

The Propagation of Slow Wave Potentials in Pea Epicotyls¹

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Slow wave potentials are considered to be electric long-distance signals specific for plants, although there are conflicting ideas about a chemical, electrical, or hydraulic mode of propagation. These ideas were tested by comparing the propagation of hydraulic and electric signals in epicotyls of pea (*Pisum sativum* L.). A hydraulic signal in the form of a defined step increase in xylem pressure (P_x) was applied to the root of intact seedlings and propagated nearly instantly through the epicotyl axis while its amplitude decreased with distance from the pressure chamber. This decremental propagation was caused by a leaky xylem and created an axial P_x gradient in the epicotyl. Simultaneously along the epicotyl surface, depolarizations appeared with lag times that increased acropetally with distance from the pressure chamber from 5 s to 3 min. When measured at a constant distance, the lag times increased as the size of the applied pressure steps decreased. We conclude that the P_x gradient in the epicotyl caused local depolarizations with acropetally increasing lag times, which have the appearance of an electric signal propagating with a rate of 20 to 30 mm min⁻¹. This static description of the slow wave potentials challenges its traditional classification as a propagating electric signal.

SWPs, also called variation potentials, have been reported and described in a variety of different plant species, first in seismonastic plants such as *Mimosa pudica* (Houwink, 1935; Sibaoka, 1953; Umrath, 1959; Roblin and Bonnemain, 1985) and later in a variety of common or nonseismonastic plants (Kawano, 1955; Van Sambeek et al., 1976; Tsaplev and Zatsepina, 1980; Frachisse et al., 1985; Roblin and Bonnemain, 1985; Wildon et al., 1992; Davies et al., 1991; Boari and Malone, 1993). Like the better-known APs, SWPs are considered to be electric long-distance signals in plants. In *M. pudica*, *Bidens pilosa*, *Tradescantia*, *Vicia faba*, and many other plants, both electric signals occur together. Usually an AP spike precedes the development of the SWP, indicating a faster rate of propagation for APs (Houwink, 1935; Davies et al., 1991). These rates also determine the spike-like appearance of APs and the wave-like appearance of SWPs in extracellular recordings.

APs are induced by the coordinated activity of ion channels (Wayne, 1994), and their propagation in both plants and animals is considered to be electrotonic (e.g. Sibaoka and Tabata, 1981; Opritov and Retivin, 1982; Davies, 1987).

No similar consensus has been reached about the mode of SWP propagation. A faster propagation in the basipetal than in the acropetal direction led to the conclusion that SWPs propagate electrically (electrotonically), i.e. in a similar fashion as APs (Kawano, 1955; Tsaplev and Zatsepina, 1980). Wildon et al. (1992) also favored an electric mechanism of propagation for the uncharacterized systemic (propagating) electric signal they induced by wounding and heat treatment in tomato plants.

Many studies have suggested a chemical means of propagation for SWPs in which wounding releases a chemical substance (wound hormone, Erregungssubstanz, Ricca's factor), which is moved by the xylem flow causing electrical changes along its path of distribution (Ricca, 1916; Umrath, 1959; Van Sambeek et al., 1976; Cheeseman and Pickard, 1977a; Roblin and Bonnemain, 1985; Frachisse et al., 1985; Boari and Malone, 1993). Recently published evidence indicates that SWPs may be caused by hydraulic signals, i.e. a positive pressure wave in the xylem caused by an excision-induced release of the negative P_x in intact plants (Stahlberg and Cosgrove, 1992, 1995) or by sudden heating (torching, flaming, or burning) of plant leaves (Malone and Stankovic, 1991). The hydraulic propagation of P_x in tubes should theoretically be very fast and approach the speed of sound. If that is so, it needs to be explained how such a fast hydraulic signal relates to a SWP that slowly propagates in pea (*Pisum sativum* L.) epicotyls (Stahlberg and Cosgrove, 1992). This difference has been explained previously by the movement of wound-released solutes in the xylem in studies that used injurious leaf burning to induce positive hydraulic signal and SWPs (e.g. Boari and Malone, 1993). The noninjurious SWP induction to intact plants by basal application of small pressure steps discussed in the present work was in obvious conflict with such a model and demanded an alternative explanation.

