is usually very complex. Free polyphenols, which are phytotoxic, probably rarely exist as such in plants, but rather in combination with sugars as glycosides, which may be stimulatory to fungi (Talieva 1954; Sproston 1957).

The complex role of polyphenolic and other systems, particularly in cabbage infected by *B. cinerea,* has been extensively investigated by Rubin and his colleagues and reviewed by Rubin and Ivanova (1960) and Rubin and Artsikhovskaya (1963, 1967).

When cabbage head leaves were infected by *B. cinerea,* peroxidase activity increased considerably, some other enzyme systems were inhibited (Rubin and Chetverikova 1955), and respiratory activity was intensified around the infection site (Rubin, Chetverikova, and Artsikhovskaya 1955). There was 4–5 times as much readily oxidizable amino acid content in the resistant cultivar Amager as in the susceptible cultivar No. 1; infection resulted in greatly increased ascorbic acid oxidase activity in the resistant but not in the susceptible cultivar (Rubin and Ivanova 1958, 1959). Rubin, Ivanova, and Davydova (1961) and Rubin and Ivanova (1963) attributed the darkening of infected tissues of the resistant cultivar Amager to the accumulation of fungistatic water-soluble tannins and free polyphenols. Precursors of these materials (phloroglucinol, caffeic, and chlorogenic acids) were presumed to be oxidized by polyphenol oxidase secreted by *B. cinerea* because the enzyme is absent from healthy cabbage. Ivanova, Davydova, and Rubin (1965) also found vanillin and another unidentified phenol in cabbage to be toxic to *B. cinerea.* The oxidation products affect the activity of the fungal dehydrogenases (Ivanova and Rubin 1963; Rubin, Ivanova, and Davydova 1964*b*).

The resistant cabbage cultivar Amager had a higher peroxidase activity than cultivar No. 1 (Rubin, Artsikhovskaya, and Spiridonova 1939) and the activity was considerably enhanced when infection occurred; Rubin, Ivanova, and Davydova (1964*a*, 1965) considered that the enhanced activity would contribute to resistance. The increase in activity was the result of enzyme synthesis (Rubin, Aksenova, and Kozhanova 1973). Aksenova, Ksivan'ski, and Rubin (1966) also found that NADH-cytochrome-C-reductase, as a component of the respiratory system, plays an important part in the defence reaction. Protein synthesis is another feature in parasitized cabbage tissue (Rubin, Aksenova, and Nguyen Din Guen 1971*a*, 1971*b*; Rubin, Aksenova, and Brynza 1973) and occurs in mitochondria (Rubin 1973*a,* 1973*b*).

Brynza and Aksenova (1973, 1974) found that mitochondria from resistant cabbage infected by *B. cinerea* had higher values for RC (respiratory control) and ADP:O_2 ratio than those from healthy tissues. The mitochondrial membranes were damaged during infection in the susceptible cultivar and coupling in oxidative phosphorylation decreased; respiratory control had been lost.

Some of these results have been exploited in breeding programs by Brumshtejn and Metlickij (1963); in seeking new cabbage cultivars with resistance to *B. cinerea,* they selected seedlings showings high peroxidase activity.

The failure of *B. cinerea* or of pectinases extracted from it to attack tissues with a high polyphenoloxidase activity has long been of interest. Chona (1932), trying to explain the apparent resistance of potato tissue, found that the enzymes were inactivated by potato juice, but attributed this to the action of certain salts, particularly magnesium sulphate and potassium phosphate. Folsom (1933) noted that when *B. cinerea* attacked potato tubers, the lesion was sometimes restricted by darkened tissue. Trzebinski (1962) found a similar situation in sugar-beet roots attacked by *B. cinerea;* those cultivars having a strong polyphenoloxidase reaction were resistant, and those with non-browning tissues were not. Although *B. cinerea* is able to rot apples slowly (Cole and Wood 1961), oxidized apple juice rapidly inactivated the pectinase enzymes of an isolate from apple, but not those of an isolate from lettuce (Cole 1956).

Deverall and Wood (1961*b*) found that both *B. cinerea* and *B. fabae* produced pectinases and cellulases capable of macerating tissue of *Vicia faba,* although in the quiescent (q.v.) phase of the chocolate spot disease there is little evidence of tissue breakdown. They also found that products of phenolic oxidation inhibit pectinases, but products of pectin degradation activate latent polyphenoloxidase. They proposed a hypothesis with the following sequence of events: the fungus infects the tissue and begins to secrete cell-wall-degrading enzymes; the degradation products in turn promote the secretion of more enzymes and also provide nutrients for the pathogen. The products of cell-wall degradation also activate the latent polyphenoloxidase system of the moribund host cells; it then acts on phenols released on cell death. The resultant oxidized phenols inhibit pectinase activity and so the lesion is restricted. In the aggressive phase of chocolate spot, *B. fabae* spreads rapidly through the tissue; it was suggested that conditions of changing host metabolism permit the fungus to produce cell-wall-degrading enzymes faster than they can be inactivated. A similar hypothesis seems to hold for the resistance of young tomato stem tissue to infection by *B. cinerea* (Jarvis and Wilson, unpublished).

Young tomato-stem tissues, compared with old tissues, are more resistant both to the growth of *B. cinerea* through them and to the germination of conidia in their vessels; germination is inhibited in the latent phase of the disease (see PART 4, "Latency"; also Jarvis and Wilson, unpublished). If conidia lie ungerminated in a vessel, local browning — apparently phenolic

in nature — occurs in the cell wall. Young tissue had a generally higher polyphenoloxidase activity, depending on the enzyme substrate, than old tissue and the activity was not increased by activators of latent polyphenoloxidase; old, susceptible tissue had a low polyphenoloxidase activity, which was increased by activators of the latent enzyme. Although these results do not seem entirely compatible with the Deverall and Wood hypothesis, the results can be explained in terms of pectinase inhibition: young, resistant tissue, with a very active polyphenoloxidase system, inhibits pectinase activity; old tissue, because of the low, non-activated state of its polyphenoloxidase system, does not.

Thomas and Orellana (1963*b*) could not relate the resistance of capsules of some cultivars of castor bean to their phenolic content (indeed *B. ricini* can tolerate relatively high concentrations), but in a subsequent paper (1964) they associated resistance with the inactivation of fungal enzymes by means of oxidation products of phenols from damaged host-cells. Capsules of resistant cultivars had a relatively low content of flavanols and related compounds, and significantly more active peroxidase and polyphenoloxidase systems.

On the basis of these findings, Thomas and Orellana (1963*b*) devised two simple biochemical tests for susceptibility. In one, they sprayed capsules with a commercial pectinase preparation; after incubation, susceptible capsules became brown and macerated while resistant capsules remained green and firm. In the other test, crushed tissue was treated with reagents (ferric chloride, vanillin-sulfuric acid, or potassium ferricyanide) for oxidized phenols; a positive color reaction indicated resistance. Esuroso (1969) used the pectinase test to screen potential cultivars for Nigerian conditions and according to test results, no cultivar was considered suitable.

Sproston (1957) investigated the role of glycosides in the resistance of *Impatiens balsamina* using as a test fungus *B. allii (B. aclada),* which is not normally a parasite of this host. Conidia germinated on the leaves and penetrated them but a dark-color reaction occurred and no further growth took place. Kaempferol, quercetin, and 2,3-dimethoxy-2-methoxy-1,4-naphthoquinone were isolated from the affected tissues. Sproston considered them too phytotoxic to exist as such in the healthy plant and thought that they probably occur as glycosides that are broken down in the host-parasite combination to release the fungitoxic phenolic moiety, which may then be oxidized.

Sokolov, Chekhova, Eliseev, Nilov, and Shcherbanovskii (1972) found 1,4-naphthoquinone to be lethal to *B. cinerea* at 10 μg/litre and the related juglone and plumbagin at 2 μg/litre and 10 μg/litre.

Schmitt (1952) found that a defence reaction of seedlings of *Lepidium sativum* to *B. cinerea,* the deposition of melanic pigments on cell walls and the development of a cortical cambium, was enhanced in high light intensities, but not in low intensities.

The ultrastructure of the *B. fabae* — *Vicia faba* relationship was investigated by Abu-Zinada, Cobb, and Boulter (1973). They found that the cytoplasm of invading hyphae was slightly less dense than that of external hyphae and that at the interface there were lomosome-like structures in the fungus, perhaps the sites of hydrolytic enzyme production. At the periphery of the lesion, host cells contained large volumes of cytoplasm, numerous Golgi bodies, and a well-developed endoplasmic reticulum. Host cells also contained various unidentified bodies and inclusions, and Abu-Zinada et al. suggested that unidentified electron-dense bodies in the extracellular spaces of the host might be remnants of fungal mycelium acted upon by enzymes of the host. Incubating mycelium in an extract of bean leaves infected by *B. fabae* resulted in considerable disorganization of fungal fine structure.

