ECTOMYCORRHIZAL FUNGI WITH EDIBLE FRUITING BODIES 2. *BOLETUS EDULIS*[1]

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Hall, Ian R. *(New Zealand Institute for Crop & Food Research Limited, Invermay Agricultural Centre, Private Bag 50034, Mosgiel, New Zealand),* **Lyon, Anthony J. E.** *(Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom),* **Wang, Yun and Sinclair, Liane** *(New Zealand Institute for Crop & Food Research Limited, Invermay Agricultural Centre, Private Bag 50034, Mosgiel, New Zealand)* ECTOMYCORRHIZAL FUNGI WITH EDIBLE FRUITING BODIES, 2 *BOLETUS EDULIS Economic Botany 52(1)44–56, 1998* Boletus edulis *sensu lato (penny bun mushroom, cep, cèpe de Bordeaux, porcino, Steinpilz) is a complex of at least five species (or sub-species) of mycorrhizal fungi which grow primarily with hosts in Fagaceae, Pinaceae, and Betulaceae. They occur in a wide variety of habitats throughout the Northern Hemisphere and have been accidentally introduced into South Africa and New Zealand. The fruiting bodies have a very strong flavor and are widely used both commercially and domestically, particularly in Europe and North America. The vegetation, climate, and soils where* B edulis *grows and methods that have been used in unsuccessful attempts to cultivate it are described*

Hongos Ectomicorrizicos Con Cuerpos Fructiferos Comestibles, 2. Boletus edulis Boletus edulis sensu lato *(champiñón, penny bun mushroom, cep, cèpe de Bordeaux, porcino, Steinpilz) es un complejo de por lo menos cinco especies (o subespecies) de hongos micorrízicos que se crían principalmente sobre hospedadores en las familias Fagaceae, Pinaceae y Betulaceae Se encuentran en una gran variedad de hábitats a través del Hemisferio Norte y han sido accidentalmente introducidos a Sud Africa y Nueva Zelandia. Los cuerpos fructíferos tienen un sabor muy fuerte y son ampliamente utilizados tanto comercial como domésticamente, particularmente en Europa y Norte América Se describen la vegetación, clima y suelos donde crece* B. edulis *y los métodos utilizados en intentos fallidos para cultivarlo.*

Key Words: mycorrhiza; fungus, *Boletus edulis*, ecology, cultivation

Boletus edulis Bull.: Fr. sensu stricto, *B. aereus* Bull.: Fr, *B. aestivalis* Fr., *B. pinophilus* Pilát et Dermek and *B. reticulatus* Boud. are a group of allied ectomycorrhizal fungi with edible fruiting bodies that are often grouped together as *B. edulis* sensu lato (Fig. 1) (Breitenbach and Kränzlin 1991; Phillips 1981). Because it takes a specialist to distinguish between these species (R. Watling pers. comm.) they are often marketed together using common names including cep and penny bun mushroom (English), cèpe de Bordeaux (French), Steinpilz (German), porcino (Italian), zhutui mo (pig leg mushroom, North China) and dajiao gu (fat feet mushroom, South China).

Unlike most other mushrooms, *B. edulis* can be stored dried and cooked at autoclave temperatures without a significant loss of its distinctive mushroom flavor (Ney and Freytag 1980). For this reason it is in demand by soup and stew manufacturers, chefs and gourmets throughout the world. *B. edulis* is also used in traditional Chinese medicines. For example, it is the major ingredient of *shujin wan,* a traditional herbal remedy made in Taiyuan, Shanxi Province, which is reputed to stimulate blood circulation and to relax muscles and joints (Liu 1984).

Of the more than 140 mycorrhizal fungi that have edible fruiting bodies, only *Tuber melanosporum* Vitt. and *T. magnatum* Pico have been produced commercially in artificial plantations (Hall et al. 1998). The commercialization of *B. edulis* is, therefore, dependent on the collection of fruiting bodies (basidiomes) from natural forests. If methods were developed for its cultivation in host plantations like the Périgord black

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Fig. 1. Fruiting bodies (basidiomes) of *Boletus edulis* from Christchurch, New Zealand.

truffle (Giovanetti et al. 1994; Hall, Brown and Byars 1994) the increased in-season supply should find a ready market. Also, as chefs prefer to work with fresh produce rather than preserved there is the possibility that *B. edulis* could be produced in Southern Hemisphere countries for out-of-season Northern Hemisphere markets.

This paper is the second in a series of three on edible ectomycorrhizal mushrooms and reviews published information on *B. edulis* sensu lato and our research findings in order to provide a basis for future studies directed toward developing techniques for its routine cultivation.