To analyze this problem we made direct measurements of pressure propagation in pea epicotyl segments of different lengths and compared them with the rates of SWP propagation. Our results indicate that the kinetic appearance of SWPs is caused by radial pressure propagation rather than by axial propagation of an electric, chemical, or hydraulic signal. This model led to the surprising conclusion that a SWP appears to be a static phenomenon rather than the result of a genuinely propagating electric signal.

Abbreviations: AP, action potential; ΔP_x , step change in P_x ; GR, growth rate; KCN, potassium cyanide; P_x , xylem pressure; SWP, slow wave potential; V_m , membrane potential; V_s , surface potential.

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MATERIALS AND METHODS

The materials and methods used in this study have been described in detail (Stahlberg and Cosgrove, 1992, 1995) and will therefore be given here in an abbreviated form. Six-day-old, dark-grown pea (*Pisum sativum* L. cv Alaska) seedlings with straight epicotyls of approximately 120 mm in length were selected for the experiments. All measurements were made under a green safety light.

Electrical Measurements

The root plus 10 mm of basal epicotyl were incubated in a vial with tap water and enclosed in a root pressure chamber. The upper part remained outside the pressure chamber and was fitted into a recording chamber (like the one described in figure 1 of Stahlberg and Cosgrove, 1992), which provided a compartment filled with solution (10 mol m^{-3} KCl) at a distance of 40 mm from the pressure chamber to measure the V_m and three compartments to measure the electric V_s at three positions along the epicotyl: **B** (basal, 30 mm above the pressure chamber), **C** (central, 60 mm above the pressure chamber), and **A** (apical, 90 mm above the pressure chamber).

GR

When in a vertical position, the epicotyl hook of the pea seedling was linked with a displacement transducer and an analog integrator to measure the GR (Cosgrove, 1981).

P_x Measurement

The upper parts of 120-mm-long epicotyls of intact pea seedlings were excised under water. The stele at the end of the decapitated stump was exposed and isolated with epoxy (5 Minutes Epoxy, Devcon Corp., Wood Dale, IL) from the bulk of the peripheral epicotyl tissue and air spaces (Fig. 1). The cut end of the decapitated epicotyl was stripped of the surrounding tissue with a fixed-hole wire stripper, exposing about 8 mm of the stele with a diameter of 0.3 mm. Five millimeters of the stele were sealed with epoxy into a tight-fitting piece of rubber tubing. The other end of the tubing was fitted tightly over the end of the glass capillary of the pressure probe. The remaining 3 mm of stele and the air spaces of the peripheral tissue were iso-

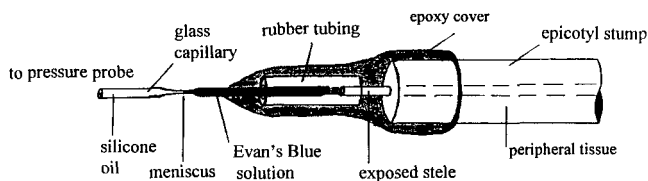


Figure 1. Connection of decapitated epicotyls to the pressure probe for the measurement of P_x in horizontally positioned pea seedlings (not to scale). The root and 20 mm of the epicotyl base are submerged in 10% Hoagland solution and enclosed in a pressure chamber. The glass capillary of a pressure probe is connected to the exposed stele of the decapitated epicotyl end by rubber tubing covered with fast-setting epoxy glue. After the glue dried, epicotyl stumps reestablished a P_x slightly below atmospheric pressure.

