RECENT ADVANCES IN ECOLOGY AND SYSTEMATICS OF MORELS.

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RÉSUMÉ — Le présent article fait la synthèse des avancées récentes dans le domaine de la biologie et de l'écologie des morilles avant de présenter des résultats nouveaux, susceptibles, d'éclairer le débat sur la notion d'espèce dans ce groupe dont la systématique est controversée. Des expériences de confrontations menées avec différentes "espèces de morilles" montrent que l'association à une plante supérieure peut être spécifique. Cependant, le fait que des facteurs bactériens puissent modifier la nature de telles associations incite à une utilisation prudente de telles spécificités d'association comme critère de caractérisation des espèces de morilles. Parmi les approches modernes, c'est l'analyse de l'espaceur ITS de l'ADN ribosomal qui est la mieux adaptée à cette caractérisation et à la révision systématique des *Morchellaceae*. Des exemples sont fournis au sein du groupe des morilles rondes.

ABSTRACT — The paper summarises recent advances in the field of the biology and ecology of morels and presents new results aiming to highlight the species definition in this group with controversial systematics. Experiments using different morel species show that the association with plants can be specific. However, as bacteria may modify their nature, the specificity of the associations must be used cautiously as criterion to characterise morel species. Within the modern approaches, the analysis of the ITS-region appears as the most adapted to characterise true species and to revise the systematics of the *Morchellaceae*. Examples within the group of the yellow morels are given.

KEY WORDS: *Morchella*, ecology, systematics, associations with plants, review

MOTS CLES: *Morchella*, écologie, systématique, associations avec des plantes, revue

Morels are often one of the first spring edible mushrooms collected in temperate regions (Weber, 1995). The stipitate mitrate ascomata with folded to spongiform hymenium make the genus *Morchella* easy to define (Chadefaud, 1960). In contrast, the fact that Korf (1973) and Jacquetant (1984) distinguished respectively 3 and 28 species illustrates

the debatable species definition. The basic difficulty here is that within each taxon, the ascomata display high macroscopic morphological variations (fig. 1), whereas the microscopical features of the hymenium are remarquably homogenous within all *Morchellaceae*. In this context, Gessner (1995) recently underlined the importance to consider also biological and ecological features in order to distinguish form variations respectively reflecting ecotypes and true species. The present article constitutes an attempt to follow this line of thought. A review of known biological and ecological features and the presentation of new results on the specificity of associations between morels and plants will be used to highlight the most recent advances on systematics of this fungal group which base on molecuiar biological investigations.

