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Physiology
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propylene oxide appears much more promising as a technique (129, 265). Analogously, the insect pathogen *Cordyceps militaris* forms perithecia on dead pupae but not on autoclaved pupae (261).

The relation of the host to sporulation has one other dimension, the influence of the host on the intensity and on the type of sporulation. This has been most thoroughly studied in relation to the appearance of the telial stage of rust fungi. From the work of Morgenthaler (210) and Waters (301) we may list factors that encourage or hasten the development of the telial stage:

1. Exposure of the host to low temperature or to slow drying.
2. Starvation of the host by dark incubation.
3. Growth of the fungus on a partially resistant host.
4. Wounding of the inoculated leaf.
5. Transfer of detached leaves from sucrose to water.

Obviously, effects of this type must be indirect for the obligate parasites, but the pattern seems clear that telia form under conditions of privation; the analogy to Klebs' conclusions is close. The factor that is dominant in nature is not known; it is most probable that drying out in autumn is dominant (91, 108), but simple starvation cannot be dismissed.

Perithecial formation in *Erysiphe graminis*—also an obligate parasite—is more rapid if the relatively resistant older leaves of the host are infected (114). Here again, we may speculate that resistance of the host accelerates the reproduction of the pathogen by depriving it of some essential factor.

Host influences on spore size merit brief mention. Uredospores of rust fungi are smaller on a resistant host than on a susceptible one, and they are smaller if the host is held under conditions unfavorable to its growth (187, 188, 268). Similar findings on other fungi have been summarized by Fischer and Gäumann (98).

13. CONCLUSIONS

The major barrier to generalizing about reproduction in the fungi is the repeated failure of experimental work to discriminate adequately between growth and sporulation; too often, only one is measured quantitatively. Consequently, many of our hypotheses on reproduction must leave open the possibility that the factor concerned may act on growth rather than specifically on the formation of spores.

The most inclusive generalization is that reproduction is initiated by factors which check the growth of an established mycelium without

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too drastically poisoning its metabolism. Studies on the effect of light, especially ultraviolet light, are the most important evidence, in view of the well-established lethal action of radiation. Gross mutilation by scraping or cutting induces sporulation in a few fungi (195, 206, 233); in scraped cultures of *Alternaria solani* Kunkel (179) observed that conidiophores arise from broken hyphae. Initiation of sporulation as the result of temperature changes, exhaustion of nutrients, and various treatments of the host plant of a pathogen are all consistent with the injury hypothesis.

Granted that a check in growth initiates sporulation, we can only speculate on the intimate mechanism. Perhaps the most promising suggestion is that injured or moribund cells release substances which act on surviving cells and divert them into a new developmental path.

It must be noted that a contrary hypothesis, that sporulation requires specific positive stimuli rather than the negative stimulation of injury, could easily be built up. In particular, the ready sporulation of many fungi on the living host plant or on cold-sterilized plant materials argues for nutritional factors which must be present in some threshold amount to permit sporulation or which must be synthesized by the fungus before reproductive activity can begin.

Less inclusive, but important and more firmly based, generalizations may be listed briefly in conclusion:

1. Reproduction occurs, in general, over a narrower range of environmental conditions than does growth; this is especially clear in findings on temperature, acidity, mineral, and oxygen requirements. The optimum for reproduction may be the same as or different from that of mycelial growth.

2. Klebs' principle, that reproduction is favored by depriving an established mycelium of one or more nutrients, is valid in general, especially for carbon and nitrogen sources. It must be qualified only to take account of the fact that for some nutrients—certain vitamins and minerals—the absolute amount required for sporulation is higher than that which supports growth. This qualification essentially only changes the definition of the "established mycelium" to indicate that it must have certain materials in high concentration.

3. There is no conclusive evidence for a specific nutritional factor required for sporulation and not required at all for growth. Specific endogenous hormones are, however, established as vital to reproductive activity, or at least to the orderly development of reproductive structures once these are initiated.

4. The requirements for sexual and asexual reproduction in a given

species are usually not alike, so that in a sense the two types compete. Apart from the relatively trivial generalization that the larger sexual structures must require more energy for their formation than the (usually) smaller asexual organs, there is as yet no good evidence for a universal difference between sexual and asexual reproduction; this possibility, however, should surely be explored. A few instances have been noted in which two different asexual structures have different requirements.

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