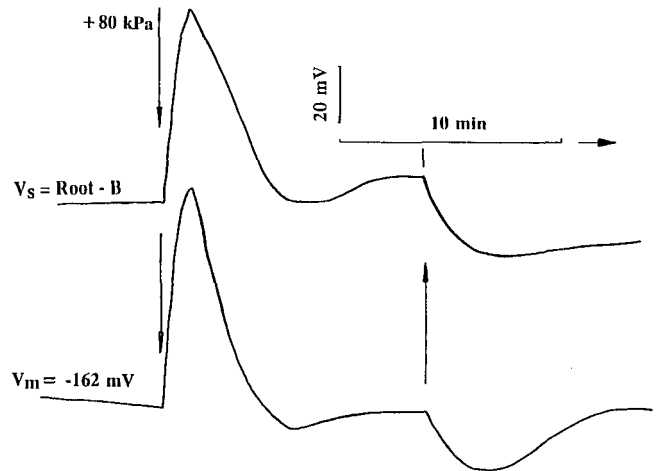


Figure 2. The effect of a step increase in P_x upon the electric V_m and V_s of the epicotyl in horizontally positioned, intact pea seedlings. At the time indicated the pressure in a chamber with the root and 10 mm of the epicotyl was increased from 0 to 80 kPa. The V_m was measured in epidermal cells at a distance of 40 mm from the pressure chamber, the V_s at a distance of 30 mm. The depolarization of epidermal cells appeared simultaneously as a negative shift in the V_s of the epicotyl (measured as the difference between epicotyl position **B** and the root). We presented the Root-B trace to emphasize the parallel changes in V_m and V_s . Example is representative of 10 similar experiments.

lated from the tubing (containing the open xylem vessels) by a layer of epoxy. The glass capillary (A-M Systems no. 6015, Everett, WA) was pulled in the middle to a small diameter of about 100 μm , which allowed easy observation and adjustment of the meniscus between the phases of silicon oil (in contact with pressure transducer of the probe) and 1% aqueous Evans blue solution (Sigma) (in contact with the cut end of the stele) inside the capillary. Five millimeters of capillary plus the adjacent tubing collar, 3 mm of exposed stele, and 5 mm of epicotyl surface were completely sealed with epoxy. The epoxy cover reduced the elasticity of the tubing and prevented a direct (and artifactual) connection between the open cut ends of the xylem vessels and the bulk of the peripheral epicotyl tissue with its large, air-filled intercellular spaces.

RESULTS

Epicotyl Cells Transduce a Pressure Signal into a Voltage Change

We applied a step-like increase in external air pressure to the roots of intact pea seedlings. Epicotyl cells outside and at 40 mm from the chamber underwent a rapid, large, and transient depolarization (Fig. 2, lower trace). When the imposed root pressure was released, the cells showed a response that varied from no change to a small, transient hyperpolarization. This result indicates that epicotyl cells convert an increase in P_x into a transient depolarization of their V_m . This V_m signal was also detected by extracellular

electrodes at the surface of the epicotyl (Fig. 2, upper trace). Although the V_s of position B was measured about 10 mm below the location of the microelectrode, the changes in V_m and V_s were very similar and can be expected to be identical when measured at the same position. Although V_s was recorded over a 3-mm-long agar surface contact, the time course of the V_s change was not much larger than that of the V_m signal. We conclude that V_s recordings are sufficiently precise to follow the path of the V_m depolarization in a noninjurious fashion.

To test the propagation of the depolarization we measured V_s along the epicotyl at three positions separated by a distance of 30 mm (Fig. 3). When the root was pressurized to 60 kPa, a depolarization appeared within 40 to 60 s first