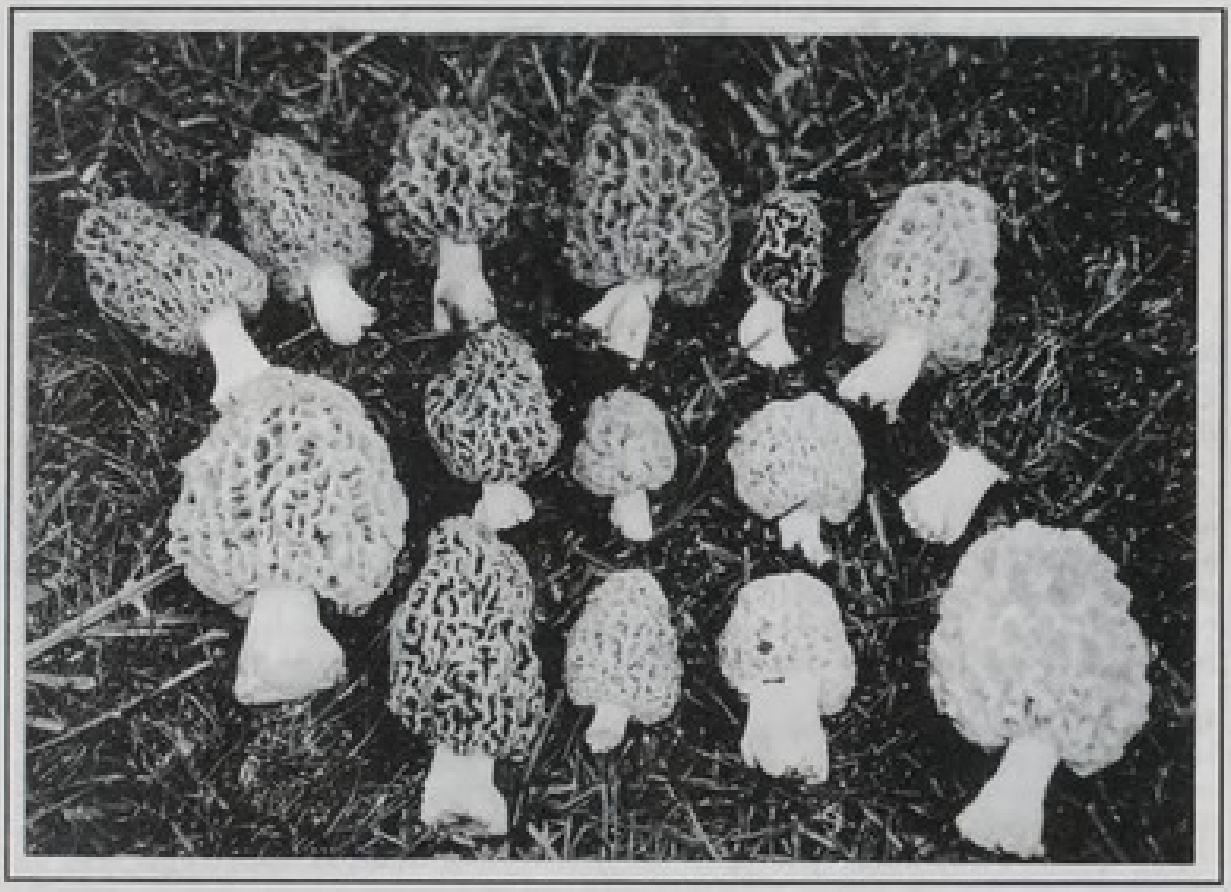

Fig. 1. — Morphological variability of fruitbodies within the taxon *Morchella vulgaris*.

BIOLOGICAL AND ECOLOGICAL CYCLES

The observation by Molliard (1905) and Matruchot (1909) that morels fruit at the expense of preformed sclerotia constituted a crucial step of the ancient effort to elucidate morel biology and ecology. The central biological role of sclerotia was confirmed by the experimental work of Ower (1982 & 1986), which resulted in mastering the fructification under culture conditions. In addition, ecophysiological field investigations allowed Buscot (1989) to demonstrate the biennial life cycle of morels in temperate regions and revealed that sclerotia constitute the mycelial structure which overlives the cold season and provides the nutrients for the ascomata development in early spring. Both latter functions of sclerotia were confirmed by biochemical (Buscot & Bernillon, 1991) and experimental ecophysiological investigations (Buscot, 1993), which also supported the observation by Mayr (1982) that morels form two types of sclerotia. The first type represents the storage and overlive structure described above, while the second one can be considered as abortive ascomatal primordia.

A second crucial step in the elucidation of morel biology was the hypothesis by Hervey *et al.* (1978) and its confirmation by Volk and Leonard (1989) that the mycelium can become heterokaryotic after forming vegetative anastomoses. In their representation of the life cycle (fig. 2), the latter authors considered that only sclerotia formed by such heterokaryotic mycelium, which they termed secondary mycelium, are able to produce ascomata (Volk & Leonard, 1990). Buscot (1993) showed that heterokaryons are being formed under low nutrient availibility, while monosporal strains segregate when cultivated on nutrient rich media. He related this duality of mycelial somatic interactions with the two ecological strategies (see fig. 3) which morels show in nature (Buscot, 1992a). Within the so called "pioneer strategy", morels behave as ruderal organisms, colonising temporary recently disturbed soils on which they display a high fructification abundancy (Kaul, 1975; Turnau, 1984, 1987; Carpenter *et al.*, 1987; Duchesne & Weber, 1993). In the so called "perennial strategy", they grow in stable ecosystems over several years and form fruitbodies only sparsely. Considering the effective nutrient availability in both ecological situations, Buscot (1992a) hypothesised that non self incompatibility between monosporal mycelial strains should be enhanced in the pioneer strategy, while heterokaryons should predominate in the perennial strategy. He related the homokaryotic stage with the saprotrophic nutrition in the pioneer strategy and respectively the heterokaryon formation with the capability to form trophic associations with plant roots in the perennial strategy (see below association with roots). Thus, as is summarised in figures 2 and 3, Volk and Leonard (1990) considered heterokaryosis from the point of view of its role for the reproductive cycle, while Buscot regarded it as a somatic feature allowing the fungus to adapt to an ecological situation marked by enhanced competition for nutrient and complex associations with other organisms.

Additionally to describing morel sclerotia, Molliard (1905) also established a link between the anamorph *Costantinella cristata* and the conidial stage of *Morchella elata*. Paden (1972) confirmed this observation and Gams (pers. communication) obtained conidia of *M. elata* in pure culture. Thus, this feature can be considered as well established. To our knowledge however, *M. elata* is the only morel taxon in which conidia were described and as conidial germination has never been reported, their biological function remains unclear. This conidial stage has been included in the biological life cycle proposed by Volk and Leonard (1990, see fig. 2).

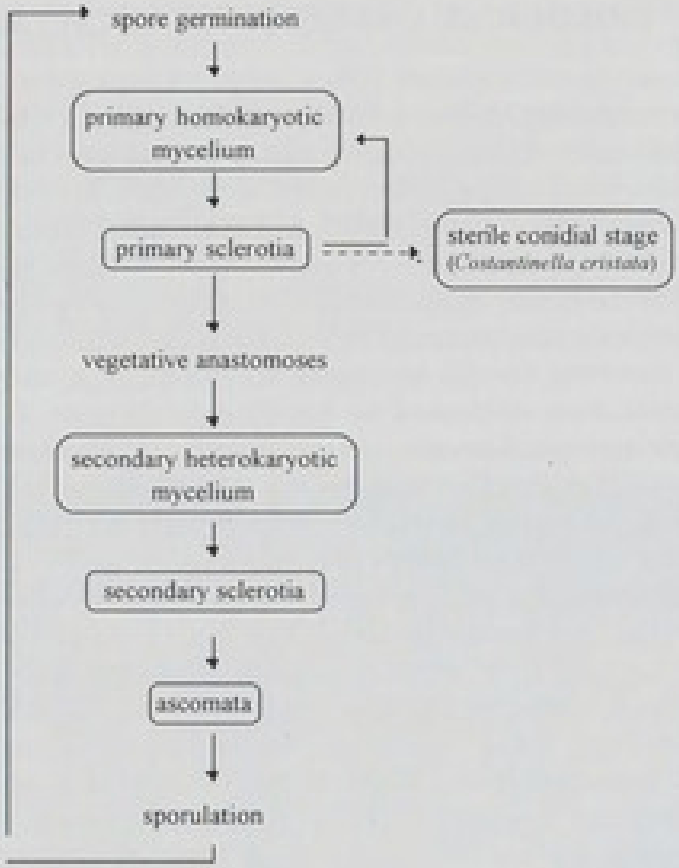

Fig. 2. — Biological life cycle of morels according to Volk and Leonard (1990).

