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Hydraulic Signals

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SUMMARY

Hydraulic signals are ubiquitous in plants. They can pass throughout the hydraulic continuum of the plant very quickly, especially in the xylem. They may permit integration of whole-plant responses. Their effect on stomata could be important; change in the environment (and water potential) of one leaf will be transmitted hydraulically and will affect the aperture of stomata throughout the shoot, by a hydropassive mechanism. Wound-induced hydraulic signals are a special case. The basipetal mass flows associated with these signals can sweep elicitors from wound sites to the remainder of the plant at rates of about 10 mm s^{-1}. This could be the mechanism by which rapid, whole-plant defence responses to localized attack are coordinated.

1. INTRODUCTION

Hydraulic signals are self-propagating changes in water (fluid) pressure. By this broad definition they are ubiquitous in plants, occurring throughout the continuous water phase in the apoplast between neighbouring cells, across cell membranes, and within all hydrated cells. At the molecular level, osmotic forces can also be considered to develop by miniature transmembrane hydraulic signals (Dainty & Ferrier 1989). In this paper, the focus is on systemic hydraulic signals which could coordinate physiological responses. These travel through the xylem.

Under the microscope mature xylem conduits appear as open tubes without internal membranes. The axial flow of water through such conduits will be determined only by gradients of hydrostatic pressure, in accordance with the Hagen–Poiseuille law (Nobel 1991). Xylem conduits are of large diameter relative to the capillaries which exist in the walls between cells. The xylem system therefore offers a pathway of relatively low resistance to axial water flow (Ziegler 1991). The major resistances to water flow through the plant occur outside the xylem, across tissues of the root and leaf. Given typical values for transpiration rate and xylem vessel radius, only small axial pressure gradients will occur within the xylem (Nobel 1991). Thus, most of the xylem will normally be at roughly the same pressure, perhaps to within a bar (0.1 MPa), at least in vegetative herbaceous plants. In trees, enormous vertical gradients in xylem pressure could exist (Tyree & Sperry 1989; but see Zimmermann *et al.*, this volume). The hydraulic capacitance of xylem has never been measured *in vivo*. However, the walls of xylem conduits are usually heavily reinforced, even in elongating tissues, and they are probably relatively inelastic. The hydraulic capacitance of xylem will therefore be small. Because of this combination of low resistance and low capacitance, change in pressure at one part of the xylem can equilibrate rapidly (i.e. with a short half-time) throughout the entire xylem. The front of pressure waves will propagate at up to the speed of sound (1500 m s^{-1} in water).

Because neither the xylem nor water itself are totally inelastic, hydraulic signals must involve a physical displacement of water (mass flow) as well as a propagation of pressure. However, the mean rate of mass flow will be far less than that of pressure propagation.

Flow in the xylem is generally acropetal, from roots to leaves. But this directionality is not a property of the xylem. There is no evidence that the xylem has rectifying properties. Directionality is imposed by the apoplastic gradients of hydrostatic pressure and, usually, water potential, which exist from roots to transpiring leaves. If these gradients were reversed, then flow in the xylem would also be reversed.

Some plant tissues such as fruit (Jones *et al.* 1985) flowers (Darlington & Dixon 1991) and others (Morse 1990) may have limited xylem connections with the stem. Most leaf tissues, however, have extensive connections, and the xylem ramifies to all parts of the tissue. In leaves of wheat seedlings, almost every cell is within four cells of the nearest xylem vessel (not shown).

Experiments with dyes, and anatomical observations of xylem architecture (Darlington & Dixon 1991) indicate that the xylem may be divided into discrete sectors, and that neighbouring leaves may not be fed from the same sector. However, dye movements are not necessarily good indicators of the pathway of water flow (Canny 1990). Experiments with several different species indicate that leaves throughout the shoot behave synchronously following a local change in the water status of one leaf (Malone 1992; Boari & Malone 1993). An example from tomato is shown in figure 1. This shows that the entire xylem of the shoot functions as a single hydraulic unit. If there are discrete sectors of xylem in the shoot, then the various sectors can be separated only by pathways of low resistance. When the water status of one leaf of a wheat seedling is altered, leaf thickness changes synch-

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ronously at all positions along a neighbouring leaf, regardless of the length of intervening xylem (Malone 1992). This shows that the major resistance to water propagation between leaves is not the xylem. It is the pathway from the xylem into leaf cells. Taken together, these observations confirm that a change in the pressure of apoplast water in one leaf of the herbaceous plant will propagate quickly, *via* the xylem, to other leaves of that plant.