The resistance to *B. cinerea* of flowers of *Paeonia* spp., *Primula sinensis, Forsythia europaea, F. suspensa, Gentiana lutea,* and *Antirrhinum majus* was investigated by Jung (1956) and Schönbeck (1968). In no case was the ovary entered; stigma secretions enhanced spore germination, but growth was halted in the style, which remained turgid long after other flower parts had withered. The resistance of the style was unaffected by changes in temperature or light, by its age, or by wounds. A fungal inhibitor, which enhanced pollen tube growth, was present in the stigmas and styles; it was water-soluble and destroyed by ultraviolet light and exposure to 60°C. Jost, Volken, and Kern (1964) suggested that an inhibitor found in the stigma and style of *Trifolium pratense* accounted for the failure of *B. anthophila* to attack female parts of the flower.

Schönbeck (1966) found a principle in the stigma of *Tulipa* that inhibited the growth of *B. cinerea* but stimulated that of *B. tulipae,* its normal pathogen. The concentration of the active principle was low in stamens, bulb, and roots, but high in petals and very high in green leaves. It was probably α-methylene butyrolactone (Bergman and Beijersbergen 1968).

Later, Schroeder and Schönbeck (1970), Schroeder (1972*a*), and Schönbeck and Schroeder (1972) attributed resistance to the presence of tuliposides (1-acylglycosides) that were released by the pistil because of increased cell permeability caused by *B. cinerea* and, to a lesser extent, by *B. tulipae.* Under the influence of *B. cinerea,* the tuliposides became degraded to lactones with a high antibiotic activity, whereas under the influence of *B. tulipae,* acids with a low activity were formed.

Schroeder (1972*b*, 1972*c*) further showed that *B. cinerea* and *B. tulipae* differed in their production of pectinases and of citric and oxalic acids.

In *Cyclamen persicum,* Schlösser (1971, 1973) showed that the saponin cyclamin, which *B. cinerea* cannot detoxify, could be responsible for the resistance of leaves. The concentration of cyclamin in stems, however, was considered low enough to permit their parasitism.

Arneson and Durbin (1968) investigated the role of the glyco-alkaloid α-tomatine in resistance of tomato to various fungi. In general, non-tomato

pathogens were more sensitive in vitro to α-tomatine than tomato pathogens; *B. cinerea,* a pathogen of tomatoes, was inhibited at 0.013 M. Arneson and Durbin concluded that α-tomatine was present in leaves at toxic concentrations (about 10^{-3} M), but it was localized in tissues and intracellular sites and could be avoided by some fungi. Verhoeff (personal communication) considered that *B. cinerea* could detoxify α-tomatine, so this substance was probably unimportant in resistance to the fungus.

Brown (1915) and Nelson (1956) had suggested that some resistance might be associated with the chemical and/or physical states of pectic materials in cell walls, and Hondelmann (1969) and Hondelmann and Richter (1973) attributed the relative resistance of fruit of certain strawberry cultivars to a low ratio of soluble to insoluble pectin. Those berries with a high ratio were less firm and more susceptible to *B. cinerea.*

This ratio is possibly influenced by the calcium content of the fruit. Indeed Silvestrov (1961) was able to reduce by about 90% the incidence of gray mold in strawberries by liming the plantation at a rate of 800–900 kg/ha (about 15–20 g/plant), although this result may have other explanations based on altered pH values in soil and altered metabolism in the host or in the parasite. Similarly, Stall (1963) and Stall, Hortenstine, and Iley (1965) reduced the incidence of gray mold in tomatoes; a lower content of phosphorus in the tissue also contributed to resistance. Tissue with a high Ca and a high P content was as susceptible as that with a lower Ca and lower P content. Again, Krauss (1971) found that lettuce plants with an increased Ca content had increased resistance to gray mold. When he found that high levels of nitrogen increased growth and decreased resistance, he suggested that the Ca level in the plant had been relatively decreased. He further suggested that the observed resistance of P- and N-deficient plants was the result of their relatively high Ca content and smaller cells. In plants with adequate Ca, the incidence of the disease was less affected by anion concentrations, the pectin was less soluble, and the cell membranes were less permeable.

Francot, Geoffroy, and Malbrunot (1956) and Bolay, Bovay, Neury, and Simon (1967) reported Ca-induced resistance to *B. cinerea* in grapes.

Deverall and Wood (1961*a*) found Ca-deficient bean plants more susceptible to *B. fabae* and suggested that their cell walls were more easily penetrated and degraded by the fungus. Similarly, Thomas and Orellana (1963*b*, 1964) attributed the resistance of capsules of some castor-bean cultivars attacked by *B. ricini* to a relatively high content of insoluble pectin and high contents of calcium and magnesium, both of which contribute to pectin insolubility (Joslyn 1962).

Other physical changes occur in infected tissues and there are differences between susceptible and resistant tissues. Rubin and Sipilov (1963) detected wide differences in the electrical potential difference from the external environment to cell contents between resistant and susceptible cabbage tissues

and between tissues infected by *B. cinerea* and those not infected. Aksenova and Savchenko (1966) found the permeability of protoplasm in resistant cabbage tissue to be increased by 12% on infection by *B. cinerea* and by 120% in a susceptible cultivar. Infection resulted in the displacement of the isoelectric point. It also resulted in an increase in mitochondrial size and in ribosome number in the susceptible cultivar No. 1, but not in the resistant cultivar Amager (Rubin, Aksenova, and Nguyen Din Guen 1971*b*). Although enhanced protein synthesis was associated with ribosomes in infected Amager and with mitochondria (Rubin 1973*b*), there was protein degradation in infected No. 1 (Aksenova, Rubin, Savchenko, and Brynza 1968; Rubin, Aksenova, and Nguyen Din Guen 1971*a*, 1971*b*; and Rubin, Aksenova and Kozhanova 1973).

Aksenova and Savchenko (1965) found that in the resistant cultivar Amager, energy-storing processes were retarded immediately around an inoculum of *B. cinerea,* and the intensity of oxidative phosphorylation increased just outside the inoculation zone. In the susceptible cultivar No. 1, energy storage remained unaltered near the inoculum, and in the surrounding zone phosphorylation increased at first, then decreased.

Other biochemical differences in infected tissues of resistant and susceptible cabbage cultivars were noted by Ozereckovskaya and Voronkov (1964), in tissues both at the site of infection and at some distance from it. In susceptible tissues, oxygen absorption was stimulated by 2,4-dinitrophenol, the content of inorganic phosphate decreased, and that of alcohol increased.

The overall nutrition of plants is important in determining their resistance as well as their predisposition (q.v.). Horne and Gregory (1928) associated the resistance to *B. cinerea* of the fruit of some apple cultivars to a low water content, high acidity, a high K content, and a low N content. Colhoun (1962) lowered the resistance of apple fruit by injecting urea and potassium phosphate into the branch; both materials together were more effective than either alone.

Verhoeff (1965) examined the effects of N, P, K, Mg, and lime as soil amendments on the extension of lesions caused by *B. cinerea* on tomato stems and petioles, and on the rate of mycelial growth through the tissues. Higher levels of soil N resulted in slower rates of lesion extension, especially on stems, and in slower rates of mycelial growth. For a given level of soil N, higher rates of K decreased the rates of lesion development; the N:K ratio was therefore important. Lesions developed more rapidly near the shoot apices. These effects were also demonstrated under commercial conditions (Verhoeff 1968).

In strawberry, the correct use of maganese, copper, and boron as trace-element fertilizers reduced the incidence of *B. cinerea* in the fruit (Dorozhkin and Grishanovii 1972).

Phytoalexins

A phytoalexin, a substance formed or activated only in the host–parasite combination (Deverall 1972), was recognized first by Purkayastha and Deverall (1964*b*, 1965) in a disease caused by a *Botrytis* sp. Diffusates from leaves of *Vicia faba,* infected by *B. cinerea,* contained substances that inhibited the germination and germ tube growth of both *B. cinerea* and *B. fabae.* Relatively less antifungal material was present in diffusates from lesions caused by *B. fabae.*

Infection drops in bean-pod cavities and containing spores of *B. cinerea* became inhibitory to the growth of germ tubes within 18 h (Deverall 1967). The inhibitor, which was ether-soluble, counteracted the stimulant effects of sucrose, glucose, fructose, galacturonic acid, or several amino acids that were also present in the drops. Drops containing spores of *B. fabae* contained relatively large amounts of a UV-absorbing, biologically inactive substance.

