required to reduce the methylene blue. It is clear that the long lag phase observed when methylene blue was present before all the oxygen was removed is due to an inhibition by methylene blue of the systems of the cell which consume oxygen.

Summary.—The rates of the exchange reaction and of the reduction of various dyes and other acceptors have been compared in a number of different microorganisms. While the activation of hydrogen, as measured by the exchange reaction, appears to be relatively simple, the utilization of the activated hydrogen for chemical reduction requires cofactors or additional enzyme systems.

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*GROWTH RESPONSE OF SINGLE-GENE DWARF MUTANTS IN MAIZE TO GIBBERELLIC ACID**

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Gibberellic acid, $C_{19}H_{22}O_6$, was first isolated by Cross[1] from the *Fusarium moniliforme* Sheldon stage of *Gibberella fujikuroi* (Saw.) Wr. It is a tetracyclic dihydroxy lactonic acid, identical to gibberellin X, reported by Stodola *et al.*,[2] and distinct from gibberellin A, isolated by Yabuta and Hayashi.[3] Both gibberellic acid and gibberellin A markedly stimulate stem and leaf elongation in a number of higher plants.[3, 4] Of particular interest to geneticists is the report of Brian and Hemming[4] that slow-growing varieties of peas (*Pisum*) will respond more than fast-growing varieties to applications of gibberellic acid. They also reported a similar differential growth response to applications of gibberellic acid between tall and dwarf varieties of broad bean (*Vicia*) and French bean (*Phaseolus*), concluding that

the causes for dwarfism in these plants are probably the same as those acting in peas.

In the present study, it is shown that normal growth can be induced in dwarf mutants of maize by the addition of gibberellic acid. Certain other mutants for dwarfism in maize show no growth response or only a very slight response to this compound.

MATERIALS AND METHODS

Of the six mutants segregating from the stocks[5] used in these experiments, *anther ear-1*, *dwarf-(5232)*, *dwarf-1*, *dwarf-(8201)*, and *dwarf-(4963)* are nonallelic to each other and are controlled by simple recessive genes. The sixth mutant, *dominant-dwarf*, is a simple dominant of unknown linkage. All mutants appear as dwarfs from the seedling stage to maturity, mature mutants being less than half the height of mature normals.

Gibberellic acid was prepared as aqueous stock solutions from two samples.[6] The first sample consisted of an equal mixture of gibberellic acid and gibberellin A. The second sample was pure gibberellic acid, $[\alpha]_D^{25}$, = 92°. Gibberellic acid was applied by placing a volume of known concentration on the surface of the first unfolding leaf of 8-day-old seedlings or on the upper leaves of older plants. In each treatment gibberellic acid was applied to at least six normal and six mutant plants. All experiments were replicated at least twice.

EXPERIMENTAL

Response of Different Mutants to Gibberellic Acid: Experiment 1.—Normal and mutant seedlings from each of the six stocks were given single applications of 10 μg. of gibberellic acid (pure sample) per plant at the time of emergence of the first seedling leaf from the coleoptile. The growth response of treated normal seedlings over that of nontreated normal seedlings was slight and was not evident until several days after application. However, the mutants *anther ear-1*, *dwarf-(5232)*, *dwarf-1*, and *dwarf-(8201)* showed a growth response that was evident within 24 hours following treatment. These four mutants continued to respond, so that at 2 weeks of age they were very similar in height to treated normals of the same age. However, without further applications of gibberellic acid, they slowly returned to the dwarf habit of growth. Normal and *dwarf-1* seedlings, with and without treatment, are shown in Figure 1. In marked contrast to the response of the above four mutants, *dominant-dwarf* seedlings showed no growth response and *dwarf-(4963)* seedlings only a very slight growth response.

These mutants, *dominant-dwarf* and *dwarf-(4963)*, were tested further by repeat runs. Ten μg. of gibberellic acid (pure sample) per plant was added to normal and mutant seedlings at the time of emergence of the first leaf, and supplementary additions of 5 μg. per plant were given at daily intervals for 5 days. With this amount applied over the period of 5 days, normal seedlings showed unusual elongation of leaf blades as well as of leaf sheaths. *Dominant-dwarf* seedlings showed no growth response. *Dwarf-(4963)* seedlings showed some growth response, but they still retained the dwarf growth habit, remaining less than half the height of nontreated normal seedlings.

In other tests these two mutants were given a single application of 100 μg. of

gibberellic acid (pure sample) per plant. Again *dominant-dwarf* seedlings showed no response and *dwarf-(4963)* seedlings only a limited response.