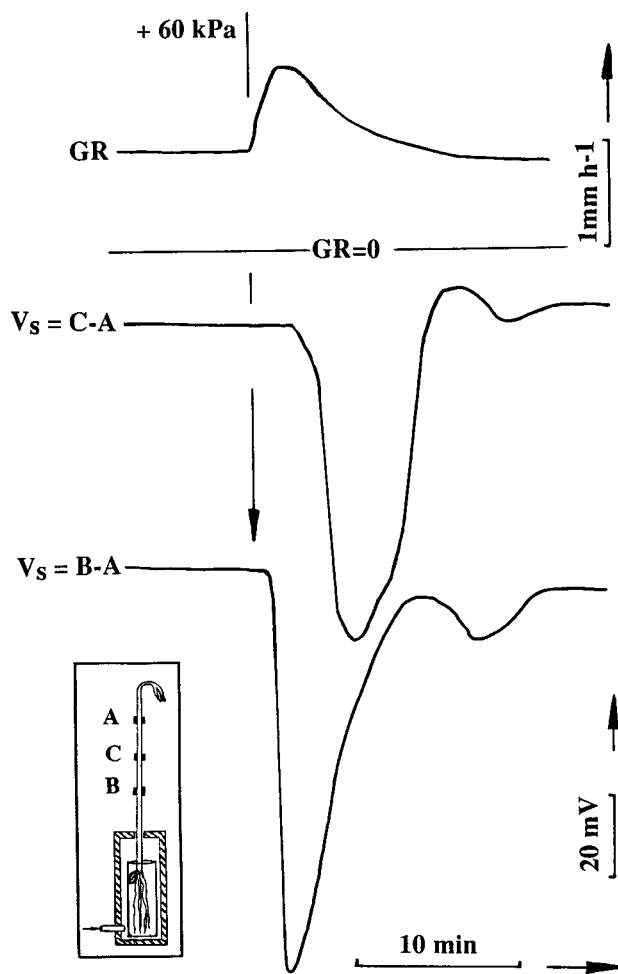


Figure 3. The effect of a step increase in P_x upon the GR and electric V_s of different positions along the epicotyl axis of vertically positioned, intact pea seedlings with an epicotyl length around 120 mm. The first response is an immediate, transient rise in the GR of epicotyl, which shows that the pressure wave reached the subapical growth region (roughly at 90–120 mm from the pressure chamber). The negative shift in V_s (representing a depolarization of the cells in this position) appears first in position B (30 mm above the pressure chamber; negative shift in the B-A trace without a simultaneous change in the C-A trace), and approximately 1 min later in position C (60 mm above pressure chamber). This example represents more than 20 repetitions with similar results.

at position B (as indicated by a negative V_s shift in the B-A trace without a simultaneous change in the C-A trace) and then reached position C within another 60 to 100 s. Our results show that the depolarization moved at speeds varying between 20 and 30 mm min^{-1} and that it had the appearance of a SWP (Stahlberg and Cosgrove, 1992).

Metabolic Inhibitors Do Not Interrupt the Propagation of the SWP

The induced SWP depolarization depended on metabolic energy and was suppressed by KCN, sodium azide, 2,4-dinitrophenol, sodium cholate, carbonylcyanide-*m*-chlorophenylhydrazine, and *p*-chloromercuribenzenesulfonic acid. When KCN replaced KCl in the agar at position B, it reduced the depolarization to 0 to 50% of the signal strength in C (Fig. 4, lower trace). The suppression at position B did not interrupt SWP propagation beyond that area, where position C underwent a normal depolarization. Such a behavior is in conflict with the concept of an electrotonic propagation of the depolarization signal (Sibaoka and Tabata, 1981). Note also that the inhibitors depolarized the cells at position B before the SWP was induced (see legend to Fig. 4), so that the absolute value of the depolarization did not differ much between treated and untreated positions. The repolarization of the SWP in the treated position, however, restored a sizable polarization of the epidermal cells and points to an interesting interference of the SWP with metabolic processes (Fig. 4, lower trace).

