On the Heterothallism of Phytopathogenic Fungi.

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The subject of sexuality among fungi is extremely broad and it has been reviewed fully by H. KNIEP in his celebrated work "Die Sexualität der Niederen Pflanzen. Jena. 1928." Important discoveries have since appeared in voluminous amount. The writer here wishes to present and discuss briefly the works dealt principally with the heterothallism among the phytopathogenic fungi.

Heterothallism in Fungi.

In heterothallic type of fungi, the sexual reproduction is completed by the union of male and female gametes formed on separate mycelia; while in homothallic type the uniting gametes are produced on different branches of the same mycelium. The phenomenon of heterothallism was first discovered by BLAKESLEE in 1904 on *Mucor Mucedo*, a phycomycetous fungus. He found no morphological difference between the mycelia of two sexes but their union was essential for the zygospore production. He applied + and − to these mycelia.

Phycomycetes.

Phycomycetous fungi are especially suitable for studying heterothallism and there has been numerous researches conducted on the lines of genetics and hybridization. BURGEFF's works (1912 - 1929) on the inheritance of factors for physiological characters made use of *Phycomyces*, phycomycetous fungi closely related to *Mucor*.

One of the first phytopathogenic fungi studied in this group is the genus *Phytophthora*. In *Phytophthora faberi* sexual bodies had not been known for a long time, but ASHBY (1922) observed their formation when he mated the fungous mycelium isolated from cacao in Jamaica with that of cocoanut palm. In *Phytophthora* some species are definitely heterothallic but with others, as in *P. palmivora*, there occurs various types: homothallic, heterothallic-like homothallic, heterothallic, and neutral. Their relationship is said to be complicated (ASHBY, 1929; NARASIMHAN, 1930; LEONIAN, 1931). Similar facts have been proven by H. DE BRUYN (1937) on *Peronospora parasitica*.

Basidiomycetes.

With agaricaceous fungi, many noteworthy studies have appeared, and they dealt principally with such fungi as *Coprinus*, *Schizophyllum*, *Collybia*, and others. Among the plant pathogenes, inheritance in *Sclerotium rolfsii* has been studied by GOTO (1939). The present writer has been working with such edible mushrooms as *Cortinellus berkeleyanus*, *Pleurotus ostreatus*, and *Collybia velutipes*. However, their relation to plant disease is slight and discussions on these fungi will be reserved for other occasion. The principal basidiomycetous fungi causing plant diseases are the species of rust and smut-fungi.

Rust fungi.

CRAIGIE's (1927) discovery of the occurrence of heterothallism among the rust fungi offered an important contribution to the knowledge of sex among this group of fungi. He found that pycnospores, the function of which had long been thought to be lost, play an important rôle in the life cycle of rust fungi, and spermatia function as sperm cells as they are produced in pycnia or spermagonia. He discovered this fact in the rusts of sunflower, *Puccinia Helianthi*, and cereals, *Puccinia graminis*.

Later, CRAIGIE (1928, 1931), HANNA (1929), ALLEN (1930–1934), BROWN (1932, 1935) and LAMB (1935) reported that, in general, heterothallism occurs in those strains of fungi that have a well developed pycnia, and Miss ASHWORTH (1931) further showed that fungi with poorly developed pycnia are normally homothallic.

After the function of pycnospore had been clarified, studies on the mechanism of diploidization of the cells of aecial primordia have been conducted. HANNA (1929) thinks that the germinated pycnospores pass through the ostioles of pycnia and proceed down to the cells of aecial primordia where they unite to form the diploid condition. Miss ALLEN (1934) is of this opinion. CRAIGIE (1933) reported that the pycnospores of sunflower rust unite with a kind of special hyphae which are short, irregularly curved, and of various lengths. He called this "flexuous hyphae." Recently, BULLER (1938) reported a similar observation on the stem rust of wheat. Pycnospore fuses at the tip or at the side of the flexuous hypha, but when it is at the side, it sends out a fusion peg.

ANDRUS (1931) observed a type of hyphae arising from the stomatal aperatures of the bean leaves affected with *Uromyces appendiculatus*. He observed that these are trychogynes whose bases are egg cells in aecidia, and they unite with spermatia. He had shown by a certain staining reaction, that the nuclei of spermatia can be differentiated from the fertilized egg cells. Miss RICE (1933) also saw similar hyphae in her cytological study of rust and confirmed them to be trychogynes.