Deverall, Smith, and Makris (1968) also found a phytoalexin in diffusates from lesions in pods of *Vicia faba* and *Phaseolus vulgaris* if the lesions were caused by *B. cinerea.* An inhibitor was also found in diffusates from the larger lesions caused by *B. fabae* and it was concluded that *B. fabae* was able to detoxify the inhibitor. Deverall and Vessey (1969) found that the phytoalexin in *V. faba* was an ether-soluble acid formed by apparently healthy cells in advance of hyphae of *B. fabae* or *B. cinerea* and also in response to physical injury. Deverall and Vessey thought that the greater ability of *B. fabae* to detoxify the phytoalexin could explain its greater pathogenicity in the aggressive phase of the bean chocolate-spot disease, and similarly that *B. cinerea,* because of its poor ability to detoxify the phytoalexin, had relatively poor pathogenicity on bean (Deverall and Wood 1961*a*).

The phytoalexin was characterized and named wyerone acid by Letcher, Widdowson, Deverall, and Mansfield (1970) and Fawcett, Firn, and Spencer (1971). The biosynthesis of wyerone acid in the host was greatly stimulated by the presence of the pathogen, and the phytoalexin reached a maximum concentration 4 days after inoculation; it then appeared to be metabolized — possibly to wyerone, an antifungal ester, which had been found in healthy seedlings of *V. faba* by Fawcett, Spencer, and Wain (1969). Balasubramani, Deverall, and Murphy (1971) noted high respiratory activity in parasitized leaf discs, which, they thought, might reflect inhibitor production. High polygalacturonase activity also occurred in and around lesions despite the presence of a polyphenoloxidase system known to be inhibitory in vitro (Deverall and Wood 1961*b*).

Further work on the detoxification of wyerone acid was done by Mansfield and Widdowson (1973). *B. fabae* reduced wyerone acid, both in vitro and in infection droplets in bean-pod cavities 1–3 days after inoculation. Though wyerone acid was metabolized by *B. cinerea* slowly in vitro, reduced wyerone acid could not be detected. Mansfield, Porter, and Widdowson (1973) identified the *B. fabae* metabolite of wyerone acid as 3-[5-(hydroxy-*cis*-hept-

4-enyl)-2-furyl]-*trans*-prop-2-enoic acid, which compares with CH_3CH_2CH = CHC ≡ CCO (C_4H_2O) CH = CHCOOR, where R is H, CH_3 for wyerone acid and wyerone, respectively.

Whereas Mansfield and Deverall (1974*b*) thought that wyerone acid production was confined to dying cells in lesions, Mansfield, Hargreaves, and Boyle (1974) suggested that it was also formed in individual, but not all, living cells in lesions caused by *B. cinerea.* They thought that phytoalexin production could be triggered initially by cell death in response to fungal invasion or that metabolites released from dead cells might induce synthesis of wyerone acid in adjacent living cells. Another possibility was that fungal metabolites might act as specific inducers of phytoalexin production in live cells; wyerone acid might then reach phytotoxic concentrations in some host cells.

Attempting to explain the pollen-induced enhancement of infection, Deverall and Rogers (1972) found that pollen diffusates were pH-dependent and that they considerably reduced the antifungal activity of wyerone acid, as did some other components of natural media.

In 1974 Mansfield and his students (personal communication) found three other fungal inhibitors accumulating in bean tissues after inoculation with *B. cinerea.*

Another phytoalexin, lyubimin, was formed in potato in response to infection by *B. cinerea* (Metliskii, Ozeretskovskaya, Chalova, Vasyukova, and Davydova 1971), and yet another in *Ginkgo biloba* (Christensen and Sproston 1972).

Cruikshank and Perrin (1963), studying phytoalexin production in pea pods inoculated with various fungi, found that *B. allii (B. aclada),* not a pea pathogen, induced the formation of pisatin in sufficient amount to inhibit fungal growth. *B. cinerea,* a wound pathogen, induced the formation of somewhat more pisatin and was moderately inhibited by it. Normal pea pathogens were not inhibited.

In fruits of *Capsicum frutescens,* inoculation by non-pathogenic fungi induced the formation of a sesquiterpene, capsidiol (Stoessl, Unwin, and Ward 1972; Gordon, Stoessl, and Stothers 1973; and Ward 1973), but *B. cinerea,* a pathogen of pepper, induced only small amounts. *B. cinerea* was apparently able to detoxify capsidiol by oxidation, first to a ketone, capsenone, then to other undetermined compounds (Ward and Stoessl 1972*a*, 1972*b*; Stoessl, Unwin, and Ward 1973).

There are many resistance mechanisms against *Botrytis* spp. and no single chemical or physical resistance mechanism can be considered general. The host–parasite combination must be regarded as a complex entity with interactions between many enzyme systems in host and parasite; some of these interactions are significant in the direct restriction of the fungus.

QUIESCENT INFECTIONS

Many *Botrytis* diseases are characterized by a period of varying or indefinite duration when the fungus is apparently inactive in a symptomless host (latent) or when a lesion is visible but not extending (nonaggressive, as opposed to aggressive when lesions are expanding). The latter terms were apparently first used by Beaumont, Dillon Weston, and Wallace (1936) to describe leaf and petal spots in tulip caused by *Botrytis tulipae;* the terms were later applied by Wilson (1937) to the chocolate spot disease of *Vicia faba* caused by *B. cinerea* (sic, = *B. fabae*) and by Brooks (1939) to rose petal spotting caused by *B. cinerea.*

The terms aggressive and nonaggressive, although descriptive in this context, are unfortunately liable to be confused with the term aggressive that is used by van der Plank (1968) to denote pathogenicity operating against oligo- and polygenic resistance.

Although latent and quiescent infections by *Botrytis* spp. have not always been recognized as such, they appear relatively common and include the following:

B. cinerea:

strawberry and rye leaves	Kerling (1964)
potato leaves	Holloman (1967)
strawberry flowers	Rose (1926), Powelson (1960), Jarvis (1962*a*), Jarvis and Borecka (1968), Schönbeck (1967*b*), and Borecka, Bielenin, and Rudnicki (1969)
raspberry flowers	Jarvis (1962*a*)
black currant flowers	Bennett and Corke (1973), Jarvis (unpublished)
grape flowers	Natal'ina and Svetov (1972*b*), Parle and Dodanis (1973), McClellan (1972), McClellan and Hewitt (1973), and McClellan, Hewitt, La Vine and Kissler (1973)
Macadamia flowers	Holtzmann (1963) and Hunter, Rohrbach, and Kunimoto (1972)
eggplant flowers	Marras and Corda (1970)
apple flowers	Edney (1964), Bondoux (1967), and Olivier and Bondoux (1970, 1972)

pear flowers	Mezzetti and Pratella (1961)
globe artichoke in storage	Link, Ramsey, and Bailey (1924)
tomato fruit, ghost spot	Read (1936), Ainsworth, Oyler, and Read (1938), Darby (1955), Owen and Ferrer (1957), Ferrer and Owen (1959), Verhoeff (1970), and Kishi, Albuquerque, and Yumoto (1972)
onion	Clark and Lorbeer (1973*a*, 1973*b*)
sunflower seedlings	Tircomnicu and Iescu (1973)
vascular system of *Ribes alpinum*	Brierley (1918*a*)
vascular system of tomato	Wilson (1963), and Verhoeff (1965, 1967, 1968)
petals generally	Trojan (1958)
Cyclamen petals	Wenzl (1938*a*)
rose petals	Brooks (1939), and Wenzl (1938*b*)
Chrysanthemum petals	Taylor and Muskett (1959)
B. fabae:	
leaves of *Vicia faba*	Wilson (1937), Yu (1945), Bremer (1954), and Sirry, Ashour, and Hegazi (1966)
B. allii:	
onion leaves	Elarosi, Michail, and Abd-el-Rehim (1965)
B. elliptica:	
rosette leaves of *Lilium candidum*	Cotton (1933), Taylor (1934)
B. convoluta:	
Iris rhizomes	Maas and Powelson (1970)
B. tulipae:	
tulip petals and leaves	Beaumont, Dillon Weston, and Wallace (1936), and Price (1967, 1970)
B. narcissicola:	
Narcissus petals and bulbs	Jarvis (unpublished)

It seems likely that most petal flecking by any species of *Botrytis* is nonaggressive infection.

The factors determining whether visible lesions are of the aggressive or nonaggressive type have been examined only in few cases. In the bean chocolate spot disease, Wilson (1937) found that aggressive lesions were formed only when a sufficiently large concentration of spores was used in the inocu-

lum, and when the plants were kept in a high relative humidity to maintain the necessary water film around the spores for some days, at a temperature between 15°C and 20°C. Wastie (1962) thought that if the primary lesions, each caused by penetration from a single spore, were widely spaced on the leaf, the host defence mechanism prevented their further development, but if lesions were sufficiently close together, at some critical degree of crowding, apparently some synergistic effect between lesions overcame resistance.