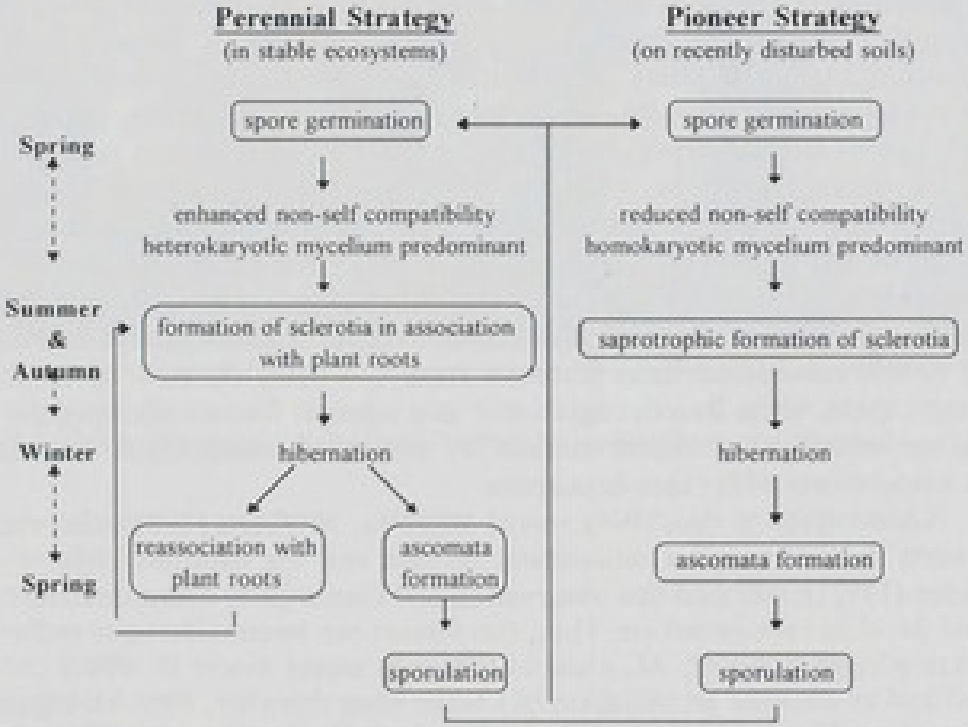

Fig. 3. — Biological and ecological life cycle of morels according to Buscot (1992).

ASSOCIATIONS WITH HIGHER PLANTS IN NATURE

The morel fidelity to vegetation types and to particular plant species is well known by morel hunters and is well documented (table 1). This feature was also largely used for species characterisation by authors such as Jacquetant (1984), who distinguishes a great number of taxa in morels. For example, within the yellow morels (*sectio adnatae* sensu Jacquetant), an association with sand dune vegetation is a crucial characteristics to identify *M. spongiola var. dunensis* (Romagnesi, 1963) and respectively, an occurence in a ash tree forest is a helpful even if not a definitive criterion to characterise *M. vulgaris* (Clowez, 1992). Nevertheless, several of the described associations of morels with plants have to be interpreted cautiously for two reasons. Firstly, within mixed vegetation types, the exact connection to a specific plant species was often not verified. Secondly, the nature of the associations was mostly not investigated. In certain cases however, connections between ascomata and plant roots or rhizomes could be traced and the kind of association characterised. The spectrum of such thoroughly characterised associations appeared to range from parasitism to ectomycorrhizal symbiosis (tab. 2). In the latter case, field observations suggest that the mycorrhizal formation occurs in spring at the same time as fruiting (Buscot & Kottke, 1990; Buscot, 1994) and represents the beginning of a new vegetative cycle within the perennial strategy (Buscot 1992a).

EXPERIMENTAL INVESTIGATIONS ON ASSOCIATIONS WITH PLANTS

While the potential to parasitism was confirmed experimentally, the formation of true mycorrhizas under controlled conditions was not successfull until now (Buscot, 1992b). Nevertheless, with seedlings of *Picea abies*, the author obtained formation of mycorrhiza-like modified short rootlets after inoculation of *M. esculenta* precultivated on a nitrogen rich medium which also enhanced the proliferation of two bacteria (*Bacillus circulans* and *Acinetobacter johnsonii*), probably originating from the spore surface (Fig. 4). Complementary assays to highlight these results are presented here briefly.