Under windy conditions, transient distortion of the stem of the plant will impose rapid local changes in xylem pressure. These will propagate throughout the xylem, as hydraulic signals. However, such transient pressure ripples will involve very little mass flow and they will be confined largely within the xylem. Change in hydrostatic pressure within the xylem *per se* will have little physiological significance because the mature xylem is dead. In the case of hydraulic signals propagating from tissue to tissue, the mass flow component will be much greater than for the isolated xylem. This is because the cells of a tissue are elastic, and their hydraulic capacitance is much larger than that of xylem. A significant volume of water will have to flow into such a tissue to impose a pressure change on it. The magnitude of pressure changes associated with mass flow between tissues will depend on the hydraulic capacity of the transmitting tissue relative to that of all the receiving tissues. Where change in local xylem pressure is sustained by the hydraulic capacity of a transmitting tissue, or by continued water loss from nearby cells, then pressure throughout the xylem, and turgor pressure of all cells of the shoot will be affected. This could have major physiological consequences. Some examples are considered below.

2. HYDRAULIC SIGNALS IN THE UNWOUNDED PLANT

Small steps in hydraulic pressure applied (clamped) to the cut end of an excised cereal leaf induce marked and very rapid (< 1 s) changes in stomatal aperture throughout the leaf (Raschke 1970). These movements occur because of changes in the back-pressure from epidermal cells adjoining the stomata. Stomata are caused to open further when epidermal turgor falls and *vice versa*. These hydropassive effects tend to accelerate the initial change in turgor by their influence on transpiration. In the intact plant, stomata must compensate actively for such hydropassive changes, otherwise a small initial drop in xylem pressure could lead to accelerating transpiration. This could continue until major loss of water removed the epidermal back-pressure on stomata. In a changeable environment, variations in the transpiration rate of exposed parts of the plant will propagate as hydraulic signals throughout the shoot. Any local pressure change will be buffered by the hydraulic capacity of the entire plant. Nevertheless, this means that stomata throughout the plant will experience frequent and rapid hydropassive microfluctuations in aperture. They must actively counter these fluctuations to avoid amplification of the initial effect. It is difficult to envisage any viable control mechanism for these short-term compensations other than one based on feedback control from some component of leaf turgor pressure. Of course, other factors (light, ABA) will influence stomatal aperture over the longer term, possibly by changing the 'set-point' of turgor pressure around which the feedback control mechanism hunts. The characteristics of the feedback control mechanism may be reflected in the stomatal 'bounce' which often follows changes in environmental conditions (Hashimoto *et al.* 1984). Systemic hydraulic signals could synchronise the response of the entire population of stomata in the shoot.

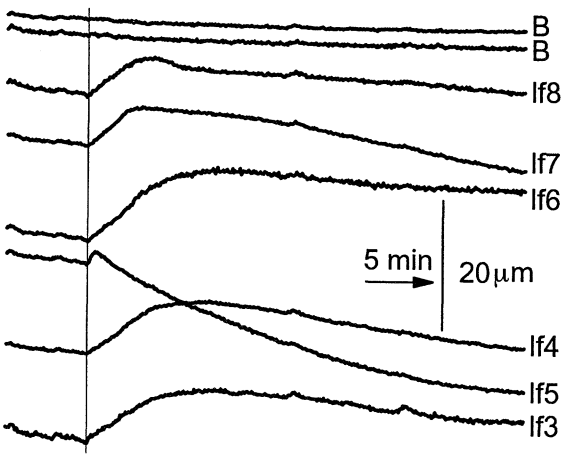

Figure 1. Systemic wound-induced increases in leaf thickness in tomato. The lines show simultaneous transducer recordings of leaf thickness in various leaves of an individual tomato plant. Leaf numbers are shown at the right (the oldest leaf would be number 1). Two blank transducers (B) which did not contain leaves, were also run on the same system. At the time indicated by the long vertical line, one leaflet of leaf 4 was scorch-wounded for 3 s using a cigarette lighter. The transducer system is described in Malone (1992).