Leach (1955) investigated the chocolate spot disease of beans again. Although Wilson (1937) had been confident that *B. cinerea* was the cause of the disease in East Anglia, Ogilvie and Munro (1947) had ascribed it to *B. fabae* in the west of England. Leach found that leaf spots caused by *B. cinerea* were inconspicuous compared with those caused by *B. fabae* and frequently *B. cinerea* affected only the epidermal cells (reminiscent of ghost spot in tomato), whereas *B. fabae* caused necrosis deep into the mesophyll. Leach considered aggressive infection to result from one or more of four conditions: (i) the infection of tissue damaged by frost, hail, insects, etc.: (ii) very heavy leaf spotting; (iii) infected flowers and moribund and dead flowers lying on leaves; and (iv) the senescence of lightly spotted leaves. Dead flowers were almost always infected only by *B. cinerea,* and *B. fabae* appeared on them only when it was sporing profusely on the lower (senescent) leaves as the epidemic progressed. Thus, any environmental factors leading to premature senescence, such as poor soil drainage or deficiency of potassium or phosphorus, would also lead to aggressive leaf infection, the epidemic phase of the disease.

B. cinerea is usually a nonaggressive pathogen on leaves of *Vicia faba,* but *B. fabae* causes spreading lesions; this situation has been studied by Wastie (1962), Deverall and Wood (1961*a*), Purkayastha and Deverall (1964*a*, 1965), Purkayastha (1966), Deverall, Smith, and Makris (1968), Deverall and Vessey (1969), and Abu-Zinada, Cobb, and Boulter (1973) in the terms of infectivity and resistance mechanisms, and is more fully described in the PART 4, "Resistance".

Price (1967, 1970) found that a high concentration of spores of *B. tulipae,* such as could be provided by rain-splashed spores, was required in the inoculum to give an aggressive lesion on tulip leaves, and that prolonged humid conditions were also required. In humid conditions, nonaggressive lesions became water-soaked but rarely enlarged. They were mostly confined to the upper leaf surface and were more numerous if the wax was removed from the leaf before inoculation.

Latency

As defined by van der Plank (1968), the latent period is the time needed for a generation of a pathogen, that is, the period from the arrival of infective propagules at the host surface until the new pathogen colony becomes a source of infection. By contrast, the time needed for symptoms to appear is the incubation period.

Because tissues newly infected by *Botrytis cinerea* act as an effective inoculum, latency may be quite short (sensu van der Plank 1968), but the incubation period, and the latent period, as defined by the appearance of conidia on lesions, may be quite long and have important implications in the design of control measures.

Powelson (1960) demonstrated the presence of *B. cinerea* in symptomless strawberry flowers and fruit by growing the fungus from surface-sterilized pieces of tissue, especially tissue from the stem end of berries; 74% of isolation attempts from the stem end yielded *B. cinerea,* compared with 6% successful isolations from the distal portion of the berry. Powelson showed that a high proportion of necrotic flower parts (petals, stamens, and calyces) contained the fungus, and that when flower parts were removed after pollination, the incidence of ripe fruit rot was considerably reduced under greenhouse conditions that favored the disease. Similarly, the application of captan three times during flowering significantly reduced the incidence of fruit rot in the field and the incidence of symptomless infection in marketable fruit. Invasion of receptacle tissue usually occurs by growth of the mycelium internally.

Jarvis (1962*a*) confirmed that these quiescent infections occur in strawberries and showed that they also occurred in raspberries and (Jarvis, unpublished) in black currants. The occurrence of *B. cinerea* was greatest in floral parts that had been slightly damaged by frost. The period between flower infection and the appearance of fruit rot may be as long as 5 or 6 weeks, but the onset of symptoms can be accelerated in very wet weather to appear, unusually, in unripe green fruit. Often the rot does not appear until after the fruit is picked, and its appearance may well depend on conditions of storage and marketing, although there is little information on this.

Jarvis and Borecka (1968) established a correlation between the incidence of blossom blight and latent infections in strawberry flowers resulting in fruit rot. Flower susceptibility to infection resulting in fruit rot, however, was not related to the rate of growth of the fungus in fruit tissue but the incidence of calyx and total flower lesions was related to the growth of the fungus through fruit tissue from a spore inoculum.

The presence of latent infections in grape flowers was also established by Natal'ina and Svetov (1972*b*), McClellan (1972), McClellan and Hewitt (1973), and McClellan, Hewitt, La Vine and Kissler (1973). In California, *B. cinerea* infects the stylar end of the flower and becomes latent in the necrotic stigma and style tissue. Later, as the berry develops, the fungus may become aggressive and rot it in mid-season, despite the absence of the rain normally associated with late-season grape rots.

Wilson (1963) found a quiescent condition in the glasshouse tomato stem rot disease caused by *B. cinerea.* Here, lesions are usually found at the sites of deleafing scars left after the removal of senescent lower leaves in the early part of the growing season, but there is often a long delay between deleafing and aggressive development of the fungus, sometimes up to 12 weeks (see PART 4, "Infection").

The incubation period varied with the age of the plant at inoculation and with the position of the inoculated node on the stem; the younger the plant and the higher the node (and hence the younger the tissue), the longer the period.

Tichelaar (1967) found that *B. allii* is able to attack young onion plants without impeding their growth. Using radioactive phosphorus as a label for conidia, he showed that the mycelium in the leaves is at first restricted to the colorless epidermal cells and that the infection remains symptomless. As the leaves age, the mycelium penetrates the adjoining leaf parenchyma and grows down into the neck of the bulb. The presence of the fungus in symptomless bulbs can be demonstrated by treatment with methyl red because invaded tissue has an acid reaction of pH 4.2 compared with pH 6.6 for healthy tissue. The reaction zone extends for about 1 cm beyond the hyphae. The characteristic neck-rot symptoms caused by *B. allii* were rarely found in the field in the Netherlands, but appeared in storage, evidently as a development of this symptomless mycelium. Tichelaar found plants of all ages to be susceptible to infection, older plants being slightly more susceptible, and the fungus was detected in bulbs 4–7 wk after leaf inoculation.

Jarvis (unpublished) believes that there may be a similar symptomless growth of *B. narcissicola* down beheaded flower stalks to the *Narcissus* bulb, and the situation may be comparable in onions where the brown stain disease caused by *B. cinerea* appears on previously symptomless bulbs in storage (Clark and Lorbeer 1973*a*, 1973*b*).

The tomato fruit ghost spot disease caused by *B. cinerea* (Read 1936; Ainsworth, Oyler, and Read 1938; Darby 1955; Owen and Ferrer 1957; and Ferrer and Owen 1959) was considered by Verhoeff (1970) to be a case of latent infection. Like previous workers, he could find no mycelium in the necrotic cells by any of the histological methods he used, although he was able, for the first time, to re-isolate the fungus. He concluded that despite the apparent failure of the fungus ever to develop further in the fruit, ghost spot represented a latent condition, or more correctly, a quiescent infection.

Little is known of the factors maintaining the equilibrium of the host–parasite combination in a quiescent state or of the changes permitting the fungus to become aggressive (Verhoeff 1974), although Thatcher (1939, 1942) put forward a hypothesis in terms of increasing host cell permeability and the relative osmotic pressures of host and parasite cells (see PART 4, "Pathogenesis"), which could apply in this case.

There is some circumstantial evidence that water content of the affected tissues may be one of the determining factors. Jarvis (1963) noted that heavy rain after a long dry period resulted in an increase from 86.8 to 90.1% in the water content of strawberry fruits. This effect, simulated by supplying water via a cotton wick threaded through the pedicel of strawberry and raspberry fruits, in all cases accelerated the onset of the quiescent–aggressive transition of *B. cinerea*. In six raspberry cultivars, the volume of the concavity at the top of the receptacle, which could perhaps be regarded as a water-holding

container, was correlated with susceptibility to *B. cinerea*. Similarly, the appearance of fruit rot from the stem end in wet fruiting seasons may represent early development of latent infections (Jarvis 1964).

Wilson (1964) advanced the onset of the transition of *B. cinerea* in tomato stems by irrigation, as compared with that in plants held just above the wilting point.

Temperature changes may affect the termination of latency; for example, Vanev (1966) found the incubation period in grapes to be temperature-dependent. Stevens (1919) and Stevens and Wilcox (1920) noted that the temperatures of various small fruits when picked were as much as 8°C or 10°C higher than ambient temperature, especially if the fruits were isolated. Physiological changes induced by picking may affect the course of latency, although there is no evidence on this point.

Results that may be interpreted in part as early onset of aggression occurred in stem rot (*B. cinerea*) on tomatoes grown in soils of relatively low nitrogen status (45 ppm) (Verhoeff 1968). In soils with more nitrogen (165 ppm) there were fewer stem lesions at a given stage of crop development and the plants were in a more vigorous vegetative state. This effect seems to be one of delayed aging or senescence.

The transition usually occurs in older tissues, and the determining mechanisms, like some of those of general susceptibility, and aggressive and nonaggressive lesions, may well be connected with physiologic processes of aging and senescence, which are more fully discussed in PART 4, "Resistance".