Distribution, Hosts and Pathogens of *Boletus Edulis*

Boletus edulis is found from the north of Scandinavia to the south of Italy and Morocco, and throughout Asia and North America including Mexico and in a wide range of habitats (Arora 1986; Breitenbach and Kränzlin 1991; Phillips 1981; Zang and Bi 1991). For example, in California *B. edulis* is found in coastal forests, dry interior oak forests and savannas and interior high montane forests of mixed conifers and hardwoods. Although it does not occur naturally in the Southern Hemisphere it has been accidentally introduced to New Zealand (Wang et al. 1995) and South Africa where it has been reported to occur at the Cape of Good Hope (Pearson 1950) and the Southern Natal Midlands (J. M. Theron pers. comm.; Marais and Kotzé 1977).

Some hosts for *B. edulis* sensu lato include *Abies, Castanea, Castanopsis, Fagus, Keteleeria, Lithocarpus, Pinus, Picea, Quercus,* and *Tsuga* (Table 1) but the various component species that make up the taxonomic complex are associated with different hosts in different locations. For example, in Southern England, *B. aestivalis, B. reticulatus* and *B. aereus* are found under *Quercus robur* L., while *B. pinophilus* is found primarily under *Betula pendula* Roth and *Pinus sylvestris* D. Don, and *B. edulis* sensu stricto under *Q. palustris* Muenchh., *Q. robur, Q. petraea* Mattuschka and *Fagus sylvatica* L.

Boletus edulis can be found growing on isolated trees although it is more likely to be found in woodlands or forests. While it is often found on mature trees, in Scotland it is also found in

TABLE 1. SOME HOST PLANTS FOR *BOLETUS EDULIS* SENSU LATO.

Location	Host	Reference
China	*Castanopsis* spp	Wang et al. 1995
	Keteleeria spp.	
	Picea spp.	
	Pinus spp.	
	Quercus spp.	
Europe	*Abies* spp.	Watling 1970
	Betula pendula Roth	Breitenbuch and Kranzlin 1991
	Castanea sativa	Moser 1983
	Fagus sylvatica L	
	Picea spp.	
	Pinus sylvestris L	
	Q robur L.	
	Q. petraea Mattuschka	
	Q. palustris Muenchh.	
Japan	Fagaceae	Imazeki and Hongo 1974; Imazeki, Otani and Hongo 1988
	Pinus spp.	
New Zealand	*B. pendula*	Wang et al. 1995
	Fagus sylvatica	Sinclair unpublished data
	Quercus cerris	
	Q. palustris	
	Q. robur	
	Ulmus procera Salisb	
North America	*Abies* spp	Arora 1986
	Castanea spp.	
	Fagus spp.	
	Lithocarpus spp.	
	Pinus spp	
	Picea spp.	
	Quercus spp.	
	Tsuga spp.	
South Africa	*Pinus radiata* D Don	D.T Mitchell pers. comm.
	P. patula Schlecht et Cham.	van der Westhuizen 1977
	P taeda L	Marais and Kotzé 1977

birch woodland that is only 10 years old with about 75% cover (R. Watling pers. comm.). On *Betula* and *Pinus, B. edulis* can dominate in a soil and does not seem to be part of a fungal succession, although with oak and beech this may not be the case (R. Watling pers. comm.). Pests of *B. edulis* include *Sepedonium chrysospermum* (Bull.) Link (Kroeger 1996), and various mushroom flies (e.g. Santini 1983) while diseases can be caused by viruses (Huttinga, Wichers and Dieleman van Zaayen 1975).

In New Zealand, *B. edulis* sensu lato is found primarily in an area about 80 km^2 around the city of Christchurch (43°S) from sea level to an altitude of about 280 m (Wang et al. 1995). In April 1994 a poor specimen of *B. edulis* was found under a 15-year-old *B. pendula* at Lake Pukaki, about 270 km to the south of Christchurch. The distribution of *B. edulis* in Christchurch and the ages of trees on which it has been found suggests that it was introduced more than 100 years ago on the roots of a tree imported into New Zealand by an early European settler. It then became established in two large parks (Hagley and Victoria Parks) and at a Ministry of Works nursery. From these areas it then spread to many parts of Christchurch City on the roots of young, transplanted trees. The nursery supplied plants for stabilization work around hydroelectric lakes, which may explain how the fungus spread to Lake Pukaki.