Hydraulic signals may also trigger systemic changes in the surface electrical potential of some plants, with or without wounding (Malone & Stanković 1991; Stahlberg & Cosgrove 1992). The physiological significance of these electrical changes is largely unknown but they may be associated with hydraulic effects on stomata. This is because hydraulic signals will activate compensatory stomatal responses (as discussed above) and these will be associated with changes in electrogenic activity at guard cell membranes. Such membranes are close to the leaf surface and they could dominate its electrical potential (Bowling 1989; Malone & Stanković 1991).

Palta *et al.* (1987) showed that hydraulic signals from the shoot may control the transport properties of root cells in sugar beet. These authors noted that 'physical signals propagated through the hydraulic continuum of the plant would offer a potentially ubiquitous system of integration within plants'. Hydraulic signals induced by excision have been shown to alter elongation rate in a number of organs (Stahlberg & Cosgrove 1992) presumably acting via cell turgor pressure.

Some organs of the shoot, such as the fruits of apple,

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tomato, and cucumber, and the heart leaves of lettuce, do not transpire much water. However, they are connected to the xylem of the shoot and they will be influenced by the diurnal oscillation in shoot water status. The resulting ebb and flow of xylem sap into these organs could provide an important vehicle for the supply of xylem-borne nutrients, especially calcium (Jones & Higgs 1985). The process of transpiration itself involves a standing hydraulic signal from leaves to roots.

3. WOUND-INDUCED HYDRAULIC SIGNALS

Localized wounds can induce rapid and systemic responses in many plants. These include changes in surface electrical potential (Malone & Stanković 1991) and systemic activation of defence genes (Ryan & An 1988). Various theories have been advanced regarding the nature of the systemic signal transmitted from wound sites. These include hydraulic (Dutrochet 1837), electrical, chemical, and various metaphysical explanations. Haberlandt (1890) believed that hydraulic signals moving through live cells (outside the xylem) were responsible for signal transduction in 'sensitive' plants like *Mimosa* spp. However, it was later shown that the signal in these plants would traverse large areas of heat-killed tissue, in which there could be no turgid cells. The signal would also travel apparently unhindered through substantial lengths of stems which consisted of alternating live and dead regions (Cunningham 1895). A current theory of long-distance electrical ('electrotonic') signal propagation in plants (Wildon *et al.* 1992) is also endangered by these observations because cell-to-cell electrical transmission would likewise require functional (live) membranes. MacDougal (1896) was unable to propagate signals reliably by applying pressure pulses to the cut ends of excised twigs of *Mimosa*. He concluded that 'hydrostatic disturbance does not constitute an impulse'. More recently, Tinz-Füchtmeier & Gradmann (1991) were also unable to detect systemic hydraulic signals during wound-induced signal transduction in *Mimosa*.

In contrast to these negative findings, Malone & Stanković (1991) reported rapid systemic hydraulic signals in response to localized wounding. They showed that localised wounds cause large (up to 100%) and rapid (half-time about 2 min) increases in turgor pressure in epidermal cells throughout the leaves of the wheat seedling. Associated effects of localised heat wounds on the thickness of other leaves on the plant (figure 1) have been demonstrated in a variety of species (Boari & Malone 1993). These systemic increases in pressure and leaf thickness cannot be accounted for by water entry across the root because they occur on wounding of seedlings deprived of external water by excision of their roots (Malone 1992). The water for systemic swelling of these seedlings must come from the damaged tissue. Ion movements and localised growth can lead to redistribution of water in excised tissues (Matyssek *et al.* 1991) but these changes occur over hours and are clearly distinct from the rapid water movements induced by wounding.