Implications of quiescence in disease control

Disease control measures can be directed against quiescent infection in two ways: (i) chemical prophylaxis may be timed so that fungicides are brought into contact with newly alighting conidia or with germ tubes and (ii) crops may be manipulated to retard the quiescent–aggressive transition to a point at which yield is least affected.

An example of the first approach is the retiming of fungicide programs, which has brought considerable benefit in raspberry and strawberry crops (Jarvis 1966*b*; Borecka 1967). However, the precise stages in flowering at which to spray are difficult to define because of the long sequence of flower development on the cymose inflorescences and because of the considerable variation between cultivars, localities and seasons (Jarvis 1969). Similarly, bloom-time application of captan and early bloom-time applications of benomyl were effective in controlling early *Botrytis* rot in grapes (McClellan et al. 1973). Attempts to control tomato stem rot by applying fungicides at deleafing have not been successful (Wilson 1963), probably because fungicides are sucked past the spores in vessels, but the systemic fungicide benomyl has proved more successful (Fordyce 1969).

In the second approach, over-irrigation of soft fruit and tomatoes would appear to be a predisposing factor (Jarvis 1963; Wilson 1963) and, in tomatoes, the provision of adequate nitrogen to the soil delays the appearance of stem lesions (Verhoeff 1968).

In picked strawberries and raspberries, avoiding high storage temperatures, including those resulting from insolation, delays the appearance of fruit rot. Stevens (1919) and Stevens and Wilcox (1920) showed that the temperature in picked small fruits exposed to direct sunlight could be as much as 8°C to 10°C higher than the ambient temperature, and that the incidence of gray mold in the market was higher in insolated fruit than in shaded and cooled fruit. They stressed the value of removing 'field heat' and Harvey and Pentzer (1960) among many others have discussed the merits of refrigerated transport in disease control.

Preharvest fungicides have also been shown to reduce storage losses in strawberries (Gilles 1964; Jordan 1973; among others), in raspberries (Mason 1973), and in grapes (Harvey 1955*b*; McClellan, Hewitt, La Vine, and Kissler 1973).

DISEASE ESCAPE

Some plants and tissues have an intrinsic resistance to *Botrytis* spp., for example, peanut cultivars (Alexander and Boush 1964), strawberry cultivars (Barritt, Torre, and Schwartze 1971; Barritt 1972; Kolbe 1971; Priedite and Ozolina 1971; and Naumova 1972), raspberry cultivars (Barritt 1971; Kolbe 1973; and Mel'nikova 1972), as well as lettuce cultivars to *B. cinerea* (Ogilvie and Croxall 1942), and onions to *B. squamosa* (Bergquist and Lorbeer 1971). Such resistance, however, is never absolute and is most likely of the polygenic type.

Brown, in his review (1934), points out the desirability of using various disease-escape mechanisms as adjuncts to chemical control. Some plants have a habit that reduces the likelihood of infection. Darrow (1966) noted that firm-fruited strawberry cultivars were less susceptible to *B. cinerea* than soft-fruited cultivars, as were those with less dense foliage, although their exposed early flowers were more susceptible to frost damage. Hughes (1965*a*, 1965*b*) also commented on the adverse effects of dense foliage. Esmarch (1926) suggested that strawberry cultivars with long stiff inflorescences, holding flowers and fruit clear of the foliage canopy, would be less susceptible to *B. cinerea,* and indeed, Koch (1963) bred such a cultivar. Tompkins (1950) noted that *Begonia* cultivars with red flowers and hairy stems were more resistant to *B. cinerea* than cultivars with light-colored flowers and smooth stems. A similar observation was made by Jennings (1962) and Knight (1962) in the case of raspberry canes; the more resistant cultivars had relatively hairy,

spineless, waxy and nonpigmented canes, and Jennings attributed escape, at least in part, to a greater runoff of surface water.

Nelson (1949) found the compactness of the fruit bunch to be important in the susceptibility of grapes; the looser bunches had less crushing damage and *B. cinerea* spread less rapidly from berry to berry by direct growth. Jarvis (1962*a*) found this also to be true in strawberries and raspberries, where the length of the peduncle as a path for mycelial growth was also probably important in berry-to-berry spread.

Thomas and Orellana (1963*a*) also found the structure of the flower raceme of castor bean to be important in its susceptibility to *B. ricini;* compact inflorescences were more severely attacked than loose inflorescenses, and staminate flowers were very susceptible, as were cultivars with short internodes. The presence of a waxy bloom appeared to offer little protection. The compact inflorescences and short internodes favored surface water retention and hence improved the likelihood of infection. Strawberry cultivars with staminate flowers are also more susceptible to *B. cinerea* (Risser 1964). Further, Lemaître (personal communication) noted that strawberries that become red before attaining their maximum volume are generally less susceptible than those that redden late, and they also tend to be firmer. Lemaître also thought that strawberries having a marked neck with the calyx raised clear of a convex receptable, those with superficial rather than sunken achenes, and those with readily falling petals were all less susceptible to gray mold.

Inflorescence habit can be manipulated to some extent (Vidal 1962; Vidal, Nebout, and Cattoen-Vidal 1963). Weaver, Kasimatis, and McCune (1962) sprayed developing inflorescences of grapes with a gibberellin, and Jarvis (1963) similarly sprayed those of raspberries; treated pedicels were appreciably longer, the fruit bunches therefore looser, and there was less gray mold.

Abdel-Salem (1934) and Brown (1934) attributed the differences in susceptibility to *B. cinerea* of two lettuce types, cos and cabbage, to their different growth habits; the cos type was much less attacked in summer, though both were equally susceptible as seedlings.

The speed with which tissues attain maturity, as opposed to senescence, may also be of importance in disease escape, especially in lignifying tissues. Thus, Lamberti (1965) found that early-ripening grape cultivars were less susceptible to *B. cinerea* than late-ripening cultivars.

There are many ways in which crop management techniques may be modified to promote disease escape: Brown and Montgomery (1948) planted lettuce on ridges and in hollows; the plants on the ridges had a greater incidence of gray mold because, it was suggested, they were predisposed by greater frost damage. Crüger (1962) discussed the ways of manipulating the glasshouse environment to avoid gray mold in lettuce. Similarly, Schellenberg (1955) reviewed the problem in vineyards.

The predisposing effect of dense plant spacing is frequently recorded in the literature. There is the additional effect of an accumulating inoculum on crop debris, for example, in Douglas fir seedlings (Halber 1963) and in flax (van der Spek 1960). The situation is also aggravated by the presence of weeds, which serve as hosts for *B. cinerea* (Wormald 1942) and induce a microclimate favoring infection (Robinson 1964). Campbell (1949) found that, in addition to density of plantings of beans, row orientation with respect to the prevailing wind had an effect, because he noted more gray mold in rows at right angles to the wind. Wilson (1937) noted a similar pattern in the incidence of chocolate spot, and Kovacs (1969) observed that strawberries protected from the prevailing wind by a hedge, 4 m high, had almost twice as much gray mold as plants 40 m away from the hedge. Jarvis (1961), however, could not explain the uneven distribution of gray mold in a raspberry plantation in terms of wind direction.

Vyskvarko, Mikhailyuk, Pliss, Vaselashku, Vasilaki, and Yuresko (1971) succeeded in reducing the incidence of gray mold on grapes by removing some of the leaves with a magnesium chlorate spray.

Deep planting can predispose plants to infection as occurred in *Gerbera* (Garthwaite 1963), but in *Begonia semperflorens* the promotion of active adventitious rooting by the use of long-day cultivation compensated for the loss of main roots attacked by *B. cinerea* (Sironval 1951).

In poorly managed glasshouses where ventilation is restricted, crops are particularly susceptible to infection by *B. cinerea,* and control of gray mold then becomes largely a matter of manipulating ventilation efficiently (Crüger 1962; Wilson 1963; and Winspear, Postlethwaite, and Cotton 1970).

The rate of fungal growth relative to the speed of the host's defence reaction offers a means of manipulating the environment in favor of the host. Controlling temperature is the simplest and most usual way, for example, cool storage; controlling the atmosphere is another simple way (Harvey and Pentzer 1960; Haas and Wennemuth 1962; and Redit 1969). Temperature control was shown by McColloch and Wright (1966) to be important in avoiding rot by *B. cinerea* in stored bell peppers. The decay of wound-inoculated peppers and the rate of fungal growth in vitro generally increased with temperature in the range 0–21°C, but more decay occurred at 10°C than at 13°C. Naturally infected peppers decayed fastest at 4°C; little rot occurred at 10°C and 13°C. Peppers, prestored at 0°C and then spore-inoculated and transferred to 55°C, rotted at rates proportional to the duration of their stay at 0°C.

In certain bulb diseases, including those of *Allium* spp., the success of infection of the emerging shoot from mycelium established in the neck probably also depends on the relative growth rates of the fungus and shoot. The shoot of tulip (Price 1967), narcissus (Jarvis unpublished), and onion (Tichelaar 1967) may become infected in this way when the tip is still in the neck or at any point along its length or it may escape infection if the fungus

fails to grow fast enough through scale leaf tissue. The relative growth rate must be determined by many edaphic, nutritional, and meteorological factors.

