Phytochemistry, Vol 24, No. 1, pp 177–178, 1985.
Printed in Great Britain

0031–9422/85 $3 00 + 0.00

DISTRIBUTION OF HYDROXAMIC ACIDS IN *ZEA MAYS* TISSUES

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(*Revised received* 7 *June* 1984)

Key Word Index—*Zea mays*; maize; *Triticum durum*; wheat; Gramineae; 1,4-benzoxazin-3-ones.

Abstract—The hydroxamic acid content of leaves of cereals correlates well with resistance to aphids. In maize these compounds were absent from xylem exudates and guttation drops. Lateral veins of leaves of 7-day-old maize plants contained 8 mmol/kg fr. wt while the entire leaf contained only 4.2 mmol/kg fr. wt. In leaves of 20-day-old plants, these amounts decreased by *ca* one-third. In mesocotyls, the cortex and central vascular cylinder contained 1.3 and 2.2 mmol/kg fr. wt, respectively. In 12-day-old wheat plants, the complete leaves and their veins contained 2.4 and 6.4 mmol/kg fr. wt respectively. Thus, the concentration of hydroxamic acid was always higher in the vascular bundles.

INTRODUCTION

Plant secondary metabolites may be important in protecting plants against herbivores and plant pathogens. For example, hydroxamic acids from the Gramineae have been suggested as resistance factors to several insects [1–3]. DIMBOA, the main hydroxamic acid from maize and wheat extracts, is toxic and deters feeding in the greenbug *Schizaphis graminum* (Rondani) at concentrations lower than those usually found in plant sap [4]. Hydroxamic acids are found in roots, shoots and leaves of maize but their location in the tissues of these organs is unknown [5]. Secondary metabolites, such as cyanogenic glucosides in *Sorghum*, may be compartmentalized in plant tissues [6]. In this paper we report that in maize hydroxamic acids are preferentially concentrated around vascular tissues.

RESULTS AND DISCUSSION

Hydroxamic acids were not homogeneously distributed among the various parts of maize leaves of 7- and 20-day-old plants (Table 1). The concentration in the lateral veins was higher than that in the rest of the leaf. Additionally, hydroxamic acids were not detected in guttation drops or xylem exudates. Similar results were obtained when several leaves of a 35-day-old plant were analysed (Table 2). The concentration was always higher in lateral veins than in the complete leaf. This was also observed in leaves of a 12-day-old plant of *Triticum durum* cv SNA-3. The concentration of hydroxamic acid in the vascular tissues of these leaves was 6.4 mmol/kg fr. wt while the concentration in the complete leaf was only 2.4.

Hydroxamic acids were present in mesocotyls and roots (Table 3) and, as previously reported [3], their concentration decreased as plants became older. Also, hydroxamic acids were more concentrated in the stele (vascular cylinder) than in the cortex.

It has been proposed that hydroxamic acids may play a role in iron transport because of their high affinity for this element [7, 8]. The absence of these compounds from xylem exudates and guttation drops, as well as the high concentration of organic acids in xylem exudates [9], suggests that hydroxamic acids are not important in transport of metals through to xylem. However, they could participate in plant mineral nutrition in other plant compartments.

The high concentration of hydroxamic acids observed in stele tissue of leaves of maize and wheat may be of importance for the resistance of the plants to aphids. The greenbug *Schizaphis graminum* feeds predominantly from the phloem and secondarily from mesophyll tissue of its host plant [10]. Phloem and other tissues found in the stele may be protected by the high concentration of hydroxamic acids against aphid feeding because of their toxic and feeding deterrent properties [4].

Table 1. Hydroxamic acid distribution in leaves of maize

Leaf part*	Hydroxamic acid (mmol/kg fr. wt) 7-Day-old plants	20-Day-old plants
Complete leaf	4.2 ± 0.1	1.3 ± 0.1
Central vein	4.8 ± 0.1	1.0 ± 0.1
Lateral veins	8.0 ± 0.2	2.7 ± 0.2
Guttation drops	n.d.	n.d.
Xylem exudate	n.d.	n.d.

* Plants were grown in a greenhouse. The second leaf to appear was used for analyses. Guttation drops were obtained from the tips of leaves. Xylem exudates from leaves were obtained by making a transverse section of the leaves and collecting drops that accumulated on the leaves attached to the plants. The numbers (± s.e.) are the mean of two samples of several leaves each. n.d. = not detected.

Table 2. Hydroxamic acid content in various leaves of a maize plant

Leaf*	Hydroxamic acid (mmol/kg fr. wt) Central vein	Lateral vein	Complete leaf
Second	0.6 ± 0.1	0.9 ± 0.0	0.8 ± 0.1
Third	1.0 ± 0.1	3.2 ± 0.2	0.9 ± 0.1
Fourth	1.9 ± 0.2	4.8 ± 0.3	1.9 ± 0.2

*Plants were grown in a greenhouse for 35 days. Leaves were ordered from the oldest (first to appear) to the youngest. The first leaf was not analysed because of its senescent state. The numbers (± s.e.) are the mean of two samples of several equivalent leaves of various plants.

Table 3. Hydroxamic acid content in cortex and vascular cylinder of roots and mesocotyls of maize seedlings

Plant part	Hydroxamic acid* (mmol/kg fr. wt) Root 4†	Root 8	Mesocotyl 4†	Mesocotyl 6	Mesocotyl 7	Mesocotyl 8
Cortex	3.1	1.0	3.6	5.9	1.1	1.3
Vascular cylinder	4.5	2.3	7.5	6.1	3.1	2.2
Complete organ	3.5	1.5	5.7	6.2	1.9	1.4

*Plants of maize were grown in the dark at 28°. Values represent the mean of two samples. Standard errors were similar to those recorded in Tables 1 and 2 and are omitted for the sake of simplicity.

†Plant age (days).

EXPERIMENTAL

Plant tissue. Plants of *Zea mays* cv T129s and *Triticum durum* cv SNA-3 were grown in soil in a greenhouse under permanent light, being irrigated with tap H_2O. Temp. varied between 22° at night and 28° during the day. Plant tissues were homogenized in distilled H_2O and centrifuged at 3500 *g* for 15 min. The supernatant fluid was adjusted to pH 3 (1 M HCl), extracted into Et_2O (2:1 v/v, Et_2O–extract) and evapd to dryness. This extract was used for quantitation of hydroxamic acids as previously described [3].

Separation of tissues. Primary and secondary veins from leaves were separated using carborundum as described in ref. [11] and then by mechanical separation with a dissection needle under a stereoscope. Cortex and stele from dark-grown plants were separated by twisting the mesocotyl at its base to break the cortical cylinder but not the stele [12]. The stele was then pulled out from the base of the mesocotyl. The separated cortical and vascular cylinders were used for analyses of hydroxamic acids. Vascular cylinders from principal roots were obtained by making a longitudinal cut 3–5 mm below the transition zone which allowed the removal of the cortex.

Acknowledgements—This research was supported by the Agency for International Development (Grant 484) and the Universidad de Chile (Grant No. 1654).

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