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Effect of Absence of Developing Grain on Carbohydrate Content and Senescence of Maize Leaves

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ABSTRACT

In maize (*Zea mays* L.) grown under normal conditions in Rhodesia, prevention of pollination or removal of the ears after flowering caused premature senescence of the leaves above the ear, preceded by the appearance of a purplish red color. In plants from which the ears had been removed the concentration of sugars and starch increased markedly in both upper and lower leaves, the increase being greater in the upper leaves.

The removal of flowers or of developing fruits has been observed to delay senescence in a number of annual plants (5). In contrast, we have noticed in Rhodesia that the removal of developing ears causes leaves of maize plants to wither prematurely. Two experiments were conducted to investigate this problem.

METHODS

In both experiments the locally bred single-cross hybrid 59H17, known commercially as SR52, was grown under normal conditions on fertile soil at a density of 31,000 plants per hectare (12, 500 plants per acre).

In the first experiment, we investigated the effect of ear removal or prevention of pollination on leaf senescence. There were four treatments, *viz.*, a control, ear removal 13 or 27 days after silk emergence, and covering the silks during the period of pollen shedding. Plots consisted of 10 plants in four replicates.

At the time of flowering the area of every leaf was measured on 20 plants. Subsequently, the green, *i.e.*, unwithered, leaf areas were estimated at weekly intervals until 8 weeks after flowering, and the green leaf area above and below the ear was calculated (1).

In the second experiment we studied the effect of ear removal on carbohydrate accumulation. This experiment consisted of two treatments in three replicates, namely, a control and ear removal 19 days after flowering.

Samples of leaf laminae were harvested from both above and below the ear on three occasions, namely, 7, 17, and 28 days after ear removal. Each sample consisted of 10 laminae, obtained by collecting either the middle two of the laminae above the ear, or the middle two of the laminae below the ear from each of five plants. Parts of some laminae had withered by the time of the third harvest, and these parts were discarded.

The samples were always collected shortly before noon and within half an hour were placed in a forced draught oven at a temperature of 110 to 120 C for 20 min and then dried for about 6 hr at 60 to 70 C.

The dried samples were finely ground and analyzed for total nonstructural carbohydrates with Clarase 300 (9). Since fructosans do not occur in maize (2), the results represent total sugars plus starch, expressed as glucose. In addition, reducing and nonreducing sugars were determined after extraction with alcohol (8); the replicate samples for the third harvest were analyzed separately, but for the first two harvests composite samples from the three replicates were used for the sugar determinations. Starch was calculated by difference: (total nonstructural carbohydrates minus total sugars) $\times$ 0.9. All analytical results are expressed as percentages of the dry matter.

RESULTS

Experiment 1. Both the removal of ears and the prevention of pollination hastened the withering of leaves, but the effect was confined largely to leaves above the ear (Fig. 1). With both treatments the leaves above the ear developed a purplish red color (probably due to accumulation of anthocyanin) 4 to 5 weeks after flowering; a few plants showed this on one or two leaves below the ear. These leaves soon began to wither rapidly and were quite dry about 8 weeks after flowering. (Colored leaf was rated as green as long as it remained unwithered.) The upper leaves of the untreated plants remained green until about 6 weeks after flowering and were still partly green after 8 weeks. Lower leaves which showed no discoloration with any treatment senesced in the normal way from the base of the shoot upwards, and the treatments had little effect on the green lamina area below the ear.

Experiment 2. All leaves were fully green at the time of the first harvest. At the second harvest a few of the upper leaves of the plants without ears showed some purplish red color, but all other leaves were green. By the third harvest, the upper leaves of the treated plants showed varying degrees of discoloration and some withering; the upper leaves of the intact plants were still green, and so were the lower leaves of both intact and treated plants, apart from some normal senescence.

Whereas only relatively small changes occurred in the leaves of the intact plants, all three carbohydrate fractions increased markedly in the leaves of the plants from which the ears had been removed (Table I). In these plants combined sugars and starch reached approximately 27% in the upper leaves and approximately 17% in the lower leaves, compared with 12 and 10%, respectively, in the leaves of intact plants. Treatment differences at the last sampling date were statistically significant for all carbohydrate fractions determined.