In South Africa *B. edulis* is found at altitudes between 900 and 1500 m in the Southern Natal Midlands growing with *P. patula* Schlecht. et Cham., *P. radiata* and *P. taeda* L. (J. M. Theron pers. comm.; Marais and Kotzé 1977). *B. edulis* has been picked commercially in these plantation forests and exported fresh to Germany. Although Dickinson and Lucas (1979) reported that *B. edulis* was present in Australia, no collections are deposited in the herbarium at the Royal Botanic Gardens in Melbourne (T. May pers. comm.; Watling and Gregory 1989). Mushrooms assumed to be *B. edulis* collected in 1996 on the lower slopes of Mt Wellington, Hobart, Tasmania, proved to be *Leccinum scabrum* (Fr.) S. F. Gray (brown birch bolete).

Consumption and Prices

There is very little information available to gauge world consumption of *B. edulis* sensu lato. Official records show that 1049 tons of *B. edulis* were sold in France in 1987 (value of Ff53,496,000[2]), more than 1000 tons in Germany in 1987 (>DM10,000,000) and 2387 tons in Italy in 1988 (*L*28,132,006,000) (New Zealand Trade Development Board 1989). However, these official figures do not include the very large quantities that are picked by individuals and consumed privately or sold directly to restaurants. Further substantial quantities are also harvested in, for example, Austria, China, Finland, India, Indonesia, Mexico, Morocco, Norway, Spain, Sweden, Switzerland, USA and Eastern European countries. World consumption of the equally popular chanterelle (*Cantharellus cibarius* Fr.) has been estimated at 200 000 tons (Baker 1997) although, unlike *B. edulis,* it is not as badly affected by worms and insects. Our educated guess of total annual worldwide consumption of *B. edulis* is, therefore, between 20 000 and 100 000 tons.

The main international markets for *B. edulis* are currently North America, France, Italy and Germany. Prices depend on quality and whether the mushrooms are sold fresh, dried or preserved. In September 1991 French pickers received Ff50–100/kg for fresh *B. edulis* (Fenoglio 1991) when small button-grade mushrooms probably from Poland retailed in Hamburg for DM120/kg. In season, *B. edulis* wholesale in the USA for US$10–55/kg although fruiting bodies harvested in April command more than US$200/kg (Mushroom Growers Newsletter 1997). Wholesale prices in the small New Zealand market have been as high as NZ$80/kg, but have fallen to NZ$20/kg when supply exceeded demand (C. D. Pratt pers. comm.) or when large quantities of *L. scabrum* were available and substituted for *B. edulis.* Whole or part fruiting bodies that have been dried, frozen or preserved in brine fetch the lowest prices. These forms are favored by manufacturers of processed foods such as mushroom stock, soups and stews for their low price and because a year-round supply of a predictable, albeit poor, quality is guaranteed. Fresh *B. edulis* have been exported from the Southern Natal Midlands of South Africa to cater for the off-season market in Germany (G. Halley pers. comm.) but we have been unable to establish the quantities involved. Dried *B. edulis* has also been exported from South Africa (J. M. Theron pers. comm.). Bulk supplies of broken caps of "*B. edulis,*" either dried or pickled in brine often contain pieces of caps of other boletes such as *Leccinum scabrum.* Boletes exported from Chile in brine in the 1970s were *Suillus luteus* (Fr.) O. Kuntze (Anonymous 1978).

Mushroom imports to Germany, particularly those from Eastern European countries, are screened for radiation by the German authorities because dangerously high levels have been found in the past (Haselwandter, Berreck and Brunner 1988). Contaminated shipments are always returned to the sender. Some boletes, such as *Xerocomus badius* (Fr.) Kühn, also accumulate heavy metals (Brown and Hall 1989; Gadd 1993; Kalac, Burda and Staskova 1991; Korky and Kowalski, 1989; Teherani, 1988; Thomas 1992) and there are frequent reports in the German press of the dangers of heavy metal poisoning from wild mushrooms.

Yields

Partly because of the reluctance of collectors to disclose earnings from *B. edulis,* it is difficult to obtain reliable information on likely yields of this fungus per hectare of forest (Fenoglio 1991) In a French experimental plot of 9-year-old *Pinus pinaster* Ait. infected with the bolete *S. granulatus* (Fr.) O. Kuntze., 2.3 kg of fruiting bodies were produced per tree. This equated to between 600 and 1500 kg/ha (Poitou et al. 1989). Similarly, in Autumn 1995 a *Q. palustris* growing in a lawn in the grounds of the University of Canterbury, Christchurch, New Zealand, at one time had 50 button stage *B. edulis* around it. These averaged 30 g although we be-

[2] Typical 1991 exchange rates US$1 00 = DM 1 74, Fr 5 93, NZ$1.71, *L* 1290

lieve they would have grown to between 50 and 120 g before they began to deteriorate. Twenty-year-old *Betula pendula* in Christchurch have also yielded as high as 2 kg per tree. The yields from these trees were unusually high, but it would not be unreasonable to expect annual yields to range between 20 and 200 kg/ha for *B. edulis* grown in managed plantations similar to those where *T. melanosporum* is cultivated (Hall, Brown, and Byars 1994).