On a different scale, respective activities of pathogen and host at different times of the year offer opportunities to manipulate crops for disease escape.

In the chocolate spot disease *(B. fabae)* of beans, Grainger (1950) found that, although the vegetative growth of bean plants became susceptible to *B. fabae* after July, the disease had little effect on bean yield. Most of the dry weight of the seeds was already laid down by July and subsequent vegetative growth was of little value in crop production. Chocolate spot, therefore, limited yield only in years when *B. fabae* appeared early.

A disease of flax caused by a fungus cited as *Botrytis lini (B. cinerea),* however, behaved in the opposite way and was more prevalent on flax in years when chocolate spot was low. This disease did not have much effect on yield either, because the increased vigor of unaffected, competing stems compensated for the stems killed by *B. lini.*

Alekseeva and Taov (1971) reduced the incidence of gray mold on sunflower by altering the sowing time and removing infected plants at flowering, and Wilson (1937) also indicated the possibility of avoiding epiphytotics of chocolate spot of beans by sowing in the spring rather than the autumn.

Howard and Horsfall (1959) reported that the removal of fruits and succulent cane tips of rose bushes prevented the advance of *B. cinerea* downwards through the pith and into the crown.

In an unusual case, the induction of abscission in tomato leaf petioles caused by *B. cinerea* has been exploited as a disease-escape mechanism by Verhoeff (1967). Leaving somewhat longer petiole stubs than is usual in commercial practice, and inoculating them deliberately, Verhoeff succeeded in hastening their abscission to leave a healed scar with the minimum of necrotic tissue that might act as a possible saprophytic base.

EPIDEMIOLOGY

Epiphytotics caused by *Botrytis* spp. are generally associated with cool, wet, and humid weather, conditions favoring sporulation and infection and possibly also having an adverse effect on the host. These conditions are described in general terms by Anderson (1924), Heald and Dana (1924), Foister (1935), and Baker (1946). The conditions for epiphytotics in some other crops are discussed in these papers:

Grapes	Stalder (1953*a*), Bouard, Bulit, Lafon and Roussel (1970), Ciccarone (1970), Bulit and Lafon (1970, 1972), Gärtel (1969, 1970, 1971), and Lehoczky (1972)

Strawberries	Rose (1926), Stolze (1962), Devaux (1970), Kolbe (1970, 1973), Fulton (1956), and Jordan and Hunter (1972)
Raspberries	Fulton (1956)
Figs	Ricci (1972)
Glasshouse crops	Bewley (1923), Kadow, Anderson, and Hopperstead (1938), and Ogilvie and Croxall (1942)
Onions	Jones (1944), Beraha (1968), and Kaufman, Lorbeer, and Friedman (1964)
Peas	Ford and Haglund (1963)
Beans	Berger (1937), Yu (1945), Bremer (1954), Sirry, Ashour, and Hegazi (1966), Gerlach and Rudnick (1972), and Sundheim (1973)
Tobacco	Wolf (1931)
Kenaf	Withers (1973)
Flax	van der Spek (1965)
Tulips	Valaskova (1963)
Ornamental bulb crops	Moore (1949)

There are also more precisely described conditions promoting and limiting the spread of the gray mold diseases. Hunter and Rohrbach (1969) and Hunter, Rohrbach, and Kunimoto (1972) found a correlation between the incidence of *B. cinerea* on *Macadamia* racemes and the number of hours per week the leaves remained wet at temperatures between 18°C and 22°C. Bakos, Bekesi, and Szurke (1939) found a correlation between the incidence of *B. cinerea* on sunflower and rainfall; Wilson (1937) between the incidence of chocolate spot *(B. fabae)* on beans and heavy rainfall from April to July; Hogg (1956) between chocolate spot and the frequency of hours in which the relative humidity exceeded 95%; and Grainger (1950) between chocolate spot and the h/wk of saturation; McClellan, Baker, and Gould (1949) the relation between temperature and humidity and *B. gladioli* on *Gladiolus;* Page (1955), Lutynska (1968), and Shoemaker and Lorbeer (1971) the relation of rainfall, relative humidity, temperature, and light to onion diseases; Nelson (1951*b*), Stellwaag-Kittler (1969), Krumov (1969), and Bulit, Lafon, and Guillier (1970) the relation of relative humidity and the number of wet days in late summer to grape gray mold; Hennebert and Gilles (1958) and Gilles (1959) the relation of strawberry gray mold to relative humidity, surface wetness and temperature, and Hughes (1965*b*) its relation to irrigation. All of these factors act differentially in strawberries, raspberries, and grapes that are insolated and in those that are shaded and sheltered (Jarvis 1961; Kovacs 1969, Lehoczky 1972; and Lafon 1974).

The delicate balance in water relations determining whether grapes are rotted by the pourriture noble or by the pourriture grise is discussed by

Ribéreau-Gayon (1970), Séguin (1973), and Lehoczky (1972); see also PART 4, "Enology".

Forecasting

There have been relatively few attempts, using meteorological data, to forecast epiphytotics either in the field or in storage (Large 1955). Large emphasized the need to consider all aspects of the life cycle of the parasite, citing *B. tulipae,* the cause of tulip fire, as an example. Jarvis (1964) established a correlation as much as 30 days before harvesting began between the incidence of gray mold in strawberries and high rainfall and the duration of relative humidities exceeding 80% during flowering. In raspberries there was a similar correlation with weather conditions in the 5-day period immediately before harvesting, and also with conditions during harvesting; the interval between individual harvests was important — the longer the interval, usually because of bad weather, the more gray mold at the next harvest.

Hervé and Moysan (1967) found an empirical, graphical method of forecasting the incidence of gray mold in strawberries; they plotted the number of hours per day when the relative humidity exceeded 90% (ordinate), against time (abscissa). On the same graph, and with the same numerical scale for h and °C on the ordinate axis, they also plotted the mean daily temperature against time, again on its same scale. Epiphytotics usually followed when the two curves intersected at least three times within 48 h in the ordinate range 14–16. Some flexibility in interpretation was necessary; infection occurred when RH was consistently high and the temperature below 18°C (though the curves did not then intersect), and 25°C was the maximum temperature.

Jarvis (1964) considered that forecasting was probably very difficult because of the complex effects of many meteorological, edaphic, and biotic factors on host, parasite, and the host–parasite combination. The conditions affecting infection from conidia are different from those affecting infection from colonized substrates, from those affecting spore dispersal (another method of forecasting considered but rejected by Jarvis (1962*a*, 1962*b*)), and from those affecting the behavior of latent infections. Although in the case of strawberries and raspberries, a forecasting method could indicate the necessity of frequent harvesting and careful storage, it could not help in the correct timing of prophylactic fungicide applications. Infection occurs so rapidly (Hennebert and Gilles 1958; Gilles, 1959) that a mycelium, either latent or aggressive, could be established before the end of the minimum 24-h observation period (Hervé and Moysan 1967). Bulit, Lafon, and Guillier (1970) found infection of grapes by *B. cinerea* to occur when the grapes remained wet for 15 consecutive hours at 15–20°C and they suggested that control measures should then be applied, but again, with this hindsight, it is doubtful whether standard prophylactic fungicide sprays would then be effective.

Harvey (1955*a*) developed a method of forecasting the incidence of gray mold in stored grapes. He established a very close correlation in grapes surface-sterilized with 1% sulfur dioxide (a standard commercial practice) between the proportion of a sample that rotted at room temperature within 10 days and the proportion rotting of the bulk of the grapes stored at about 0°C for 10–16 wk.

INTERACTION WITH OTHER MICROORGANISMS

Evidence on the role of *Botrytis cinerea* in controlling the parasitic activity of other microorganisms is sparse and conflicting. Broadfoot (1933) found *B. cinerea* to limit the pathogenicity of *Gaeumannomyces graminis* and to be antagonistic to it on potato dextrose agar, but Lal (1939) could find no such activity. Savastano and Fawcett (1929) found that *B. cinerea* depressed the rate of decay of citrus fruits caused by *Penicillium italicum* and *P. digitatum* at 9–18°C but at 22–30°C all three fungi together rotted lemons faster than each alone.

B. allii (B. aclada) markedly interfered with the parasitic activity of *Monilia fructigena* when spores of both fungi were mixed in the inoculum for apple fruits; Vasudeva (1930*b*) explained this interference by postulating that staling products of *B. allii* in the infection drop inhibited the growth of *M. fructigena.*

In mixed inocula with *Nectria cinnabarina*, the activity of *B. cinerea* on *Prunus domestica* varied with the time of year (Mostafa 1947*a*, 1947*b*). In February, the pathogenicity of *B. cinerea* was enhanced, in April it was decreased, and in December, January, and March, the presence of *B. cinerea* increased the parasitic activity of *N. cinnabarina.* Interaction occurred both in the infection drop and in the host. *B. cinerea* and *Stereum purpureum* were mutually inhibitory.