First series of assays were performed in a gnotobiotic culture system in which axenic root systems of Norway spruce seedlings were confronted with homo- or heterokaryotic strains of *M. esculenta* and/or the bacteria isolates mentioned above (for the method, see Buscot 1992 b). The experiments showed clearly that only the morel is able to induce root modifications, as control plants and plants inoculated only with the bacteria never formed modified roots. In all assays inoculated with morel strains, the formation of mycorrhiza-like modified short roots with generally limited growth was induced (fig. 5a & e). In few cases, the modified roots displayed a prolonged growth, which confered a club-shape to them (fig. 5a). Co-inoculation with the morel and the bacteria appeared to enhance this latter event (fig. 5b & d). Furthermore, confirming the above mentioned hypothesis of a link between heterokaryosis and the capability of association with roots in nature (Buscot, 1992 a), the production of both mycorrhiza-like and club-shaped roots was clearly higher in case of inoculation with a heterokaryotic than with a monosporal strain (fig. 5). The clearest morphological effect was obtained with polysporal inoculates (fig. 4).

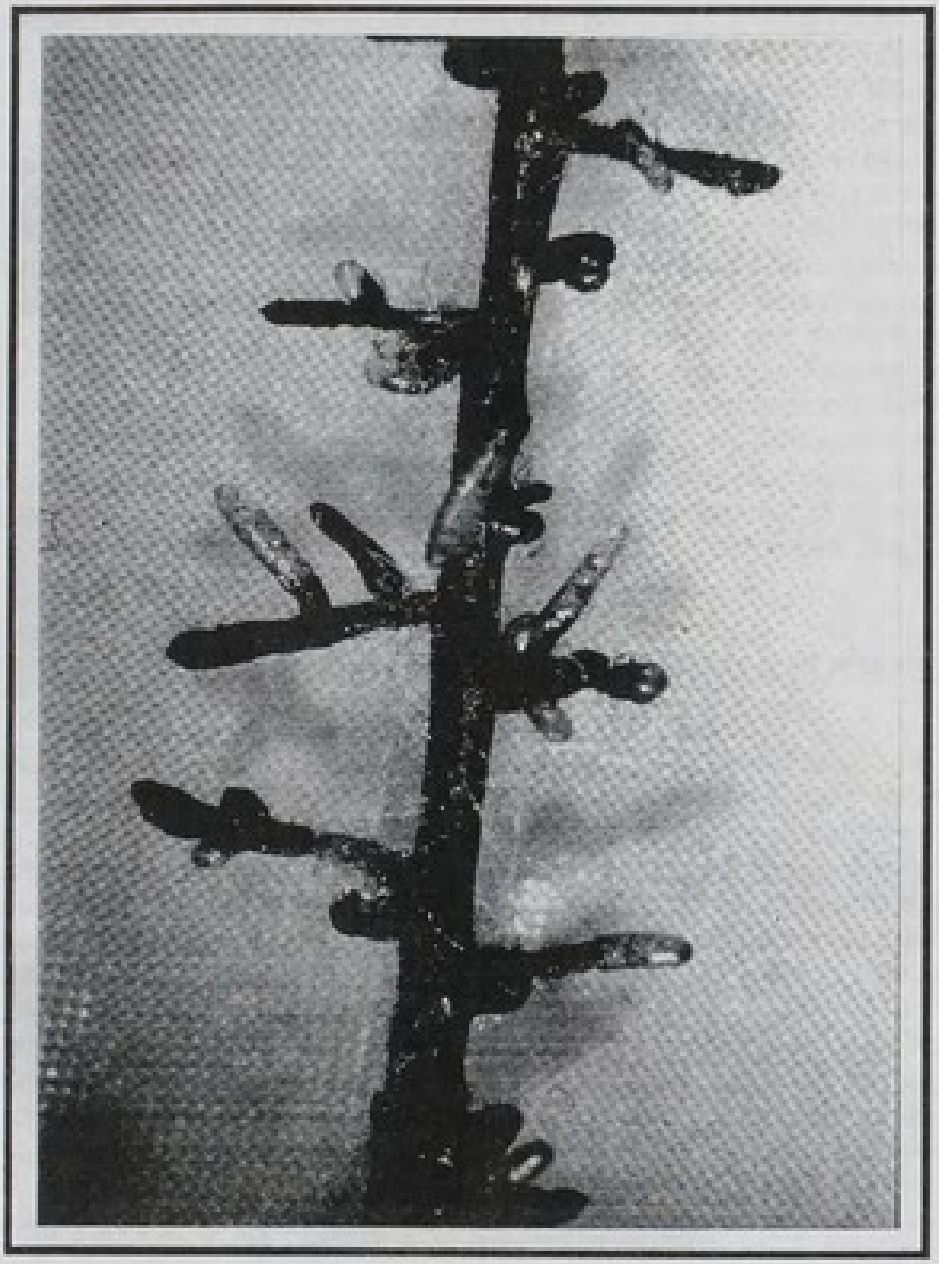

Fig. 4 — Mycorrhiza-like modified short roots of a Norway spruce seedling (*Picea abies*) infected with a polysporal inoculate of *Morchella esculenta*