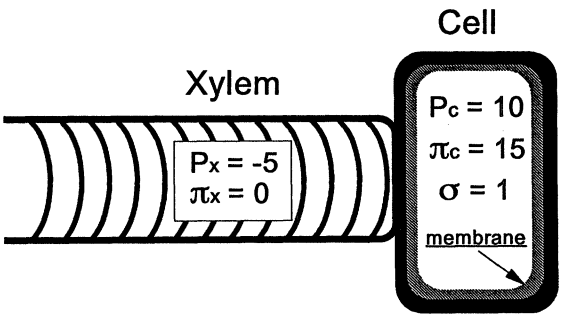

Figure 2. Diagram of wound-induced change in the driving forces on water in a system consisting of a leaf cell and adjacent xylem vessel. The driving force for water flow, J_v/L_p is given as in equation 4) example values (in bars) are shown on the diagram.

$$J_v/L_p = \Delta P - \sigma\Delta\pi. \quad (4)$$

J_v = Water flow rate; L_p = hydraulic conductance; π_c = cell osmotic pressure; P_c = cell turgor pressure; π_x = xylem hydrostatic pressure; π_x = xylem osmotic pressure; σ = membrane reflection coefficient. The effect of wounding on this driving force can be calculated as follows:

1. Prior to wounding, hydrostatic gradients are balanced by osmotic gradients and the net driving force on water is zero (equation 5).

$$J_v/L_p = (10 - {}^{-}5) - 1 \times (15 - 0) = 0. \quad (5)$$

2. On scorching, the membrane reflection coefficient is reduced to near zero. The osmotic component becomes ineffective in driving water flow. A strong net driving force (5 bar), towards the xylem, develops immediately (equation 6). The hydraulic conductance of the pathway (L_p) may also be increased on wounding, because of membrane disruption. Wounding will therefore establish a strong, xylem-borne flow of water away from the wounded region.

$$J_v/L_p = (0 - {}^{-}5) - 0 \times (15 - 0) = 5. \quad (6)$$

Localized wounding initiates hydraulic signals by destroying cell membranes (figure 2). When this happens, the reflection coefficient at the boundary of the cells falls catastrophically from near unity to near zero. Water, previously constrained within those cell membranes by osmotic gradients, is released to the apoplast where it becomes available to the nearest xylem. Because the water in the xylem is normally under tension, the available sap will be drawn into the xylem. It will relieve xylem tension locally and this will propagate throughout the shoot as an hydraulic signal.

The front of the wound-induced hydraulic signal travels through the plant at speeds in excess of 10 cm s^{-1} (Malone 1992; Boari & Malone 1993). There follows an extended phase of mass flow from the wound site, which may last for many minutes. This occurs because all cells of the shoot are in hydraulic equilibrium (or quasi-stationary state) with their nearest xylem. When xylem pressure is boosted suddenly and systemically by a localized wound, all cells of the shoot will begin to approach the new equilibrium by drawing water from their local xylem. This

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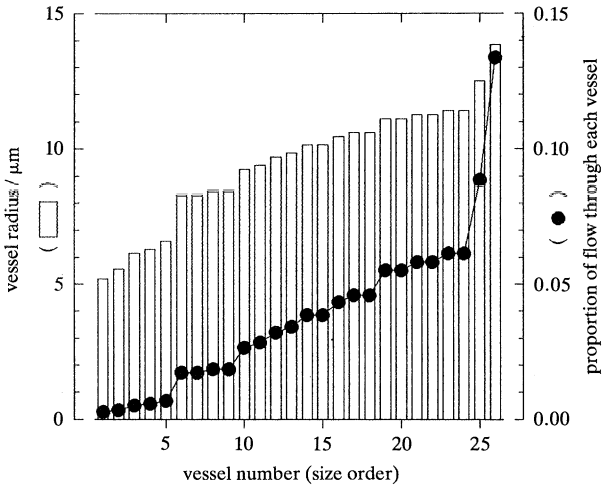

Figure 3. Xylem vessel radii in a petiole of a tomato leaflet. Petiole segments were excised by transverse cuts with a fresh razor blade and rinsed for 2 min in water. They were then plunged into liquid N_2, freeze-dried, shadowed with gold, and viewed in a scanning electron microscope. This example had 26 xylem vessels of various radii (histogram). The proportion of any flow which would occur through each vessel (circles) was calculated as $r^4/(\Sigma r^4)$.