DISCUSSION

The premature senescence of the upper leaves, caused by preventing pollination or removing the developing ears, is not in agreement with the general observation that the removal of

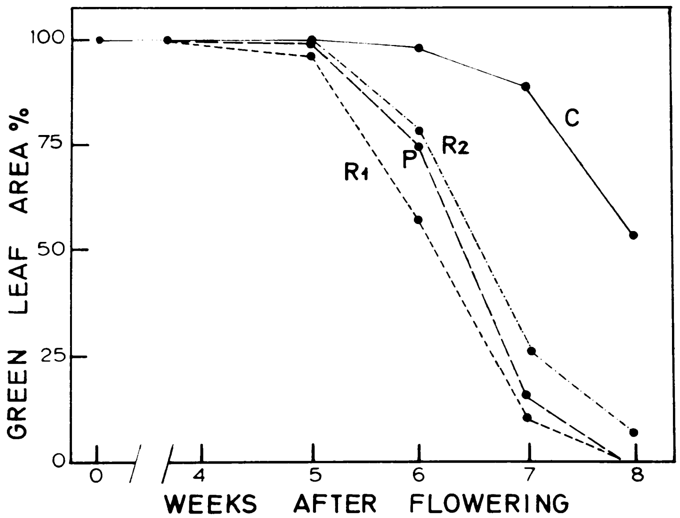

FIG. 1. Green leaf area above the ear, expressed as a percentage of the leaf area at the time of flowering. C: Untreated; P: pollination prevented; R_1 : ears removed 13 days after flowering; R_2 : ears removed 27 days after flowering.

flowers causes delayed senescence in many plants (5), nor with the results for maize obtained by Moss (6). He found that the leaves of maize plants on which pollination had been prevented were still green towards the end of the season and had a higher rate of assimilation than the leaves of normal plants which were by then senescent. No carbohydrate determinations on the leaves were done by this worker, but he found that prevention of pollination increased the sugar concentration in the stalks.

The appearance of a purplish red color (also noted by Moss) is usually considered a sign of an abnormally high carbohydrate accumulation, which is to be expected when the main "sink" for photosynthate—the developing grain—is absent.

Humphries (3) suggested that abnormal carbohydrate accumulation in the leaves might cause senescence but was unable to confirm this in subsequent work (4). However, it may be that premature senescence will not occur unless a certain critical carbohydrate level in the leaves is reached. Thus, in experiment 2 reported here, the lower leaves of plants without ears, although accumulating less carbohydrate than the upper leaves, accumulated considerably more than the leaves of the intact plants, yet showed neither discoloration nor premature senescence. Possibly, if the concentration of accumulated carbohydrate in the leaves remains below such a critical level, other factors tending to prolong their life might come into operation. Such responses may vary for different conditions and varieties.

Table I. *Leaf Carbohydrates as Percentages of the Dry Matter*

Carbohydrate	Days after Ear Removal	Upper Leaves		Lower Leaves	
		Untreated	Ears removed	Untreated	Ears Removed
Reducing sugars	7	3.46	3.59	3.91	4.94
	17	2.75	5.00	3.57	5.55
	28	2.26	6.87	4.24	8.17
Nonreducing sugars	7	7.19	8.54	6.08	5.87
	17	6.57	11.44	4.27	6.56
	28	7.66	14.82	4.87	6.85
Starch	7	0.88	1.85	0.43	0.38
	17	1.25	3.88	0.23	0.70
	28	1.66	5.73	0.67	1.66
Combined sugars and starch	7	11.53	13.98	10.42	11.19
	17	10.57	20.32	8.07	12.81
	28	11.58	27.42	9.78	16.68

The increase in carbohydrate concentration following ear removal was strikingly large: at the last harvest the upper leaves of the plants without ears contained more than twice as much total sugar and more than three times as much starch as those of intact plants. Starch appears to occur normally only in relatively small amounts in maize leaves and only in the bundle sheaths (7); all the starch may, therefore, have accumulated in these cells. Such abnormal concentrations of nonstructural carbohydrates might well interfere with some of the functions of the leaf and hence lead to premature senescence.

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