There are reports of apparent declines in the size and yields over time for some edible mycorrhizal mushrooms including *B. edulis* in Europe (Anonymous 1995; Cherfas 1991; Palm and Chapela 1997). It has yet to be determined if these reductions are simply because of the large numbers of collectors picking fruiting bodies before they have had a chance to grow to their full size, or if they are due to environmental damage such as soil compaction, acid rain, or climatic change.

Soil Conditions

Unlike the more intensively studied *T. melanosporum* (Hall, Brown and Byars 1994) there are no published details of soils associated with *B. edulis.* In an attempt to overcome this gap in our knowledge we collected and analysed *B. edulis* soils from England, New Zealand and Scotland.

UK Soils

Dr R. Watling (Royal Botanic Garden, Edinburgh) and the second author have kept records of locations near Sheffield and in Scotland where *B. edulis* have been found in the past. During the summer of 1992 soil samples were collected from different soil depths from these areas, air-dried, and then analyzed by the AgResearch soil testing laboratories at Invermay Agricultural Centre, Mosgiel, New Zealand, using standard New Zealand techniques (Cornforth and Sinclair 1984). Additional information on the sites, such as aspect, grid reference, slope, and host plants, was also gathered. The means and ranges of the soil analysis parameters are presented in Table 2 while copies of the raw data can be obtained from the first author.

The data were extremely variable which is perhaps not surprising in view of the wide range of localities that *B. edulis* can be found in. The only particularly notable characteristics of the soils were the moderate to very high available Fe concentrations and generally high C and C/N

Table 2. Mean pH and nutrient concentrations from *Boletus edulis* sensu stricto sites near Sheffield and in Scotland.

	pH	Ca (µg/ml)	K (µg/ml)	P (µg/ml)	Mg (µg/ml)	Na (µg/ml)	S (µg/ml)	Fe (µg/ml)	C (%)	N (%)	C/N ratio	Slope (°)	Aspect (°)
0–25 mm													
Minimum	3.7	0	20	1	20	1	12	528	4.3	0.23	6.9	1	0
Mean	4.3	390	90	10	67	3	40	2145	14.5	1.01	15.5	12	185
Maximum	6.1	2750	160	26	200	6	92	6700	27.6	1.80	29.7	31	350
25–100 mm													
Minimum	3.5	0	20	1	10	1	2	688	1.2	0.05	9.1		
Mean	4.1	162	51	9	37	3	26	2330	8.0	0.49	17.3		
Maximum	4.9	875	140	84	85	7	67	5860	26.8	1.7	32.7		
100–200 mm													
Minimum	3.6	0	20	1	5	1	2	484	0.7	0.04	8.0		
Mean	4.1	73	37	8	23	3	30	1725	3.5	0.20	16.6		
Maximum	4.8	500	100	60	70	6	73	4460	17.8	0.82	35.0		

ratios, which decreased with soil depth (a reflection of the mor-forming litter).

To determine the variability of soils developed beneath the various host plants, soil test data were pooled for sites where a particular host plant was found and compared with pooled data from other sites. Some statistically significant differences were detected which, again, reflect the variability of the sites where *B. edulis* was found:

Fagus sylvatica Soils

Soil-extractable Fe concentrations (0–25 mm and 25–100 mm) in *Fagus sylvatica* soils (2867 and 2778 μg/ml respectively) were greater than in non-*Fagus sylvatica* soils (1458 and 1904 μg/ml) (SED for 0–25 mm = 411, and for 25–100 mm = 382).

C/N ratio at 25–100 mm in *Fagus sylvatica* soils (19.28) was greater than non-*Fagus sylvatica* soils (15.39) (SED = 1.368).

Soil-available Ca concentration (100–200 mm) in *Fagus sylvatica* soils (25 μg/ml) were greater than in non-*Fagus sylvatica* soils (119 μg/ml) (SED = 32).

Available S concentrations (100–200 mm) in *Fagus sylvatica* soils (37.7 μg/ml) were greater than in non-*Fagus sylvatica* soils (22.3 μg/ml) (SED = 5.48).

Quercus petraea Soils

Total N concentrations (0–25 mm) in *Quercus petraea* soils (1.229%) were greater than in non-*Quercus petraea* soils (0.913%, SED = 0.143).

C/N ratio in *Quercus petraea* soils (0–25 mm) (12.31) were less than in non-*Quercus petraea* soils (16.94, SED = 1.58).

Betula pendula Soils

Available Ca concentrations (25–100 mm) in *Betula pendula* soils (243 μg/ml) were greater than in non-*Betula pendula* soils (104 μg/ml, SED = 54).

