Semi-Incompatibility in Cochliobolus carbonum

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ABSTRACT

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The formation of the "barrage" phenomenon in certain crosses of *Cochliobolus carbonum* enables detection of semi-incompatibility and reciprocal compatibility. Genetic studies indicate that semi-incompatibility is conditioned by a single gene and that semi-incompatibility and inhibition of perithecial formation are controlled by the same gene.

The recent detection of race 3 of *Cochliobolus carbonum* Nelson (6) prompted studies on the genetic control of pathogenicity and virulence of the new race. We discovered that all crosses attempted between wild-type isolates of race 3 in our collection were incompatible, whereas all isolates were compatible with some *A* or *a* mating types of races 1 or 2 of the species. The previous report (5) on the detection of a gene in *C. carbonum,* designated in allelic form as *I-i,* that inhibited perithecial formation between paired isolates when both isolates carried the *i* allele, suggested the need to identify the genotypes of race 3 isolates for that allele. Appropriate crosses between race 3 isolates and *A* and *a* isolates of races 1 and 2 with the *I* or *i* allele demonstrated that all race 3 isolates carried the *i* allele, thus accounting for the incompatibility between race 3 isolates (Dalmacio and Nelson, *unpublished*). Thus, it was necessary to pursue genetic studies of race 3 by crossing race 3 isolates with *AI* or *aI* isolates of races 1 or 2 and backcrossing race 3 ascospore isolates to race 3 wild-type isolates or by intercrossing compatible race 3 ascospore isolates. Three distinct reactions were found when backcrosses and intercrosses were attempted. Some crosses were incompatible because of common mating types or the presence of the *i* allele in both isolates. In other crosses, a clearly visible zone between paired isolates was produced in which no perithecia were formed. This phenomenon has been described as a "barrage" (1). Some crosses that exhibited barrage formation produced a row of peritheica on each side of the zone, but other crosses produced a single row of perithecia on one side of the zone.

Semi-incompatibility is a type of reproductive system in monoecious fungi in which the ascogonia of one mating partner are fertilized by the male gametes of the other, while the reciprocal cross is incompatible. The system has been demonstrated in *Podospora anserina* (Ces.) Rehm (1). The detection of semi-incompatibility in *C. carbonum* has been possible because barrage formation occurs between certain isolates. The genetic analysis of semi-incompatibility is reported herein.

MATERIALS AND METHODS

Two wild-type isolates and three ascospore isolates of race 3 of *C. carbonum* were used to make three different crosses designed to exhibit semi-incompatibility (one row of perithecia). Crossing procedures described by Nelson (3) were followed. The parental genotypes for compatibility and perithecial inhibition were as follows: *Ai* and *aI* for cross 1; *AI* and *ai* for cross 2; and *AI* and *ai* for cross 3. Twenty days after pairing, 136 ascospores were isolated from the crosses as follows: six tetrads (48 ascospores) from cross 1; five tetrads from cross 2; and 48 ascospores isolated randomly from cross 3. Seven days after isolation and growth on potato-dextrose agar, each ascospore isolate was mated with four tester isolates having the genotypes of *AI, Ai, aI,* or *ai*. Fertile crosses were characterized for their pattern of perithecial formation 15 days later.

RESULTS AND DISCUSSION

Of the 272 $A \times a$ combinations (136 ascospore isolates $\times$ two of the four testers) derived from the three original crosses that exhibited semi-incompatibility, 136 crosses exhibited semi-incompatibility, while the remaining 136 crosses demonstrated reciprocal compatibility or reciprocal incompatibility with a frequency of 69:67, respectively. Both crosses involving tetrad analyses segregated 1:1 for semi-incompatibility: reciprocal compatibility, or incompatibility. These results demonstrate that semi-incompatibility is conditioned by a single gene.

From inspection of parental and tester genotypes, we observed that all crosses that showed semi-incompatibility involved an isolate carrying the *i* allele, whereas crosses in which both isolates carried the *I* allele or *i* allele, showed reciprocal compatibility or reciprocal incompatibility, respectively. These results indicate that semi-incompatibility and inhibition of perithecial formation are controlled by the same gene.

Failure or inability to detect the barrage phenomenon may be the reason why previous investigators have not described semi-incompatibility and reciprocal compatibility in *C. carbonum*. Although some isolates of race 3 clearly exhibit the phenomenon in paired combination, the race was detected only recently. It would be difficult, if not impossible, to detect patterns of

perithecial formation without this character. Crosses and intercrosses among wild-type isolates of races 1 and 2 did not show any barrage formation.

Semi-incompatibility possibly may be explained by the inhibitory effect of the *i* allele on the trichogynal nucleus of the isolate carrying the allele. The single row of perithecia produced in crosses of $AI \times ai$ or $Ai \times aI$ occurred on the side of the barrage zone occupied by the isolate carrying the *I* allele, regardless of mating type. It seems to us that only the male gametes are functional in isolates with the *i* allele. This interpretation does not support the dominant-like hypothesis previously proposed (5). If the *I* allele were dominant over the *i* allele, crosses $AI \times aI$ and $AI \times$ or $Ai \times aI$ should give indistinguishable patterns of perithecial formation. That was not observed in the present study.

Although the phenomenon of semi-incompatibility in *C. carbonum* is similar to that reported in *P. anserina,* the genetic control of the phenomenon is clearly different. Whereas semi-incompatibility in *C. carbonum* is determined by one gene, that of *P. anserina* is determined by two nonallelic genes (1). Another point of difference is that semi-incompatibility occurs only between isolates of different races in *P. anserina,* but in *C. carbonum,* it occurs between isolates of the same race as well as isolates of different races.

Semi-incompatibility has also been implicated in *C. heterostrophus* (2, 4). Fukuki and Aragaki (2) observed in certain crosses on dialyzing membrane that most perithecia were formed at one end of the membrane strip on the side of one parent. That semi-incompatibility may actually occur in that species is supported by the report of the occurrence of a single gene that inhibits perithecial formation comparable to the one that controls semi-incompatibility in *C. carbonum* (4).

The genetic factor(s) that control barrage formation in *C. carbonum* appear(s) to be independent of the gene that controls semi-incompatibility. Certain $AI \times aI$ and $AI \times ai$ or $Ai \times aI$ combinations did not produce barrage. Study of the genetics of barrage formation is underway.

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