Also in mixed inocula, *B. cinerea* reduced the parasitic activity of *Pythium debaryanum* on *Fuchsia* sp. pistils and was strongly antagonistic to it in culture (Schönbeck and Schinzer 1970), but this report contrasts with the synergistic effect of these two organisms on lettuce noted by Basile (1952). Fehlhaber et al. (1974) later characterized the antibiotic botrydial from culture filtrates of Schönbeck's isolate as a sesquiterpene.

Purkayastha (1966) mixed equal numbers of conidia of *B. fabae* and *B. cinerea* in inocula for bean leaves, and found no significant difference in the numbers of spreading lesions caused by *B. fabae* alone, and by both fungi together. When there were twice as many conidia of *B. cinerea* as of *B. fabae* in the inoculum, there were no spreading lesions typical of *B. fabae*, and Purkayastha suggested that antifungal substances were produced in the lesion area, as had been postulated earlier (Purkayastha and Deverall 1964).

B. cinerea was shown to be very sensitive to *Trichothecium* spp. (Sidorova 1954) and *Botrytis* sp. to *Trichoderma* spp. (Matsumoto 1939; Yamamoto 1954; Likhachev and Vasin 1970; and Wells, Bell, and Jaworski 1972). The mycelial growth of *B. cinerea* was found by Ale-Agha, Dubos, Grosclaude, and Ricard (1974) to be inhibited by heat-killed spores of *Trichoderma viride* at a concentration of 10^7–10^8 spores/ml but only in the presence of ascorbic acid at 2 mg/litre, which lowered the pH to 3.1.

The growth of germ tubes of *B. cinerea* was inhibited by bacteria on the surface of *Chrysanthemum* and beetroot leaves; the effect was greater on older leaves and was reversed by removing the bacteria by various means (Blakeman and Fraser 1971; Blakeman 1973; Sztejnberg and Blakeman 1973*a*, 1973*b*; and Blakeman and Sztejnberg 1974). It was suggested that the epiphytic bacteria play some part in the resistance of *Chrysanthemum*; this resistance is more correctly called disease escape. Subsequent work by Sztejnberg and Blakeman (1973*a*) suggested that bacteria with copious polysaccharide sheaths could act as sinks for nutrients on beetroot leaves, so that spores of *B. cinerea* were unable to germinate there, an effect simulated by leaching nutrients from spores in vitro. It seems likely that this is a common phenomenom; *B. cinerea* and probably other species are common in the phyllosphere (e.g., Kerling 1964; Holloman 1967; Skidmore and Dickinson 1973; and Godfrey 1974), but never attack healthy leaves.

Kadymova (1971) also noted that certain bacteria and their culture filtrates, because they were antagonistic to *B. cinerea*, gave some control of *B. cinerea* on grapevine, and Cleary (1959) attributed the comparative absence of gray mold in lettuce affected by bacterial wilt to the antagonism of the bacterial pathogen *Pseudomonas marginalis*.

Ujevic, Kovacikova, and Urosevic (1970) found a number of bacteria and fungi antagonistic to *B. cinerea*, especially *Fusarium oxysporum*, and *Penicillium expansum* reduced the incidence of gray mold in young lentil plants.

The control of plant diseases by the use of antagonistic organisms has always been of interest (Wood and Tveit 1955) and the first gray mold disease to be investigated in this context was that of lettuce caused by *B. cinerea* (Asthana 1936; Newhook 1951*a*, 1951*b*; and Wood 1951). Many organisms that were antagonistic in vitro, including *T. lignorum* and a *Phoma* sp. and several bacteria, prevented pathogenesis by *B. cinerea* if they were first inoculated onto lesions simulating frost damage. Control was particularly effective at high temperatures but not so effective at the normal temperature of lettuce cultivation. *B. cinerea* was unable to colonize tissues already colonized by certain other organisms. Some control of *B. cinerea* in field conditions was obtained by spraying lettuce seedlings with antagonists in 1% glucose solution, but control under commercial conditions was unsuccessful. Nevertheless, prior colonization of necrotic tissues by antagonists probably accounts for some disease escape from *B. cinerea* in field conditions.

Newhook (1957) also found that colonization of dead tomato petals by *B. cinerea* was prevented by prior colonization by species of *Cladosporium*,

Penicillium, and *Alternaria;* when petals adhering to fruit surfaces after the application of fruit setting sprays were so colonized, the incidence of *B. cinerea* on them was reduced by 30–100%.

Similarly, Bhatt (1962) and Bhatt and Vaughan (1963) were able to reduce the colonization of strawberry flower parts by prior inoculation by *Cladosporium herbarum;* and Voznyakovskaya and Shirokov (1961), Muslimov (1965), and Jouan and Lemaire (1971) reduced it with various bacteria.

Sometimes, severe attacks by *Botrytis* spp. are observed after soil sterilization; these attacks have been attributed to the absence of competitive or antagonistic microorganisms. For example, Behr (1966) noted one in flax and MacWithey (1967) one in *Iris* rhizomes invaded by *B. convoluta. B. cinerea* seemed to be controlled in soil by *Trichoderma koningi,* the inhibitory effect of which increased with pH (Schuepp and Frei 1969). In contrast, Ale-Agha, Dubos, Grosclaude, and Ricard (1974) found that in vitro inhibition by dead spores of *T. viride* is enhanced by ascorbic acid at pH 3.1.

The degradation of sclerotia in soil as a method of reducing the inoculum levels of *B. cinerea* has been reported by Pohjakallio, Salonen, Ruokola, and Ikaheimo (1956), Pohjakallio and Makkonen (1957), Karhuvaara (1960), Makkonen and Pohjakallio (1960), and Ervio (1965). The parasitic organisms include *Acrostalagmus roseus (Verticillium roseum), Trichoderma viride, Trichothecium roseum, Coniothyrium minitans, Rhizopus nigricans, Sporotrichum carnis,* and species of *Verticillium, Penicillium,* and *Mucor.*

Gall midge larvae, nematodes, and mites were also found to destroy sclerotia of *B. cinerea* on stored grapevine grafted material (Gärtel and Hering 1965); indeed the midge larvae failed to spread in the absence of the fungus.

Harrison (1952) found a species of the mite *Pediculopsis* that dispersed spores of *B. gladiolorum* among plants of *Acidanthera* and *Gladiolus,* and that was unable to establish colonies in the absence of the fungus.

ENOLOGY

As a pathogen of grapevines and grape berries, *Botrytis cinerea* is an extremely important organism and its epidemiology on this host has been reviewed by Schellenberg (1955), Bouard, Bulit, Lafon, and Roussel (1970), Bulit and Lafon (1970, 1972), Ciccarone (1970), Gärtel (1967, 1969, 1970, 1971), and Lehoczsky (1972). In addition, *B. cinerea* has profound effects on the quality of wine. Either the berries rot rapidly and completely, or, in suitable conditions, they decay very slowly permitting them to dry considerably; such dry grapes are made into the valuable and distinctively flavored, sweet wines such as the Sauternes of France, the Trockenbeerenauslese of Germany, and the Aszu of Hungary. The destructive rot is known as pourri-

ture grise in France and Graufäule in Germany, and the 'noble rot' is the pourriture noble of France and Edelfäule of Germany.

Grapes affected by the destructive rot are of no value for making wine; if they are included in the must, they impart a taint that can be counteracted, however, by the addition of sulfuric acid (Mathieu 1924). As a contaminant of wine cellars, *B. cinerea* also causes a taint (Mathieu 1929) and interferes with fermentation (Le Roux, Eschenbruch, and de Bruin 1973) by the production of a toxin complex, botryticine (Ribéreau-Gayon, Peynaud, Lafourcade, and Charpentié 1955). It also decreases the coloration of red wines (Toth 1971) and spoils wine quality (Flath, Forrey, and King 1972).

Müller-Thurgau (1888) reported that grapes affected by noble rot lost about 25% of their weight, mostly as water, while their relative sugar content increased from 11.7% in mid-October to 19.6% by the end of November and their relative content of total acids from 17.4 to 22.1%. Despite the apparent rise in sugar content in the noble rot, the fungus did deplete them and at a faster rate and in relatively greater amounts than the loss of organic acids.

Similarly Moser (1967) found that sugars were utilized in grapes affected by the noble rot, but in vintage years the sugar content was initially so high that not enough sugar depleted before the grapes dried out to impair the sweetness of the wine.