Available S concentrations (25–100 mm) (32.6 μg/ml) in *Betula pendula* soils were greater than in non-*Betula pendula* soils (21.2 μg/ml, SED = 4.04).

Organic C concentrations (25–100 mm) (11.74%) in *Betula pendula* soils were greater than in non-*Betula pendula* soils (5.29%, SED = 1.76).

Total N concentrations (25–100 mm) (0.73%) in *Betula pendula* soils were greater than in non-*Betula pendula* soils (0.33%, SED = 0.122).

Available Ca concentrations (25–100 mm) (133 μg/ml) in *Betula pendula* soils were greater than in non-*Betula pendula* soils (31 μg/ml, SED = 32).

As it was possible that the fruiting bodies found under a mixed coniferous wood at two sites could have been *B. pinophilus,* data for these sites were pooled and compared with pooled data from the other sites. However, no statistically significant differences were detected.

Boletus edulis Soils in Christchurch, New Zealand

Soil samples were taken from sites where *B. edulis* had been collected in Christchurch in the past and analyzed as above. While soil chemical characteristics (Table 3) were close to the ranges in the UK soils (Table 3), some soils had relatively high levels of available soil P (Little Hagley Park and Holmwood Road) while the site in Creyke Road had a relatively high soil pH.

Climatic Requirements and Fruiting

B. edulis sensu lato is found in cool-temperate to subtropical zones. The climate of Ostersund, Sweden, represents one of the coolest areas (Table 4) while Christchurch, New Zealand, and Bordeaux are towards the middle of the climatic range (Tables 5 and 6). Escourt in the Southern Natal Midlands, South Africa, is an area with the warmest winter temperatures and highest number of accumulated degree days of areas where *B. edulis* is found (Table 7). We, therefore, believe that *B. edulis* might be grown in cool to warm temperate zones in Argentina, Australia, Chile, New Zealand and elsewhere in the Southern Hemisphere.

Fruiting of *B. edulis* generally occurs in late summer or autumn and before other Boletaceae such as *Suillus* although occasionally fruiting bodies can also develop in spring. In the UK, fruiting normally begins in August and can continue until October. However, no fruiting occurs

TABLE 3. DETAILS OF SITES WHERE *BOLETUS EDULIS* HAS BEEN FOUND IN CHRISTCHURCH, NEW ZEALAND.

Site	Host plant	pH	Soil test figures for top 100 mm of soil (extractable nutrients unless otherwise stated—Cornforth and Sinclair 1984)											
			Ca (total %)	Ca (μg/ml)	K (μg/ml)	P (μg/ml)	Mg (μg/ml)	Na (μg/ml)	S (μg/ml)	Fe (μg/ml)	B (μg/ml)	C (%)	N (%)	C/N ratio
Victoria Park	*Quercus robur*	5.3	0.5	750	80	3	195	14	24	798	1.86	5.9	0.31	19.0
Botanical Gardens	*Fagus sylvatica*	5.1	0.5	875	260	24	165	18	26	1242	1.04	3.0	0.25	12.0
Creyke Road (University of Canterbury)	*Quercus palustris*	6.5	0.9	1750	380	9	290	8	6	998	2.77	6.0	0.33	18.2
Hagley Park	*Quercus* spp.	5.4	0.5	875	244	9	185	10	14	1036	0.81	2.9	0.22	13
Little Hagley Park	*Quercus robur*	4.2	0.2	250	80	43	170	23	111	3010	1.12	5.4	0.25	21.6
Fendalton	*Fagus sylvatica*	6.0	0.7	1125	300	55	250	24	12	1032	1.35	3.4	0.25	13.6
Mairehau	*Betula pendula*	5.2	0.4	500	80	6	145	16	14	846	0.44	2.7	0.15	18.0

TABLE 4. CLIMATE DATA FOR ÖSTERSUND, SWEDEN, 63° 10′N, ALTITUDE 328 M (JOHANNESSEN 1970).

	Mean daily temp (°C)	Mean daily temp range (°C)	Temperature extreme		Mean precipitation (mm)	Thunder storms (d/mo)	Mean sunshine (h/month)	Mean windspeed (m/s)	Accumulated degree days (>10°C)
			Highest (°C)	Lowest (°C)					
January	−8.4	6.7	9.8	−33.8	34	0	26	2.0	
February	−7.1	7.2	9.2	−31.4	23	0	61	2.1	
March	−4.1	8.9	16.0	−30.0	23	0	121	2.0	
April	1.2	8.0	18.8	−18.0	29	0.14	180	2.1	
May	6.7	10.3	26.5	−6.8	31	0.3	252	2.3	
June	11.3	9.8	33.5	−1.5	69	1.4	240	2.7	
July	14.7	9.7	32.5	2.5	77	2.4	249	2.4	
August	13.4	9.3	31.3	0.2	74	1.1	204	2.1	
September	8.9	7.1	25.2	−5.2	51	0.2	126	2.4	
October	3.8	5.2	16.4	−15.2	43	*	74	2.3	
November	−0.8	4.3	12.2	−20.4	42	0	29	2.1	
December	−4.5	5.4	8.5	−31.0	36	0	10	2.0	
Annual	2.9	7.6	33.5	−33.8	532	6	1572	2.2	290.1