tends to reduce xylem pressure throughout the healthy tissue and therefore promotes further entry of water into the xylem of the wounded tissue. This continues until all the water released at the wound site is exhausted. Transpiration rates are reduced immediately after localized wounding (Van Sambeek & Pickard 1976; Wildon *et al.* 1992) possibly because the systemic hydraulic signal will close stomata hydropassively. Nevertheless, transpiration from all leaves can continue at this time. However, the source of the water for both transpiration and systemic swelling will be the wound site rather than the root medium. Proximal to the wound site, in the petiole of the wounded leaf, the wound-induced mass flow will be basipetal, ie. in the reversed direction with respect to the normal transpiration stream. This important point is not appreciated by some workers (Wildon *et al.* 1992). Basipetal (reversed) flow through the petiole of the wounded leaf will proceed as far as the next major node with the xylem (where xylem from the damaged leaf merges with the xylem of the stem). From there, the flow will be both acropetal and basipetal, and the relative magnitudes of flow in each direction will depend on the corresponding distribution of hydraulic capacitance in the plant.

Wound-induced hydraulic signals differ from other hydraulic signals in two salient respects. First, a relatively small area of wounded (transmitting) tissue can have a marked effect on turgor pressure throughout the plant. To illustrate this, consider a model tissue containing identical cells each of volume 500 pl and elastic modulus 50 bar (5 MPa). These values would not be unreasonable for epidermal cells of the wheat leaf (Malone & Tomos 1990). By definition, the volume required to raise the pressure of a healthy cell through 1 bar (0.1 MPa) will be 10 pl. Thus, breakage of only one cell would release enough water to raise the pressure of 50 healthy cells through almost 1 bar (0.1 MPa).

Second, the mass flow associated with wound-induced hydraulic signals includes solutes released from damaged cells as well as water. This factor could be particularly important for the integration of whole-plant defence responses to localized wounding. This is because the mass flow associated with wound-induced hydraulic signals may rapidly disperse soluble elicitors from the wound site throughout the entire plant. This could be the mechanism of systemic dispersal of 'systemin' (Pearce *et al.* 1991) or other 'proteinase inhibitor inducing factors' (PIIF) in tomato plants. These compounds are released from damaged leaves of tomato and they can activate defence genes in healthy leaves. Previously, it has not been clear how these elicitors might travel rapidly around the plant. The phloem is not involved (Wildon *et al.* 1992). To establish whether PIIF distribution by wound-induced hydraulic signals would be sufficiently rapid to account for the observed systemic activation of defence genes, we must consider the rate of basipetal wound-induced mass flow. This can be estimated using several approaches:

(*a*) *Transducer measurements of the magnitude of wound-induced increases in leaf thickness*

Localized scorch wounding induces a systemic increase in thickness of leaves of tomato (figure 1) and many other plants (Boari & Malone 1993). In young tomato plants (at the four-leaf stage), localized scorching causes a systemic increase of about 6 µm in leaf thickness. These leaves have an initial thickness of some 300 µm at the point of measurement. The wound-induced increase in thickness is therefore about 2%. If we assume, conservatively, that change in leaf thickness is related to change in leaf volume by a ratio of 4:1 (Kozlowski 1980, p.3) and that, in addition to the damaged leaf, the plant has three healthy leaves each with a fresh mass of 0.5 g, then the volume of water required to account for the observed swelling of the plant is

$$\frac{0.2 \times 3 \times 0.5\ \text{g}}{4} = 0.0075\ \text{g} = 7.5\ \mu\text{l}. \qquad (1)$$