The metabolism of grape constituents by *B. cinerea* has been studied by Stalder (1954), Ribéreau-Gayon (1960, 1970), Ribéreau-Gayon, Peynaud, Lafourcade, and Charpentié (1955), Sutidze (1962), Hofmann (1968), Nelson and Amerine (1956), de Jong, King, and Boyle (1968), Novák (1958), Novák and Vörös-Felkai (1958), Dittrich (1964), and Champagnol (1969) among others; see also PART 3, "Metabolism". Tartaric and malic acids are both utilized (tartaric acid more so in vitro) as well as mono- and disaccharides, starch, cellulose and some glycosides, to yield glycerol, mannitol, and ethanol; gluconic, citric, acetic, succinic, glycolic, and lactic acids; and soluble dextrans, using the enzymes glucose oxidase, laccase, tyrosinase, ascorbic acid oxidase, pectinases, and proteinase. Sutidze (1962) found tannins to be utilized and the must content to be reduced by as much as 77%. Jako and Nyerges (1967) also found the sugar content of infected grapevines to be decreased. Musts containing *B. cinerea* ferment very slowly. Ribéreau-Gayon et al. attributed this slowness to the inhibition of yeasts by a complex of 2 inhibitors; the pair are collectively termed botryticine and are destroyed by sulfuric anhydride or heat.

The reasons why one vineyard may have the noble rot and its neighbor the destructive rot are not well understood (Ribéreau-Gayon 1960). Dubos (personal communication) obtained no evidence that different races of the fungus are involved, although she did obtain evidence of differential pathogenicity of isolates from different parts of France. Pesante (1947) found some differences in the composition of musts attributable to different isolates of *B. cinerea,* while Saponaro (1953) merely found some morphological differences between vineyard isolates.

Ribéreau-Gayon (1960, 1970) found that must from healthy grapes from a destructive rot vineyard had twice the total N and ammonium N content of healthy grapes from a neighboring vineyard that had the noble rot. He (1960) also attributed the resistance of the cultivar St. Emilion to its very low N content.

In both lots of grapes, 75–90% of this N disappeared when they were parasitized by *B. cinerea*. He concluded that the N nutrition of the grapevines has a profound effect on whether the rot is noble or destructive. Noble rot vineyards tend to be on nutrient-poor, well-drained, limestone soils; the plants are deep rooted and have a constant water supply that tends to decrease at fruit maturation. By contrast, vines on richer soils have more superficial roots and a widely fluctuating water supply; their fruits mature earlier and are more susceptible to cracking (Séguin, Compagnon, and Ribéreau-Gayon 1969). Ribéreau-Gayon (1960) also found that in the noble rot of Sémillon grapes, 22% of sugars were utilized, together with 49% of the tartaric acid and 8% of the malic acid; in the destructive rot of the same cultivar, 52% of the sugars were utilized, 44% of the tartaric acid, and 28% of the malic acid. In the noble rot of Sauvignon grapes the utilization of sugars, tartaric, and malic acids respectively was 27%, 40%, and 40%, compared with 36%, 27%, and 24% for the destructive rot. The utilization of acids was relatively more important than that of sugars in the noble rot and the converse was true in the destructive rot.

In California and Moldavia SSR, attempts have been made to reproduce the effect of a noble rot in harvested grapes by Nelson and Amerine (1956), Nelson and Nightingale (1959), Nelson, Kosuge, and Nightingale (1963), de Soto, Nightingale, and Huber (1966), de Jong, King, and Boyle (1968), Flath, Forrey, and King (1972), and Trofimenko and Tikhonova (1972). This process is known as 'botrytization'; hence the verb 'to botrytize'. Mature grapes were sprayed with a suspension of spores of *B. cinerea* and incubated at 98–100% RH and 20°C for 1 day, then at 50–60% RH for 1 wk. The wine made from these grapes was very sweet, but there tended to be a marked taint and the yields were small. Promising attempts were also made to produce sweet wines by growing *B. cinerea* in sterile grape juice before fermentation and also by adding enzymes from *B. cinerea*.

PRINCIPLES OF CONTROL

Diseases caused by *Botrytis* can be controlled in many ways, yet they remain among the most economically serious diseases, both in the field and in stored and marketed products. All phases in the biology of the causal organisms must be considered in the design of prophylactic and therapeutic treatments, in the modifications of cultural practices, and in the selection of new cultivars (Wood 1961; Jarvis 1965).

Fungicides

In general, fungicides are of value only as prophylactics, but because of the rapidity of infection from conidia, little warning of the likelihood of infection can be obtained from a knowledge of relevant meteorological factors. Moreover, the conditions permitting infection to occur often do not permit fungicide applications to be made to field crops; and fungicides effective against *Botrytis* spp. in vitro are often not effective in the field because the fungicides affect host metabolism, are tolerated by the fungi, or are applied at an incorrect time and place (Gilles 1964; Jarvis 1966*b*, 1969; Müller 1964; Brandes 1971; and Lafon, Verdu, and Bulit 1972). Because many crops become affected by *Botrytis* spp. just before harvest, attention must be given to the levels of fungicides that can be tolerated in foods and in grape must (Lamberti and Quacquarelli 1965), and to fungicide efficacy in controlling rots developing after harvest. These considerations have been studied in strawberries by Gilles (1964), Freeman (1965), Maas and Smith (1972), and Jordan (1973); in raspberries by Mason (1973); and in grapes by Harvey (1955*b*), McLellan (1972), and McClellan, Hewitt, La Vine, and Kissler (1973). Fungicide applications after harvest add considerably to the costs of production and often are detrimental to food quality.

Storage diseases

Postharvest rots caused by *Botrytis* spp. often outweigh field diseases in their economic effects, although in some respects they are more amenable to control by careful storage and marketing techniques and certain other treatments: controlled-temperature or controlled-atmosphere storage, pasteurization, irradiation, fumigation and vapor-phase fungicides, and delay of ripening (Wright, Rose, and Whiteman 1954; Harvey and Pentzer 1960; Haas and Wennemuth 1962; Smith 1962; Smith, McColloch, and Friedman 1966; Sommer and Fortlage 1966; Spalding 1966; Shibabe, Ito, and Iizuka 1967; Eckert and Sommer 1967; Hansen 1967; Lutz and Hardenburg 1968; Redit 1969; Ceponis 1970; Ceponis, Kaufman, and Butterfield 1970; Sutton and Strachan 1971; Aharoni and Stadelbacher 1973; and Sommer, Fortlage, Mitchell, and Maxie 1973). There are also several ways of treating crops immediately pre- or post-harvest to ensure that they enter storage in good condition, for example, keeping produce from contact with saprophytically based inocula on the soil or on containers or in plant debris (Jarvis 1960*a*; Jenkins 1968), removing field heat by precooling (Duvokot 1965; Hall 1966; and Mitchell, Maxie, and Greathead 1964), and curing onions to dry out the neck before storage (Vaughan 1960; Harrow and Harris 1969; and Böttcher 1973).

Disease escape

Considerable contributions to control may be made by various manipulations of environment and habit that confer disease escape and these can be

supplemented by modifications of cultural practices that confer resistance (e.g., liming in the case of tomato, lettuce, and strawberry gray mold) and by the selection of new cultivars. Cultural practices that predispose to infection (e.g., over-dense crops) should be avoided. Reductions in inoculum, both mycelial and conidial, can be achieved by attention to crop hygiene, that is, the removal of alternative weed hosts, perhaps aided by specific antisporulants such as tecnazene and hexachlor-2-propanol.

Little attention has been paid to the practical possibilities of exploiting the degradation of sclerotia in or on the soil, although they are parasitized by many organisms; and the control of infection by prior colonization with other microorganisms has been shown to be feasible in certain circumstances.

Little is known of the relative importance of conidia and ascospores in infection, but ascospores are probably of greater importance than has hitherto been supposed. If they are important, then some attention to the biology of sclerotial germination, apothecial formation, ascospore discharge, and the inhibition of all of these processes could be rewarding.

Breeding for resistance

No major gene-resistance against *Botrytis* spp. is known; this is hardly surprising in view of the wide range of methods and the wide range of environmental conditions in which these species can attack their hosts. One or two intrinsic resistance mechanisms are known and some features of habit conferring disease escape (q.v.), but relatively few diseases are the subject of special attention by plant breeders. The careful techniques elaborated by van der Meer, van Bennekom, and van der Giessen (1970) for screening *Allium* spp. for resistance to *B. allii* are an exception; these techniques take into account most aspects of infection and pathogenesis. Vasileva (1973) made a study of the inheritance of resistance to *B. cinerea* in an F_1 generation of grapes.

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APPENDIX

Additional Literature

These important references were noted since the text was drafted in December 1974, or were inadvertently omitted from it, or were not discussed there. To aid in assessing the coverage of these papers, each reference is followed by key words, set in italics. These key words are in line with the BOTBIB computer-filed bibliography on *Botrytis* and *Botryotinia* spp. that is compiled at the Scottish Horticultural Research Institute and filed at the Edinburgh University Computer Centre (Jarvis and Topham: Bull. Br. Mycol. Soc. 8:37. 1974).

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