TABLE 5. CLIMATE DATA FOR BORDEAUX, FRANCE 44° 50′N, ALTITUDE 47 M (ARLÉRY 1970).

	Mean daily temp (°C)	Mean daily temp range (°C)	Temperature extreme: Highest (°C)	Temperature extreme: Lowest (°C)	Mean precipitation (mm)	Thunder storms (d/mo)	Mean sunshine (h/month)	Mean windspeed (m/s)	Accumulated degree days (>10°C)
January	5.2	7.5	19.7	−14.4	90	0.7	81	3.3	
February	5.9	8.5	22.4	−15.2	75	1.3	103	3.5	
March	9.3	10.7	25.5	−6.1	63	0.9	174	3.8	
April	11.7	11.2	30.9	−4.8	48	1.6	210	3.6	
May	14.7	11.2	33.6	−1.8	61	4.3	229	3.2	
June	18.0	11.5	38.4	2.5	65	5.4	253	3.1	
July	19.6	11.7	38.6	5.1	56	5.9	262	3.1	
August	19.5	12.1	37.1	4.7	70	6.0	243	2.8	
September	17.1	11.1	36.2	−1.7	84	3.3	195	2.5	
October	12.7	9.9	30.4	−5.3	83	1.2	158	2.5	
November	8.4	8.0	23.9	−6.4	96	0.7	84	2.9	
December	5.7	6.8	21.2	−13.4	109	1.7	60	3.3	
Annual	12.3	10.0	38.6	−15.2	900	33.0	2052	3.1	1325.5

if there is a dry summer and an early, dry autumn with frosts, such as occurred in the UK in 1991. In contrast, fruiting does not begin in northern California until early November, and continues until late December. This pattern appears to be related to a fall in temperature and accumulated rainfall (Largent and Sime 1994). In Christchurch, New Zealand, fruiting begins in late February and, if there are no severe frosts, can continue until mid-May. In Christchurch in 1994, fruiting in February was cut short by a relatively dry autumn, but irrigation on the University of Canterbury campus resulted in a second crop of fruiting bodies in late March and early April.

The trigger for fruiting seems to follow some summer rainfall during a warm spell of weather followed by frequent rain in autumn accompanied by a fall in soil temperature (J. Guinberteau and M. Mamoun pers. comm.). To determine if this was also related to fruiting in Christchurch, New Zealand, climatic data for the Christchurch Airport meteorological station (H32451, 43.483°S, 172.533°, altitude 30 m) for 1996 were obtained from New Zealand's National Institute for Water and Atmospheric Research. Daily maximum and minimum air temperatures were averaged to estimate mean daily air temperature, and potential evapotranspiration was estimated using Priestley-Taylor's method (1972). Daily totals of incoming shortwave radiation were corrected to net radiation (Jamieson 1982) and zero net soil heat flux was assumed. To provide a crude index of accumulated water deficit, potential evapotranspiration was subtracted from rainfall with accumulated water deficit arbitrarily set to zero at the beginning of January (Fig. 2). In late summer and autumn 1996, flushes in fruiting appeared to be related to rainfall, increased soil moisture, and falling air temperature, which suggests that further research on their effects is warranted.

CULTIVATION OF *BOLETUS EDULIS*

For some ectomycorrhizal fungi such as *Rhizopogon* spp., infection of host plants can be achieved by placing about 10^5 spores onto a root system (Castellano and Molina 1989). Although the germination of *B. edulis* spores can be enhanced with abietic acid (Fries et al. 1987), infections can fail to form even with the application of 10^7 spores. Modifications of the techniques described by Molina and Palmer (1982) for other ectomycorrhizal fungi have been successful in producing laboratory-scale numbers of

TABLE 6. CLIMATE DATA FOR CHRISTCHURCH, NEW ZEALAND, 43° 29′S, ALTITUDE 30 IN (NEW ZEALAND METEOROLOGICAL SERVICE 1983).