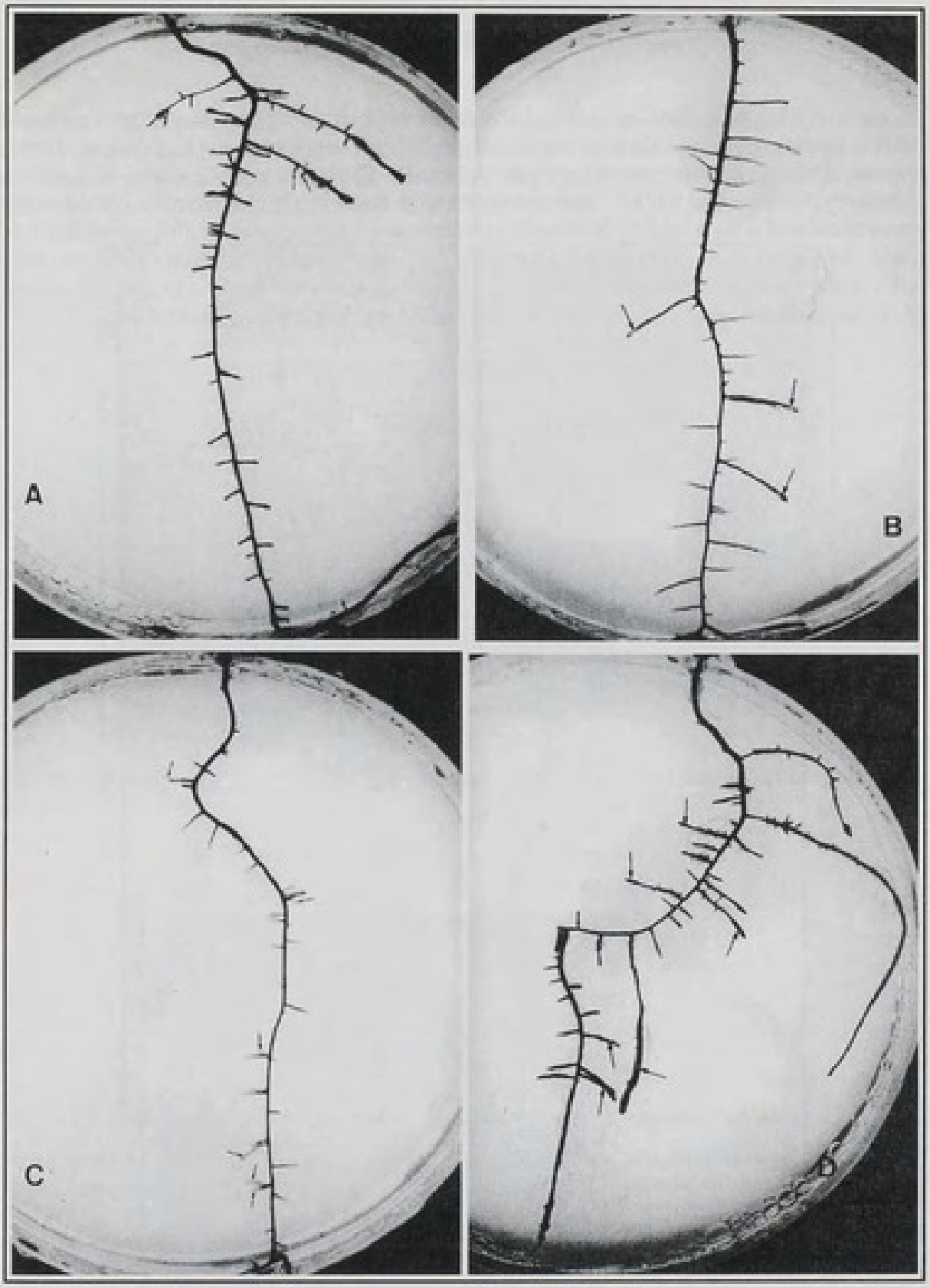

Fig. 5. — Root systems of Norway spruce seedlings inoculated with *Morchella esculenta* and eventually with *Bacillus circulans* and *Acinetobacter johnsonii*. a, single inoculation with a monosporal morel strain; b, dual inoculation with a monosporal fungal strain and with the bacteria; c, single inoculation with a heterokaryotic morel strain; d, dual inoculation with a heterokaryotic morel strain and with the bacteria (small arrows, mycorrhiza-like modified short roots with limited growth potential; large arrows, club-shap modified rootlets with prolonged growth potential).

Additional experiments were also performed to assess the specificity of different morels to plant species. Surface sterilised seeds of *Pinus banksiana* Lamb. and *Betula pendula* Roth. were germinated and precultivated on peat during 5-6 weeks in a growth chamber (photoperiod, 16/8 h; light intensity, 80 mmol m^{-2} s^{-1}; temperature, 24°C). They were inoculated with a mix of *Morchella esculenta* and *Morchella elata* and grown for 8-10 weeks. In comparison with control plants, the inoculated birches exhibited reduced shoot but a similar root development (data not shown). In contrast, in pine assays, the effects of the inoculation were higher, as both shoot and root development were reduced (fig. 6).