Propagation Rates of the Hydraulic and Electric Signal Do Not Match

In addition to inducing a SWP, a pressure step caused an increase in the epicotyl GR that started within 0 to 2 s and lasted between 6 and 10 min (Figs. 3 and 4). Growth (confined to the subapical region above position A) responded faster than V_s in more basal positions of the epicotyl, which indicates that the hydraulic signal was much faster than the depolarization. To confirm this conclusion we measured the speed of pressure propagation in the epicotyl by connecting a pressure probe to decapitated epicotyl stumps. After a short equilibration time the epicotyl restored a negative P_x in the decapitated stump (Fig. 5, example 1). The size of the negative P_x depended on the length of the attached epicotyl piece. The measurements confirmed that pressure changes propagate very quickly through the epicotyl (Fig. 5). It took several minutes, however, before the P_x steadied at a new level. Also, the established P_x changes were not always completely reversed after pressure release (e.g. Fig. 5, example 2), which led to considerable variations in the results that were reduced by averaging the propagated P_x changes of a negative and positive pressure step (50 kPa). In the beginning we attempted to reduce the variability further by excising the roots before the experiment. We found, however, neither a reduction in the variability of the results nor a significant difference in the pressure values propagated by pea epicotyls with or without roots. The discrepancy between rapid

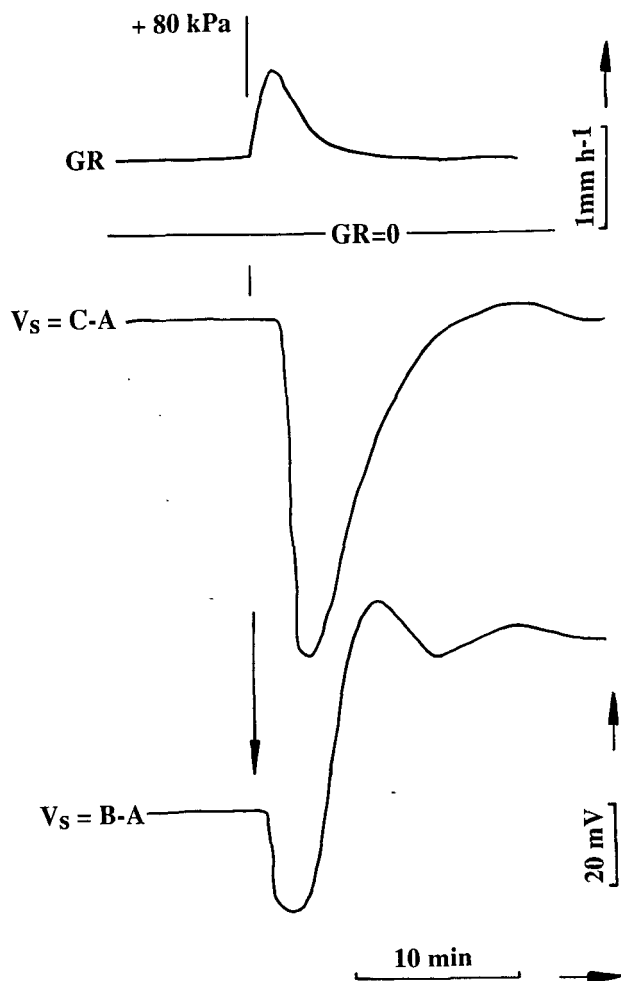


Figure 4. Local application of metabolic inhibitors does not prevent propagation of the SWP. As also shown in Figure 3, we measured the effect of a step increase in P_x upon the GR and electric V_s at different positions along the epicotyl axis of vertically positioned, intact pea seedlings. The contacting agar at electrode position **B**, however, contained 10 mol m^{-3} KCN instead of 10 mol m^{-3} KCl. The suppression of the electric signal at position **B** did not prevent the signal propagation to position **C**, which underwent a normal depolarization. Note that the inhibitors depolarized the cells of position **B** before the SWP was induced (initial V_s value for B-A was on average -65 ± 7 (SE) mV ($n = 6$) and considerably more negative than that for C-A, 5 ± 2 (SE) mV). The example represents 25 similar results with 10 mol m^{-3} KCN, 10 mol m^{-3} sodium azide, 10 mol m^{-3} sodium cholate, 5 mol m^{-3} 2,4-dinitrophenole, 1 mol m^{-3} carbonylcyanide-*m*-chlorophenylhydrazone, 0.1 mol m^{-3} sodium orthovanadate, and 0.1 mol m^{-3} *p*-chloromercuribenzenesulfonic acid application to position **B** or **C**.