	Mean daily temp (°C)	Temperature extreme		Mean precipitation (mm)	Mean sunshine (h/month)	Mean windspeed (m/s)	Accumulated degree days (>10°C)
		Highest (°C)	Lowest (°C)				
January	17.0	35.9	3.1	51	209	4.7	
February	16.8	40.0	2.7	45	186	4.4	
March	15.1	33.3	−0.1	58	163	3.9	
April	12.2	29.9	−4.0	60	150	3.6	
May	8.9	27.3	−4.2	70	125	3.3	
June	6.1	22.0	−7.2	54	120	3.1	
July	5.6	21.2	−6.8	62	122	3.3	
August	6.9	22.8	−6.7	56	145	3.3	
September	9.2	24.8	−3.8	43	162	3.9	
October	11.6	30.1	−4.2	47	200	4.4	
November	13.8	32.0	−0.7	49	207	4.4	
December	15.7	35.4	2.7	53	210	4.7	
Annual	11.6	40.0	−7.2	648	1999	3.9	971.8

plants infected with *B. edulis* and other Boletaceae (Marais and Kotzé 1977; Poitou 1978; Poitou et al. 1989; Zuccherelli 1988). However, there are problems with these techniques because *B. edulis* cultures can rapidly lose their ability to infect after just a few subculturing procedures. Infections often collapse once infected plants are transferred into unsterile media and some isolates can fail to infect (Wang unpublished data). Competition from other ectomycorrhizal fungi such as *Scleroderma* spp. can also be severe following transplantation (Meotto, Pellegrino and Craddock 1994).

Infections have also been established on seedlings by growing them with their roots in close contact with those already infected with the fungus (Ceruti, Tozzi, and Reitano 1988). This method is commonly referred to as the "mother plant technique" and is a modification of one developed by M. Joseph Talon to produce plants infected with *T. melanosporum* Vitt. (Giovanetti et al. 1994; Hall, Brown and Byars 1994; Hall and Wang 1998). Details of the techniques used by companies in Europe to produce commercial numbers of plants infected with *B. edulis* and *S. granulatus* have not been published. The Italian company Vitroplant has produced seedlings infected with *B. edulis* by growing sterile seed-

TABLE 7. CLIMATE DATA FOR ESTCOURT, SOUTH AFRICA (SCHULTZE 1972).

	Mean daily temp (°C)	Temperature extreme		Mean precipitation (mm)	Mean sunshine (h/month)	Accumulated degree days (>10°C)
		Highest (°C)	Lowest (°C)			
January	21	38	6	108	229.4	
February	21	37	8	115	207.2	
March	20	35	4	89	229.4	
April	17.5	33	1	47	231	
May	13.5	31	2	23	248	
June	11	27	5	7	258	
July	10.5	27	5	13	269.7	
August	13	31	3	15	244.9	
September	16	35	2	30	246	
October	18	38	1	63	226.3	
November	19.5	38	3	98	216	
December	20.5	37	4	117	217	
Annual	17	38	5	725	2810.5	2472

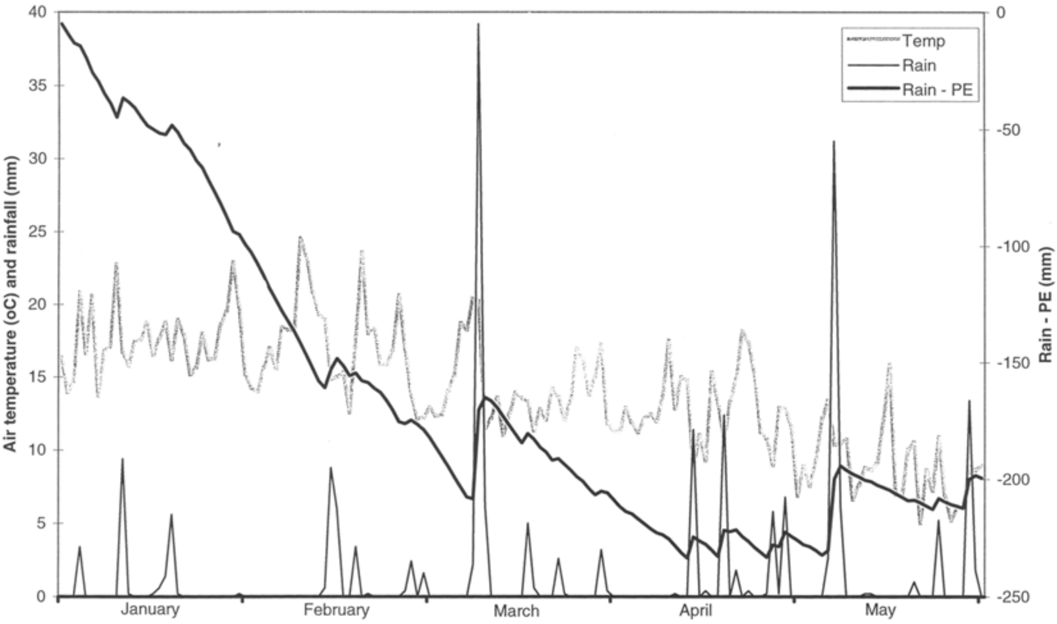

Fig. 2. Air temperatures at 100 mm depth, rainfall, and accumulated water deficit (rainfall-potential evapotranspiration (rain-PE)) in Christchurch, New Zealand, in late Summer and Autumn 1996 adjacent to an area where *Boletus edulis* fruiting bodies (basidiomes) were found.