Smut fungi.

Heterothallism in smut fungi was first studied by KNIEP (1919) in *Ustilago violaceae*. Since then STAKMAN and CHRISTENSEN (1927) showed the heterothallic

relationship in *Ustilago zeae*, DICKSON (1927) in *U. levis* and *U. hordei*, HANNA (1929) in *U. zeae* and *Sorosporium reilianum*, FLOR (1932) in *Tilletia triticina* and *T. levis*, RODENHISER (1932) in *Sphacelotheca Sorghi* and *S. cruenta*, etc.

Knowledge on the heterothallism in these smut fungi promoted the studies on hybridization, inheritance, sex factor, morphological, cultural and pathological factors of the hybrids. The genetical studies on the smut fungi were commenced by KNIEP (1926) and followed by other workers.

DICKINSON (1927) and later ALLISON (1937) found that the segregation for sex factors in *Ustilago hordei* was in the ratio of 2 : 2. HANNA and POPP (1930), HOLTON (1932) and ALLISON (1937) obtained the same results for *U. avenae*, *U. levis*, *U. hordei* and *U. medians*. In other smuts, ratios of 4 : 0, 3 : 1, and 2 : 2 have been observed (DICKINSON, 1928; HANNA, 1929; BAUCH, 1932; CHRISTENSEN, 1931; RODENHISER, 1932). DICKINSON (1927) and HOLTON (1932) have demonstrated that there were six possible arrangements of the sex groups on the promycelium of *U. levis*.

As to the segregation of factors for cultural characters DICKINSON (1927) found within *Ustilago hordei* and *U. levis*, the factors segregating in 2 : 2, 3 : 1, and 4 : 0 ratios, and that segregation for cultural characters was independent of sex factors. Other workers have found the same to be true in other smut fungi (HANNA, 1929; CHRISTENSEN, 1931; RODENHISER, 1932; ALLISON, 1937).

Ascomycetes.

Among the ascomycetous fungi, the problem of sex has been carefully studied from the pure mycological point of view, and particularly in relation to cytology and genetics. Unlike rusts and smuts, the fungi employed in these researches were principally of the genera of *Neurospora* or *Ascobolus*, and consequently there are but few phytopathogenic fungi treated. With *Neurospora* there are studies of DODGE (1928 – 1936), LINDEGREN and his collaborators (1932 – 1939), SEAVER (1937) and DICKSON (1939); and with *Ascobolus*, DODGE (1920), SCHWEIZER (1931), GWYNNE-VAUGHAN and WILLIAMSON (1932), BETTS (1936), DOWDING (1931), and BETTS and MEYER (1938, 1939). Although there are such works as SCHWEIZER's proving *Ascobolus strobilius* to be homothallic, majority of these studies brought out the point that these fungi are heterothallic.

Studies on the interspecific hybridization have also been reported; and it has progressed to a stage where chromosome maps have been constructed on some fungi whose crossing over values have been determined. The phenomenon of hybrid vigor has been demonstrated on such physiologic character as the rate of growth, proving that the F_1 generation is superior to either of the two parental stocks from which it was produced. Maternal inheritance or cytoplasmic inheritance, and other similar phenomena are also verified at present.

Conclusion.

This brief outline on the present status of heterothallism shows that whenever heterothallic fungi are associated within or among species, there is always a possibility for the development of new strains or hybrids. Moreover, the hitherto

known findings demonstrated that such newly formed organisms in many cases exhibit an increased pathogenicity or other physiologic characters than those possessed by either of the parental stocks. One of the most important ways of disease prevention, no doubt, is to develop disease resistant varieties of plants; but the constant appearance of new highly destructive strains of fungi as hybrids in nature will certainly be a grave problem in plant breeding work. Furthermore, should these new fungi increase their resistance to fungicides through hybrid vigor, the fungicides as used today would certainly not be adequate in combating diseases. For these reasons, a thorough study on the heterothallism of phytopathogenic fungi is very essential from the standpoint of plant disease control.

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