Sensitivity of Response of Mutant Seedlings to Gibberellic Acid: Experiment 2.— The four stocks segregating *anther ear-1*, *dwarf-(5232)*, *dwarf-1*, and *dwarf-(8201)* were used in this experiment. Normal and mutant seedlings were given single applications of gibberellic acid (pure sample) at the time of emergence of the first leaf. The amounts used ranged from 0.01 to 20 μg. per plant. Normal seedlings showed no observable growth response with amounts less than 0.5 μg. per plant. Mutant seedlings from each of the four stocks showed a slight but noticeable growth response with as little as 0.01 μg. per plant. Both normal and mutant seedlings

FIG. 1.—Response of normal and *dwarf-1* seedlings to a single application of 10 μg. of gibberellic acid (pure sample) per plant. Treatments given at the time of emergence of the first leaf. Plants shown are 2 weeks old.

responded to the addition of amounts greater than 1.0 μg. per plant, the growth response of the mutant seedlings being much greater than that of the normal seedlings. Mutant seedlings ultimately reached the same height as treated normal seedlings with 10, 15, and 20 μg. of gibberellic acid per plant. With only single applications, all mutant plants reverted to the dwarf habit of growth. In the range studied, the degree of response was related to the dosage: the greater the dosage, the greater the response.

Response of Mutant Plants to a Continuous Supply of Gibberellic Acid. Experiment 3.—The four mutants *anther ear-1*, *dwarf-(5232)*, *dwarf-1*, and *dwarf-(8201)* were tested for their growth response to multiple applications of gibberellic acid. Nor-

mal and mutant seedlings were given 10 μg. of gibberellic acid (mixture) per plant at the time of emergence of the first leaf. Additional amounts, totaling 60 μg. per plant, were supplied to the uppermost leaves at 2- or 3-day intervals for 8 weeks. All seedlings showed an initial response as described in the previous experiments. Normal plants showed only a slight response in later stages of growth. The four mutants continued to respond, becoming very similar to treated normal plants in size and shape. Normal and *dwarf-1* plants, with and without treatment, are shown in Figure 2.

FIG. 2.—Response of normal and *dwarf-1* plants to multiple applications of gibberellic acid (mixture), totaling 60 μg. per plant. Treatments initiated at the time of emergence of the first leaf and continued at 2–3 day intervals. Plants shown are 9 weeks old.

DISCUSSION

Evidence for the conversion of a mutant phenotype to a normal phenotype by the addition of a particular compound has been well documented in microörganisms, especially in *Neurospora*.[7] These contributions have led to many significant advances in the study of gene action.[8] In contrast to the vast amount of information of this nature for microörganisms, there are few reports for higher plants where mutants respond to a given compound to reach a normal phenotype. Langridge[9] has reported a case in the crucifer, *Arabidopsis thaliana* (L.) Hayn., where a simple recessive mutant responded to thiamine to give normal growth.

Brian's work[4] on the growth response of dwarf varieties of beans and peas to gibberellic acid suggests that this response is probably under genetic control. The four mutants of maize *anther ear-1*, *dwarf-(5232)*, *dwarf-1*, and *dwarf-(8201)* are clear examples of cases in which the ability to respond to gibberellic acid is under the control of single genes. The response of these four mutants and the lack of response of the two mutants *dominant-dwarf* and *dwarf-(4963)* indicate that the reason for dwarfism can vary, depending on the particular gene controlling the expression of the dwarfing character. Studies are being made on the mechanism of the gibberellic acid response in these mutants.

SUMMARY

1. The growth response of six single-gene mutants in maize to gibberellic acid is reported. Four of these, *anther ear-1*, *dwarf-(5232)*, *dwarf-1*, and *dwarf-(8201)*, responded by normal growth. The fifth mutant, *dominant-dwarf*, did not respond and the sixth mutant, *dwarf-(4963)*, showed only a slight response.

2. The sensitivity of response to gibberellic acid and the requirement of a continuous supply of gibberellic acid to maintain normal growth for four of the mutants are reported.

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*THE q LOCUS OF NEUROSPORA CRASSA**

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Investigations with several organisms have demonstrated that crosses of individuals carrying mutant alleles may give rise to rare nonmutant progeny. In a number of instances[1] the event which produced the exceptional offspring was shown to involve crossing over within a small chromosomal segment. In *Neurospora crassa*, Bonner[2] has described the occurrence of rare nonmutant progeny in crosses of niacin-requiring mutants, which he has designated "*q* mutants." These mutants do not form niacin-independent heterocaryons with one another, and there is evidence that all of them are blocked in the same step in niacin synthesis.[2] Apparently, no similar cases have been reported in which both a genetic study and a biochemical