pressure propagation and slow movement of the depolarization challenged the hypothesis that SWPs are caused by a hydraulic signal (Malone and Stankovic, 1991; Stahlberg and Cosgrove, 1992).

A Leaky Xylem Created ΔP_x Gradient in the Epicotyl

Figure 5 shows that a chamber pressure step of 50 kPa was reduced to 35 kPa by traversing an epicotyl length of 40 mm and to about 15 kPa within an epicotyl length of 80

mm. From these results we conclude that pressure application led to a pressure gradient in the epicotyl. The generation of such a P_x gradient could have been caused by radial leaks or a high hydraulic resistance in the xylem. Xylem vessels are known to resemble leaky tubes (e.g. Canny, 1993) and we often observed the appearance of exudate spheres at the surface of pressurized pea epicotyls. The belated establishment of a steady P_x value should also be attributed to lateral leaks and the filling of intercellular spaces. Our experiments with different epicotyl lengths showed that the reduction of the pressure step can be better explained on the basis of xylem leaks in the epicotyl than on the basis of a high frictional root resistance (Zimmermann et al., 1993).

Measuring the reduction of a 50-kPa step in a group of seedlings with their epicotyls cut to lengths from 2 to 12 cm, we created a model for the pressure gradient in the xylem of an intact pea epicotyl (Fig. 6). A linear regression line of the measured data crossed the ordinate (epicotyl length = 0) at 45 kPa (applied pressure was 50 kPa) and therefore provided a first estimate of the steepness of the pressure gradient (about 4 kPa cm^{-1}), which was used to convert chamber pressure steps into estimates of the local

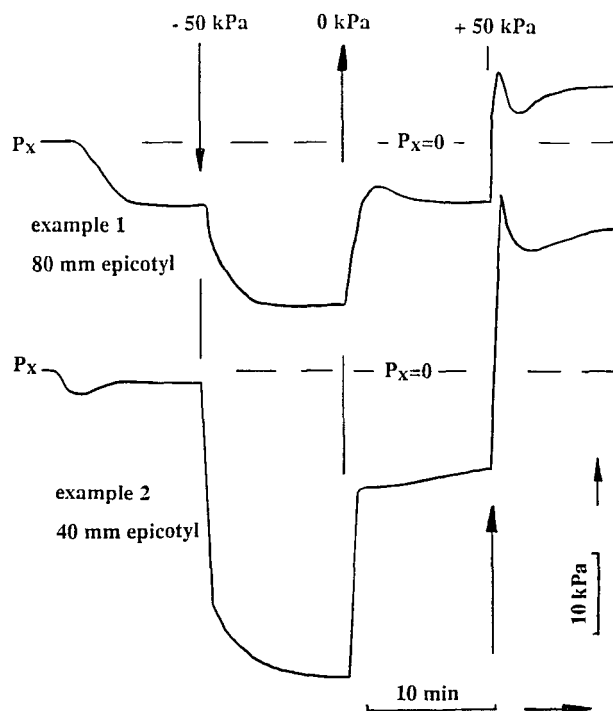


Figure 5. Examples for pressure propagation through pea epicotyl stumps of different lengths. The root and 10 mm of the epicotyl of 120-mm-long pea seedlings were placed under solution and sealed into a pressure chamber. The epicotyl outside the chamber was decapitated or cut (under water) to different lengths and connected to a pressure probe. We measured the P_x changes at the cut end of the epicotyl stumps while positive and negative pressure steps were applied to the seedling's base. As pea epicotyls increased in length, they showed an increasingly negative initial P_x and lower amplitudes of the propagated pressure steps. Examples are representative of 25 experiments with different lengths of the epicotyl outside the pressure chamber.