This volume of water must flow from the wound site, travelling basipetally through the xylem of the petiole of the wounded leaf. To determine the rate of this flow, we measured xylem distribution in transverse sections of petioles of tomato leaflets using a scanning electron microscope. The example petiole shown in figure 3 had 26 xylem vessels with a total transverse area of 7766 µm^2. From the Hagen–Poiseuille law which relates the volume flow through tubes to the fourth power of their radii, it can be calculated that 13.5% of total xylem flow along this petiole will occur in the single largest vessel (circles in figure 3). Thus, about 7.5×0.135 µl must pass down this vessel, of radius 13.5 µm, following scorching of the leaflet. The half time of the wound-induced leaf swelling (and thus of the mass flow) is observed to be about 2 min. We

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can therefore calculate the average basipetal mass flow rate through this vessel over the first 1 min from wounding as

$$\frac{7.5 \times 10^9\ \mu m^3 \times 0.13 \times (1 - e^{(\frac{-1}{2.88})}\ min^{-1})}{\pi \times (13.5)\ \mu m^2} = 8.3\ mm\ s^{-1}. \quad (2)$$

(*b*) *Estimation of the rate of basipetal wound-induced mass flow from the decrease in leaf thickness seen at sites close to the wound*

Undamaged tissue close to the wound site often shows an initial increase in thickness which is quickly overtaken by a decrease in thickness (Boari & Malone 1993). This effect is evident in the leaflet nearest to the wound site in figure 1. This downturn must reflect the arrival in the xylem underlying the healthy tissue, of some factor from the wound site which can decrease cell turgor. The factor could be cell sap flowing from damaged cells, which will contain considerable quantities of solutes (Malone *et al.* 1989) and which will draw water from the live cells by an osmotic process. Alternatively, it could be hot water arriving from the (heated) wound site. Each of these effects will decrease progressively from the wound site. In either case, the timing of the downturn indicates the rate of mass flow from the wound site to the site of measurement. In the leaves of large maize plants (where the effect can be measured with greater accuracy) we observed a downturn in leaf thickness beginning at about 20 s after the wound at a position 15 cm proximal (basipetal) to the wound site (Boari & Malone 1993). Thus, the mean rate of basipetal mass flow must have been at least 7.5 mm s^{-1}.

(*c*) *Estimation of the rate of basipetal wound-induced mass flow from the rate of tracer movement from submerged cuts*

The systemic hydraulic effects of localized scorching can be quantitatively mimicked by excision of one leaflet through its submerged petiole (Malone *et al.* 1993). Both these treatments provide an excess of water to the xylem at the treatment site and both, therefore, induce hydraulic signals with similar kinetics and rates of mass flow. The mass flow rate can be measured by monitoring the movement of tracers into the plant from the medium of submerged excision. Radiolabel can be recovered from all parts of the plant within a few minutes of submerged excision (Malone *et al.* 1993). Flow into the stem subjacent to the treated leaf is especially rapid. This basipetal flow is only slightly reduced if the phloem of the treated petiole is destroyed (heat-killed) 24 h prior to the submerged excision (figure 4), and it is increased if significant osmoticum is included in the medium of submerged excision (figure 4). The latter may more closely mimic the situation *in vivo*, where solutes are incorporated with the mass flow from wound sites. These solutes may draw extra water from cells surrounding the flow path and thus prolong the mass flow. From the counts recovered in the various plant parts, and the specific activity of the treatment solution, about 8 µl of solution must have entered the plant within the 5 min application time (control plant in figure 4). This entire volume had to pass basipetally through the xylem of the distal half of the treated petiole (which was not counted). Applying the same figures for xylem transverse area as in 1 (above) we calculate that, along the treated petiole, the mean rate of basipetal mass flow over the first 1 min from submerged excision was 9 mm s^{-1}. We have obtained similar results with various different radiolabelled tracers including Rhamnogalacturonan I, adenine, sucrose, and abscisic acid (Malone *et al.* 1993). Rhamnogalacturonan I is a large pectic cell wall polysaccharide with PIIF activity (Ryan *et al.* 1981).