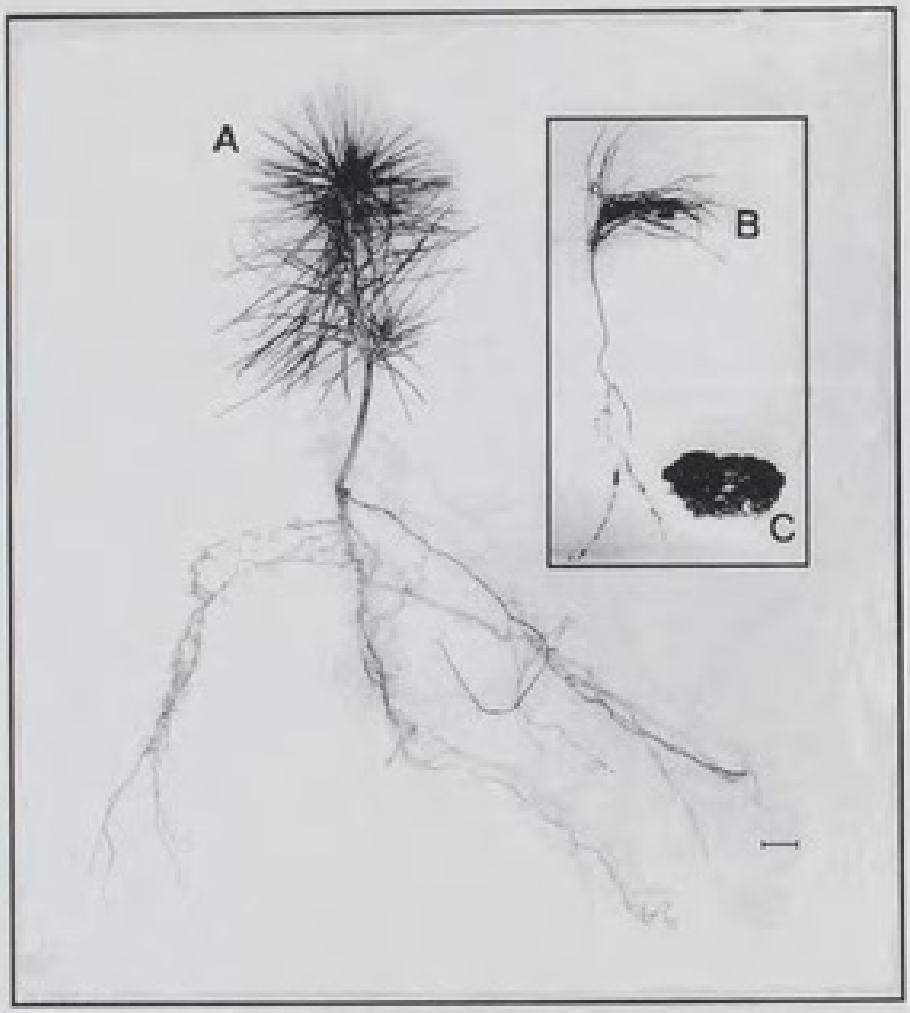

Fig. 6. — Confrontation assay between *Pinus banksiana* and a *Morchella esculenta* + *M. elata* mix. A, control plant; B, inoculated plant; C, sclerotia formed close to B roots. Scale bar represents 1 cm.

The kind of the interaction with the roots was also different according to the plant partner. Dense mycelial masses formed around root sectors of the birch trees (fig. 7), whereas large sclerotia formed close to, but not in direct contact with, the pine roots (fig. 6). With either of the plant species, a direct penetration of root tissues by the fungus could not be detected, but the remarkable number of dead plants at the end of the assays suggests a kind of necrotrophic parasitism of the fungus. Using PCR techniques described in the following section, it was possible to demonstrate that from the mixed inoculates, only *M. esculenta* developed in presence of birchs, and respectively that only *M. elata* grew in

presence of the pines (fig. 8). In additional control assays without plants, the mixed inoculum displayed a very reduced growth in the peat substrate used for the assays. Thus, this second series of experiments demonstrates clearly that morel species need a compatible plant partner to colonise certain kinds of substrates.

Fig. 7. — Detailed view of birch roots with dense mycelial masses formed by *Morchella elata* (white arrows).

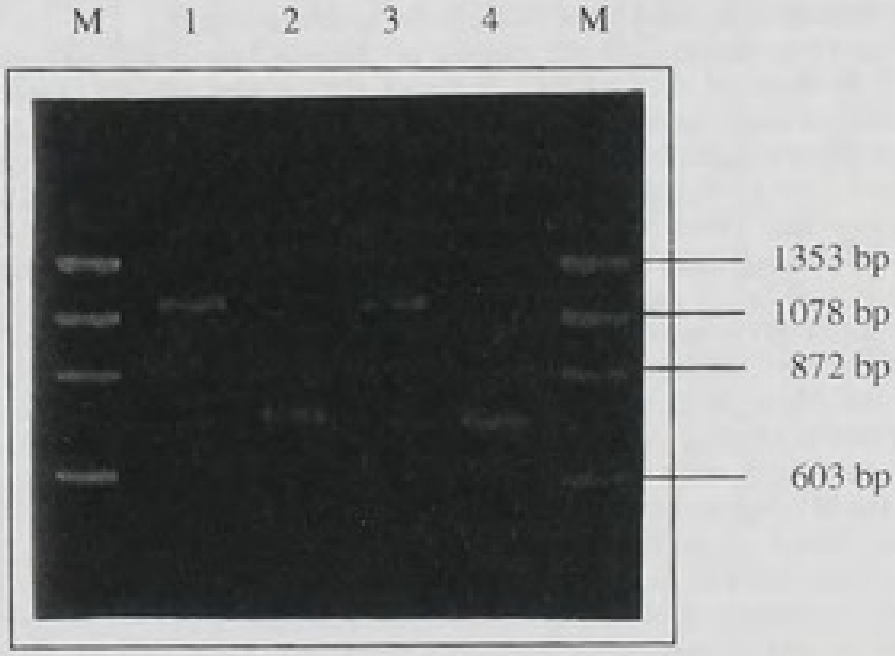

Fig. 8. — Agarose electrophoresis gel of the rDNA spacer ITS of *Morchella esculenta* (1), *M. elata* (2), the mycelial masses formed around root sectors of the birches (3) and of the large sclerotia formed close to *Pinus banksiana* roots (4). M = fragment size markers fX 174 digested by Hae III.