lings in a medium containing 10% of a culture of *B. edulis* grown in a solid medium (Zuccherelli and Capaccio 1990). Other commercial techniques probably involve the inoculation of sterile seedlings with segments of infected root or mother plant techniques.

Veselkov (1975) found that infections could be established by burying pieces of dried *B. edulis* cap in the rooting zone of suitable hosts. Similarly, Y. Wang (unpublished data) established infections on *Q. robur* with a mixed inoculum composed of infested soil and blended *B. edulis* fruiting bodies. Although these plants were heavily contaminated with other ectomycorrhizal fungi and rhizosphere organisms, the infections appeared stable, unlike those established using pure cultures. This suggests a component of the soil microflora may be required for *B. edulis* infections to be stable. The growth and establishment of mycorrhizal infections by *Cantharellus cibarius* Fr. depend on co-organisms which, at least in part, have their effect through the production of CO_2 (Danell 1994). Such three-way interactions between host plants, mycorrhizal fungi and other soil organisms have been reviewed by Fitter and Garbaye (1994).

The authors have noted that *B. edulis* is commonly found with *Amanita muscaria* (L. ex Fr.) Hooker or *A. rubescens* ((Pers.) Fr.) S. F. Gray in China, England, New Zealand, and the USA, an association also noted by J. Guinberteau (pers. comm.) in France and I. Plattner (pers. comm.) in Austria. This may be because the three species have similar ecological requirements and fruit at similar times of the year or it might reflect a biological association.

Other Boletaceae colonize discrete blocks of litter placed in the rooting zones of infected plants (Read 1992). Some organic mulches are also colonized by *T. melanosporum* and stimulate fruiting (Hall, Brown, and Byars 1994). Thus, *B. edulis* may also colonize organic components in the soil and the nutrients it gains may be involved in fruiting.

Discussion

Although plants infected with *S. granulatus* have produced fruiting bodies (Poitou et al. 1989), there are no known reports of fruiting bodies being produced from transplanted plants infected with *B. edulis.* The relatively low price of *B. edulis* compared with truffles (Hall, Brown, and Byars 1994; Hall, Zambonelli, and Primavera in press) and matsutake (Wang, Hall, and Evans 1997) may exclude establishing plantations specifically for *B. edulis* production. However, plantation forests of *Pinus* or *Quercus* would be an ideal habitat for *B. edulis.* The forest owner could gain additional income during the life of a stand and improve cash flow (Hall and Wang 1996). *B. edulis* might also be grown in conjunction with *Betula, Picea, Q. robur* or *Q. palustris* in forest beautification margins, public areas or private gardens.

Only six New Zealand native plants routinely produce ectomycorrhizas. The ectomycorrhizal fungi associated with these native trees do not appear to form mycorrhizas with exotic ectomycorrhizal trees (Hall, Brown, and Byars 1994). The ectomycorrhizal fungi on exotic ectomycorrhizal trees are, therefore, restricted to those that have been accidentally introduced in the past. For example, about 2000 fungi can form ectomycorrhizas with Douglas fir (Trappe 1977), but only a small fraction of these are found in New Zealand. This lack of competition probably contributed to the establishment of *B. edulis* in New Zealand and may allow it to become more widespread in the future. The wide range of host plants on which *B. edulis* has been found in New Zealand might also reflect this lack of competition.

Although there are very large and obvious gaps in our paper this merely reflects the few publications and the general lack of information on *B. edulis.* Our survey of the soils in New Zealand and the U.K. is an attempt to begin to fill these gaps. Regrettably, because of the value of the *B. edulis* market, it is likely that there is considerable information on the production of plants infected with the fungus that remains confidential. Still more, such as the soil and climatic requirements of *B. edulis* and other details regarding its distribution, rests in herbaria. No doubt, important observations, which have not yet been committed to paper, also rest in the minds of those interested in the mushroom. Conceivably, it is this type of information rather than details of methods for producing infected plants that holds the key to the routine cultivation of this delicacy and which we urge people to publish.

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