There is reasonable agreement in the values for basipetal mass flow rate arising from these three different methods. It can be concluded that wound-induced mass flows can transport solutes extensively and rapidly from the wound site. The rate of mass flow (*ca.* 10 mm s^{-1}) is sufficiently rapid to distribute elicitors throughout the plant within the shortest times observed for systemic wound-induced gene activation (20 min; Peña-Cortes *et al.* 1988). We therefore conclude that this is the mechanism of systemic signalling of wounding in tomato. This mechanism could operate in various other

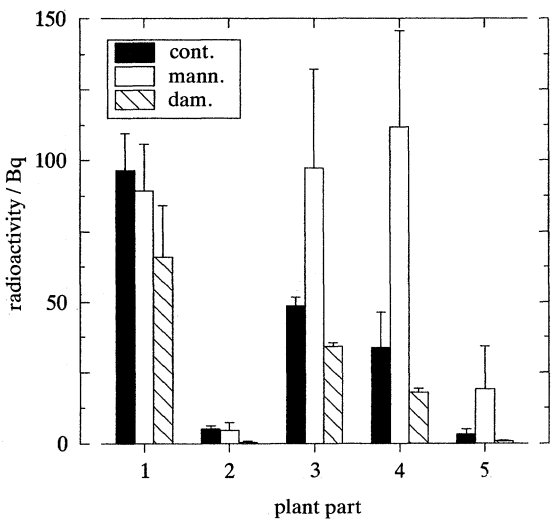

Figure 4. Movement of radiolabelled tracer from a site of submerged excision. The terminal leaflet of leaf 5 of tomato seedlings (seven-leaf stage) was excised through its petiole submerged in a solution of ^{14}C-adenine. The petiole remained submerged for 5 min, then the following plant parts, each about 2.5 cm in length, were harvested: 1, proximal half of treated petiole; 2, stem above junction with treated petiole (including the apex); 3, stem immediately below junction with treated petiole; 4, stem further below; and 5, stem base. The plant parts were frozen in liquid N_2, thawed, and centrifuged through a perforated container. Liquids thus extracted (about 70% of the tissue fresh mass) were made up to 500 µl with water and counted with 4.5 ml liquid scintillant. Counts (Bq) recovered from each part are shown. The specific activity of the applied solution was 24 Bq μl^{-1}. In some cases, 3 cm of the central region of the treated petiole was killed (by flame) 24 h prior to submerged excision ('dam'). In some cases, the tracer solution was made up to 5 bar (0.5 MPa) with mannitol prior to submerged excision ('mann'). Means of 4 plants ± s.e.

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situations where localized damage, such as that occurring on pathogen invasion, induces a systemic defence response.

With small wounds there will not be much water released and, although the kinetics of the hydraulic signal will be similar, the extent of the associated mass flow will be less. Considerable distribution of the elicitors will still occur if the wound-induced mass flow proceeds as far as the next major node with the xylem of the stem. From this node solutes (including elicitors) will be distributed with the transpiration stream even after the hydraulic signal has ceased, at least in the acropetal direction. A minimum level of wounding which will permit significant distribution of elicitors can therefore be predicted. This is based on the volume of sap required to displace the contents of the major xylem vessel(s) from the wound site, as far as the junction with the xylem of the stem. Taking, for example, the tomato petiole shown in figure 2, the most rapid flow will occur in the single largest vessel of the petiole. This has a radius of 13.5 μm. In tomato plants (at the four-leaf stage) the length of petiole from a wounded leaflet to the stem is up to about 5 cm. Thus the volume required to displace the contents of the largest vessel will be

$$\pi\ (13.5\ \mu\text{m})^2 \times 5 \times 10^4\ \mu\text{m} = 2.8 \times 10^7\ \mu\text{m}^3 \approx 0.03\ \mu\text{l}. \quad (3)$$

The fresh mass of a leaflet is about 100 mg. Thus, each will contain nearly 100 μl of water, much of it in the vacuoles. We can therefore estimate that damage to less than 1% of the cells in one leaflet could provide enough sap to fuel a wound-induced mass flow of solutes to the stem. From this, it is evident that even small wounds such as those inflicted by leaf-biting insects or by lesion-inducing pathogens, could induce basipetal mass flows which are sufficient to provide a vehicle for extensive distribution of elicitors from wound sites. It remains to be seen whether wound-induced hydraulic signals play a role in coordination of defence responses in plants growing in the field.

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