A TRAUMATOTROPIC RESPONSE DUE TO INTERRUPTED WATER TRANSPORT

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1. Introduction. Traumatotropic curvatures generally will occur in oat seedlings upon wounding them unilaterally. The curvature may be positive or negative (respectively toward or away from the wound). Weimann (1929) also distinguishes between primary and secondary curvatures regarding their occurrence within or after a period of 5 hours after wounding. The primary positive curvature may show as early as 10 minutes after wounding (STARK 1917) and will disappear after a few hours and then be replaced by a primary negative curvature. This negative curvature was observed by FITTING (1907) and others. It was not observed either by STARK or by BEYER (1925). WEIMANN showed that this negative curvature is due to a geotropic response induced by the primary positive curvature. On the clinostat the primary negative curvature was never obtained. The secondary positive curvature has been given the most attention in the literature. STARK explained it as being due to formation of special wound hormones which inhibit the growth. Beyer (1928), however, made it clear that the wound curvature was to be explained in terms of growth hormone. The incision interrupts the stream of growth hormone which travels in basal direction, causing a curvature below the wound and in a positive sense. This explanation still holds at the present time. A secondary negative curvature has also be shown to exist, it is not a geotropic response. Its mechanism is not clear as yet. A classification based upon fundamental characters of the curvatures may be rather one which is based upon the location of the curvature below or above the wound, than the one of Weimann which is based on the time of occurrence. A curvature due to an interruption of an auxin stream moving in basal direction, must necessarily occur below the interruption (incision). According to Weimann (secondary) positive curvatures, located above the wound, do not exist as was claimed by Bünning (1927). Stark, however, showed that such (primary) positive curvatures may occur within one hour after wounding. The purpose of the present study was to check up on those positive curvatures which are located above the wound, because of their possible connection with a growth factor coming from the basal parts of the plant. A unilateral incision might prevent such a "food factor" (see Went 1935) from reaching the parts above the wound and hence prevent them from growing.

2. The traumatotropic curvature located above the incision. In the small side of Avena coleoptiles an incision was made with a special knife which made it possible to make incisions of a uniform depth of 0.25 mm. This just severs the vascular bundle but does not cut the entire wall of the cylindrical coleoptile. The Avena plants were grown under standard conditions and the experiments were carried out in a physiological darkroom at 23° C. and about 90% humidity. The cuts were made 2 cm from the top of the coleoptile. Small tinfoil plates were stuck into the wound. Avena coleoptiles wounded this way show a positive traumatotropic curvature located above the wound, which starts to become visible about 20 minutes after wounding. Figure 1 shows Avena plants which had been wounded 1 hour before the picture was taken. At this time the curvature has about reached its maximum and starts to curve back (geotropically).

Since this curvature is located above the wound the possibility exists that a factor coming from the basal parts of the plant is prevented from going up. Such a factor may be either water or a food factor. According to STARK it may also be possible that a wound hormone which inhibits the growth, is set free by making the incision. The possible effect of interrupted water transport was studied first. There are two ways by which the Avena seedling may be supplied with water, viz. by suction pressure and by root pressure. The suction pressure is caused by the growing cells in which the wall tension is decreased by auxin, and also by transpiration. In order to eliminate the root pressure the roots were cut off. Then 2 incisions immediately above each other were made. In the lower one tinfoil was stuck and the other one served for the uptake of water (fig. 1). Those plants were put with their base in water in such a way that the incision was just below the surface. Controls were kept with their base in water but with the incisions in air. One hour after

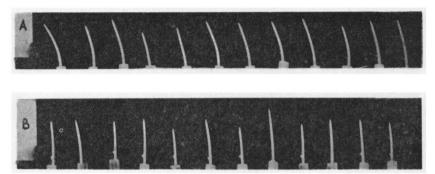


Figure 1. Positive traumatotropic curvatures of Avena coleoptiles one hour after 2 small incisions were made at the left side. In the lower incision a small piece of tinfoil was stuck. The plants at (A) have been standing in rapidly moving air; the plants at (B) were enabled to take up water through the incisions. (61110).

wounding the following curvatures were observed:

incision under water -0.5 incision in air +5.2

Which shows that uptake of water through the cut may prevent the bending of the plant. If the roots were retained the following curvatures were obtained:

incision under water +3.7 incision in air +9.3

In this case as well as in the case when the root pressure was eliminated, uptake of water through the wound reduced the curvature greatly. But with the roots present the absolute curvatures were larger. This shows that interruption of the water uptake (being either uptake by suction pressure or by root pressure, or both) leads to positive traumatotropic curvatures which are located above the incision.