In summary, the above experimental investigations firstly reinforce the hypotheses emitted by Buscot (1992a and 1993), that associations of morels with plants are crucial in the perennial ecological strategy observed in stable ecosystems and that heterokaryosis is an advantage for the fungus in this situation. Secondly, the experiments implied that not only the associations but also their nature could be specific and depend on the taxa of both partners. *M. esculenta* formed a different kind of association with the Norway spruce than with the birch and none with *P. banksiana* with which *M. elata* in turn formed a third kind of association. However, the experiments with the bacteria also demonstrate that the features of the associations can be modified by other biological factors. This suggests that using the associations with plants as a criterion for determination and as an element helping to clear the morel systematics must be done cautiously and in combination with further criteria.

LINK WITH THE SYSTEMATICS

In recent years the potential of modern biological methods to improve the morel systematics was assessed by several authors.

The isozyme polymorphism was used by Gessner *et al.* (1987) and Yoon *et al.* (1990) to characterise geographic isolates of *Morchella esculenta* from North America. Kulkarni and Kamerath (1989), Royse and May (1990) also compared different American *Morchella* species by this method. Finally, Wipf *et al.* (1996a) assessed whether isozyme polymorphism in different members of the *Morchellaceae* could be used to clarify the systematics of the familly. The analysis by the different authors allowed fine discriminations at the inter — or intraspecific levels and appeared useful in strain characterization. However, Wipf *et al.* (1996a) underlined that the exhibited polymorphism is not adequate to perform phylogenetic analysis or to clear the species concept.

The large subunit of the rDNA of *Morchellaceae* was also analysed with PCR/RFLP by Bunyard *et al.* (1994). However, the authors reported higher degrees of polymorphism between intraspecific populations than among putative species in certain cases, which illustrates further the difficulty to define species in morels. In a more recent paper, Buscot *et al.* (1996) showed that polymorphism of the internal transcribed (ITS) spacer of ribosomal DNA is more adequate to clarify morel systematics. The analysis allowed to differentiate clearly all genera in the *Morchellaceae* and confirmed both species groups recognised in all classifications, i.e. black (*sectio distantes*) (Jacquetant, 1984; Weber, 1995) and yellow morels (*sectio adnatae*), which exhibited respective ITS lengths of 740-750 and 1150-1220 bp, respectively (fig 9). Sequence analysis of the ITS region confirmed this high genetical distance between black and yellow morels (Wipf *et al.* 1996b), further suggesting that they should perhaps be considered as distinct genera, as *Mitrophora* is. Within each "genera", slight length variations and different restriction profiles of the ITS region allowed to separate several species (fig. 9).

At present, the performed molecular biological analysis reinforce the validity of taxa like the yellow morels *M. spongiola var dunensis* and *M. hortensis* which do not exhibit remarquable typological criteria but are well characterisable by their specific ecology. In contrast, the distinction between *M. esculenta* and *M. vulgaris* proposed by Clowez (1992), on the basis of ecological features is not confirmed by the molecular biological analysis (data not shown).

