Introduction

Interactions between different regions of a mycelium and between different mycelia play an important role in morphogenesis and growth of fungi. The better understood interactions are those which are mediated by substances secreted into the substrate, and which result in the initiation and growth of sexual organs. In *Achlya* and Mucorales specific sexual hormones have been identified (Barksdale, 1969; Bu'Lock, 1976; van den Ende, 1976), and diffusible, but as yet unidentified compounds play a similar role in the sexual interactions of *Ascobolus stercorarius* (Bull.) Schrot. (Bistis, 1956, 1957). Bistis also provided strong evidence that initiation of apothecia depends on a diffusible agent released by the ascogonium.

Compared to the evidence for the morphogenetic role of secreted substances much less is known about interactions between different regions of individual hyphae or of hyphal associations. Butler (1961) noted interdependence in elongation between branches on a main hypha, and Larpent (1966) showed that initiation and elongation of branch hyphae is influenced by apical dominance in the parent hypha. Nutrient levels in the substrate, translocation of cell contents towards the main apex, and internal competition between the main hypha and its branches participate in these interactions but the underlying mechanism remains to be clarified. The small size and mode of growth of individual hyphae present considerable obstacles to the study of internal growth correlations. Such studies can be carried out more readily on large hyphal associations represented by fruitbodies of many higher fungi, especially those of hymenomycetes. Differentiation and enlargement of these fruitbodies occur in an orderly manner, and must result from highly coordinated growth of numerous interconnected hyphae. This type of development virtually demands the existence of internal coordinating mechanisms. Physiological relationships among different fruitbody regions with tissue-like organization can be investigated macroscopically. Such studies have been done mainly on fruitbodies of fleshy, lamellate Agaricales which have finite growth. Nothing is known about the physiological interactions in primordia during differentiation of the fruitbody regions when cell enlargement is limited. The present review is concerned with the subsequent transitional period which is
marked by an increasing rate of cell enlargement, and with the phase of rapid fruitbody enlargement when cell elongation in the stipe attains its maximum rate. The role of the pileus in stipe elongation will be emphasized, and participation of the mycelium in this relationship will be considered. The review of published literature will be supplemented by results of recent, largely unpublished work on *Flammulina velutipes* (Curt. ex Fr.) Sing.

Role of the Pileus in Stipe Elongation of Agaricales

As early as 1842, Schmitz mentioned that complete decapitation of young agaric fruitbodies always resulted in cessation of stipe growth, but that they grew to their "destined height" even if half of their pilei were removed. He was also the first to determine by measurement that the growth zone is located in the upper portion of the stipe. Gräntz (1898) reported that stipes of *Coprinus sterquilinus* (Fr.) Fr. grew normally after being decapitated shortly before the onset of rapid elongation, and that detached whole pilei or segments expanded normally. Also the excised growth zone of the stipe was said to elongate in the usual manner. Gräntz thought that a nutritional relationship between pileus and stipe during differentiation caused subsequent coordinated expansion of these regions. He further concluded that connection of the stipe with the mycelium was no longer required during elongation provided that sufficient water was available. Continued growth and geotropic curvature of detached stipes with or without pilei, of longitudinal stipe slices, and of stipe sections were also observed by Knoll (1909) in a *Coprinus* species (probably misidentified) during rapid elongation. Streeter’s (1909) observations on transplanted stipes of *Amanita crenulata* Peck also seemed to indicate that removal of the pileus did not prevent continued elongation and geotropic response. On the other hand, Magnus (1906) mentioned that elongation of young fruitbodies of *Agaricus campestris* [probably *A. bisporus* (Lange) Imbach] continued if at least half the pileus was left on the stipe, but only occasionally after decapitation during rapid elongation. None of the authors cited measured the growth after various operations or presented quantitative comparisons with untreated controls.

The first quantitative results were published by Borriss (1934a) for *C. lagopus* [probably *C. radiatus* (Bolt. ex Fr.) S. F. Gray (Pinto-Lopes and Almeida, 1972)]. He showed that elongation soon ceased if stipes were decapitated before the onset of rapid elongation (stage III), but it continued if only a thin pileus slice with few lamellae was left on the stipe at an even earlier stage (II). Small curvatures away from the slice occurred often. Growth also continued if the stipe was decapitated just before the beginning of rapid elongation (stage IV). Measurements were given for only one specimen for each operation. Borriss stated that

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1More than one *Agaricus* species has been cultivated and the nomenclature is very confusing. It is often impossible to determine with certainty which species was used, especially in older experimental studies.