3. Artificial root pressure. The effect of root pressure can be imitated by cutting off the coleoptiles at the base and forcing water into them. This was done by cutting the seedlings at the base of the mesocotyl and sticking them in special holders. These holders consisted of thin glass tubing to which at one end a small piece of thin rubber tubing was connected by means of which the plant was held in place. The other end of the holder was connected with a water reservoir which could be raised or lowered in order to change the pressure. Figure 2

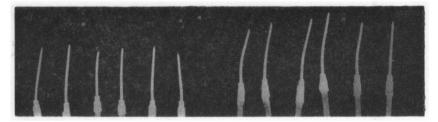


Figure 2. The effect of artificial root pressure on the traumatotropic curvature of Avena coleoptiles. The plants were photographed 1 hour after an incision was made at the right side. The water was forced into the six plants at the right with about 30 cm water pressure. The six plants at the left are controls. (61116).

shows such plants 1 hour after they had been wounded. They show the usual type of curvature as described in this paper. The curvature of the plants to which pressure has been applied is larger than that of the controls which got water but without pressure. A requirement for a successful experiment is a high humidity. The plants of figure 2 were covered with a bell jar during the experiment. If the humidity is low, pressure does not seem to have much effect on the curvature. Even ordinary darkroom humidity is generally not high enough to obtain an optimal effect. This is not only the case with artificial pressure but also with root pressure. In paragraph 2 the curvature of plants with their incision in air was 5.2 if the root pressure was cut out, and 9.3 with the root pressure. During this experiment the plants were kept in a cupboard in the darkroom. In table 2 of paragraph 4, however, the plants with their incision in air curved 12.2° if the roots had been removed, and 13.5° if the roots were present. In this experiment in which the effect of root pressure was hardly noticeable, the plants were placed in rapidly moving air. Therefore, the actual humidity around the plants was no doubt lower here than in the experiment of paragraph 2.

4. The curvatures are not due to wound hormones. According to Stark a wound hormone is released by cutting the plant tissue. It diffuses into the growing tissue and inhibits the growth. According to this view the possibility would exist that immersing of the wounded tissue in water may wash the hormones out of the wound, thus preventing the traumatotropic curvature rather than by water uptake. This possibility was ruled out,

however, in the following way. Avena plants were wounded by making double incisions and were put with their bases in water in such a way that the wound was just below the surface.

Table 1. Traumatotropic curvatures of Avena coleoptiles with their incision under water and in rapidly moving air. (61030).

1 hour after wounding; incision under water	+1	0	_3	_1	+1
the same plants 1 hour later after incision had been in air	+11	+11	+7	+10	+7

One hour later they were taken out of the water and photographed. Then they were placed for another hour in a stream of rapidly moving air (with their base in water but the incision in the air), and after this period photographed again. The results are shown in the tables 1 and 2. In table 1 some values for individual plants are given. It is clear that in most cases the curvature is practically zero if the incision is in contact with water. The plants did not lose their ability to curve traumatotropically however, because if the cut was exposed to air the curvature increased to about 10°. This could not be possible if wound hormones were responsible for the traumatotropic curvature. The table 2 shows the same results. The figures here, however, are averages of 24 plants. In the same table the effect of the roots on the traumatotropic curvature is shown again.

Table 2. Traumatotropic curvatures of Avena coleoptiles with roots and without roots; with the possibility of water uptake through the incision and with this possibility excluded. (61110).

	roots removed	roots present
First hour, incision under water Second hour, incision exposed to	+ 3.2	+ 7.8
rapidly moving air	+ 11.1	+ 14.1
rapidly moving air	+ 12.2	+ 13.5
rapidly moving air	+ 10.5	+ 11.5

Summary. If an incision is made in one side of the base of Avena coleoptiles, a positive traumatotropic curvature appears. This curvature which commences to show about 20 minutes after wounding, is located above the wound. It is proven that this

type of traumatotropic curvature is due to interrupted water uptake.

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