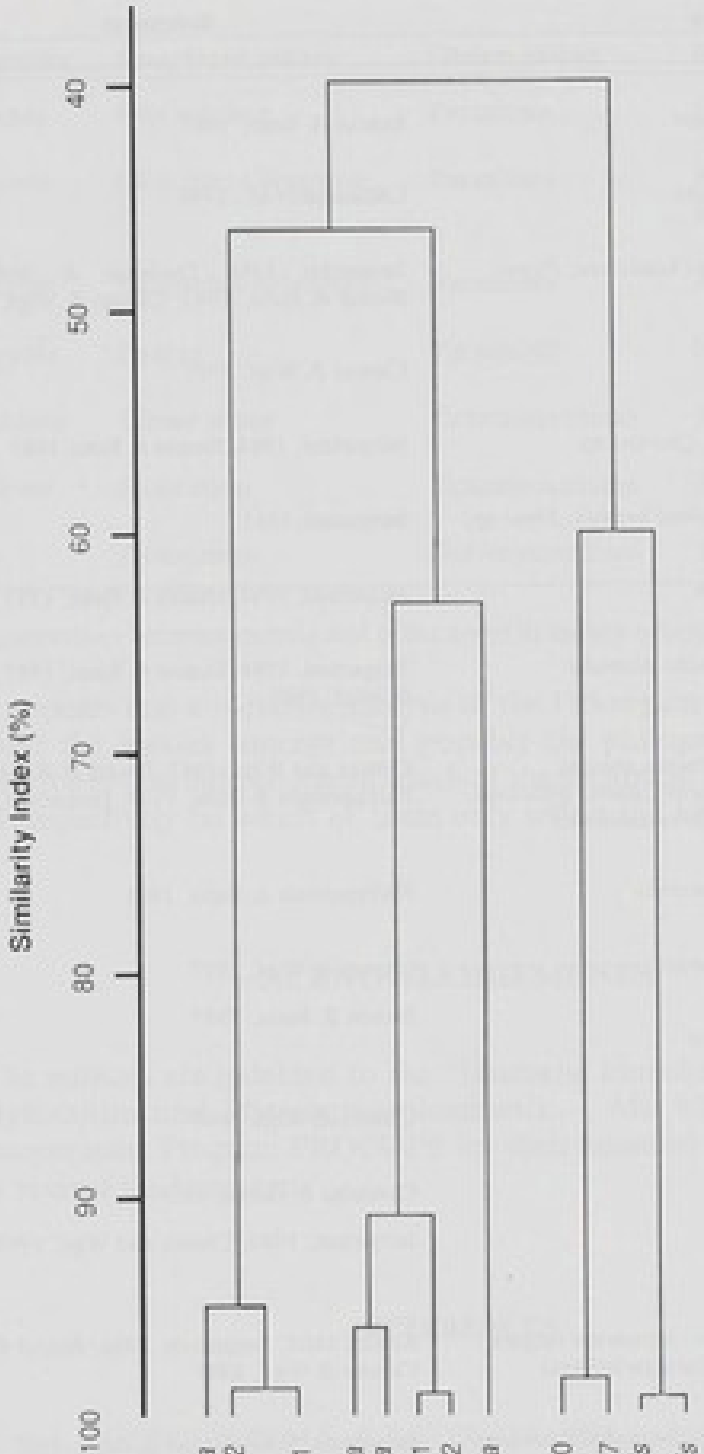

Fig. 9. — Similarity relationships of some *Morchellaceae*. UPGMA tree (Sneath and Sokal, 1973) constructed with the computer program WinCam 2.0 (PC).

Plants	References
Equisetaceae	
Equisetum hiemale	Buscot & Roux, 1987
Polypodiaceae	
(species not given)	Lakhanpal *et al.*, 1990
Pinaceae	
Abies alba, Pinus banksiana, Picea abies	Jacquetant, 1984; Duchesne & Weber, 1993; Buscot & Roux, 1987; Clowez & Wipf, 1997
Magnoliaceae	
Magnolia sp.	Clowez & Wipf, 1997
Fagaceae	
Fagus sylvatica, Quercus sp.	Jacquetant, 1984; Buscot & Roux 1987
Betulaceae	
Betula sp., Carpinus betulus, Alnus sp.	Jacquetant, 1984
Corylaceae	
Corylus avellana	Jacquetant, 1984, Buscot & Roux, 1987
Ulmaceae	
Ulmus minor, Celtis australis	Jacquetant, 1984; Buscot & Roux, 1987; Clowez & Wipf, 1997
Rosaceae	
Prunus avium; Prunus spinosa; Crataegus monogyna, Rubus fruticosus, Malus pumila, Pyrus communis	Clowez and Wipf, 1997; Buscot & Roux, 1987; Philippoussis & Balis, 1995; Jacquetant, 1984
Fabaceae	
Robinia pseudoacacia	Philippoussis & Balis, 1995
Aceraceae	
Acer pseudoplatanus	Clowez & Wipf, 1997
Cornaceae	
Cornus sanguinea	Buscot & Roux, 1987
Apiales	
Hedera helix	Clowez & Wipf, 1997
Vitaceae	
Vitis vinifera	Condamy & Cornu, 1878
Salificicaceae	
Populus nigra	Jacquetant, 1984; Clowez and Wipf, 1997
Oleaceae	
Fraxinus excelsior, Ligustrum vulgare, Olea europaea , Syringa vulgaris	Robert, 1865; Jacquetant, 1984; Buscot & Roux; Clowez & Wipf, 1997
Asteraceae	
Cynara scolymus, Helianthus tuberosus, Hieracium murorum, Taraxacum sp.	Jacquetant, 1984; Buscot & Roux, 1987
Liliaceae	
Allium ursinum	Buscot & Roux, 1987
Buddlejaceae	
Buddleja	Clowez & Wipf, 1997

Table 1 — Listing of plant species near which occurence of morels have been reported.

Morel species	Associated plants	Observations	Références
M. esculenta	*Vitis vinefera*	Parasitism	Condamy & Cornu, 1878
M. esculenta	*Oleaceae; Cornaceae*	Parasitism	Robert, 1865; Buscot & Roux, 1987
M. esculenta	*Helianthus tuberosus*	Parasitism	Roze, 1883
M. spongiola	*Poacea*	Parasitism	Romagnesi, 1963
M. semilibera	*Ulmus minor*	Ectomycorrhizas	Matruchot, 1909
M. esculenta	*Picea abies*	Ectomycorrhizas	Buscot & Kottke, 1990
M. elata	*Picea abies*	Ectomycorrhizas	Buscot, 1994

Table 2 — Association between morels and plant roots in nature which have been analysed precisely.

It appears that a sequence analysis of the ITS region of representative taxa will allow to clear the species concept and possibly the philogeny of the *Morchellaceae*. Furthermore, it will give indications on which of the ecological features really characterise species and respectively on which of them only reflect the high ecological plasticity of morels.

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