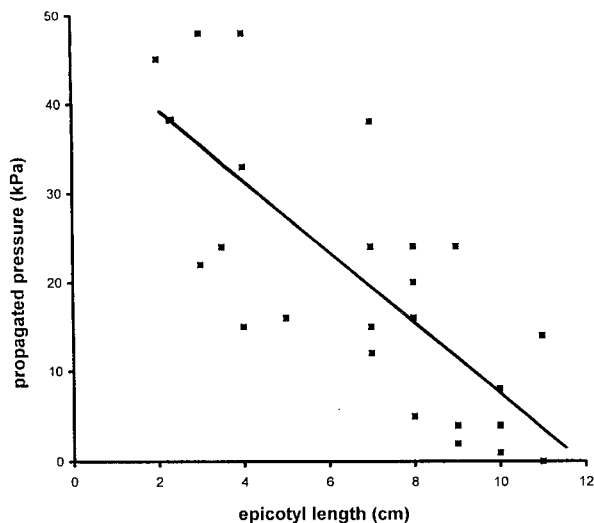


Figure 6. Regression analysis between the propagated portion of the original 50-kPa chamber pressure (positive and negative pressure steps were applied and provided an average value) and varying effective epicotyl length (the distance between the pressure chamber and the point of measurement varied between 2 and 12 cm). Note that the slope of the regression line provides an approximate value for the reduction of the P_x step in the epicotyl (about 4 kPa cm^{-1}), a value that reflects radial leaks in the xylem of pea epicotyls. The coefficient of determination is $r^2 = 0.57$, the correlation coefficient is $r = 0.75$, and the correlation is significant at $\alpha = 0.001$.

change in epicotyl ΔP_x at the electrode positions. Thus, a 50-kPa step in the chamber should create a local ΔP_x of 34 kPa at position B (30 mm), a ΔP_x of 23 kPa at position C (60 mm), and be almost completely dissipated at the hook of a 120-mm-long epicotyl.

Depolarization Depended on Size of the Applied Pressure Steps

We determined that the smallest chamber pressure step that could induce a depolarization at position B was 30 kPa or a local ΔP_x of 24 kPa (not shown). For the chamber pressures used, the depolarization at position C (rather than B) showed a complete set of changes that the electric response underwent with increasing pressure steps (Fig. 7). With increasing pressure steps (50–100 kPa) the induced depolarization decreased its lag phase from 150 to 30 s and increased its amplitude as the pressure steps increased from 50 to 80 kPa, after which it plateaued. At position B the amplitude reached its maximal value at a chamber pressure step of 60 kPa (not shown).

The lag times of the induced depolarizations increased exponentially with decreasing pressure steps at both electrode positions (Fig. 8). Depolarizations with equal lag times need higher chamber pressures at C than at B, e.g. a lag of 60 s required chamber pressures of 45 kPa for position B and chamber pressures of 90 kPa for position C. These results can be explained completely on the basis of acropetally declining ΔP_x values (see Figs. 5 and 6). The large range of different pressure steps in Figure 8 enabled us to test the likely shape of the pressure gradient in the

epicotyl. A linear gradient implies that after a parallel shift (to the left) the curve for position C should coincide with the curve for position B. This did not occur because the required shifts were larger for higher-pressure steps, and therefore it indicates an exponential P_x gradient.

Figure 8 shows that local depolarizations are timed by different local steps in P_x , which has a gradient that creates the appearance of a propagating electric signal in the epicotyl, e.g. 60 kPa caused a lag of 30 s at B and a lag of 120 s at C. The appearance of a SWP can be explained by a sequence of local depolarizations with lags timed by the P_x gradient in a leaky xylem. A SWP appears as a static phenomenon rather than the result of a self-propagating electric signal.

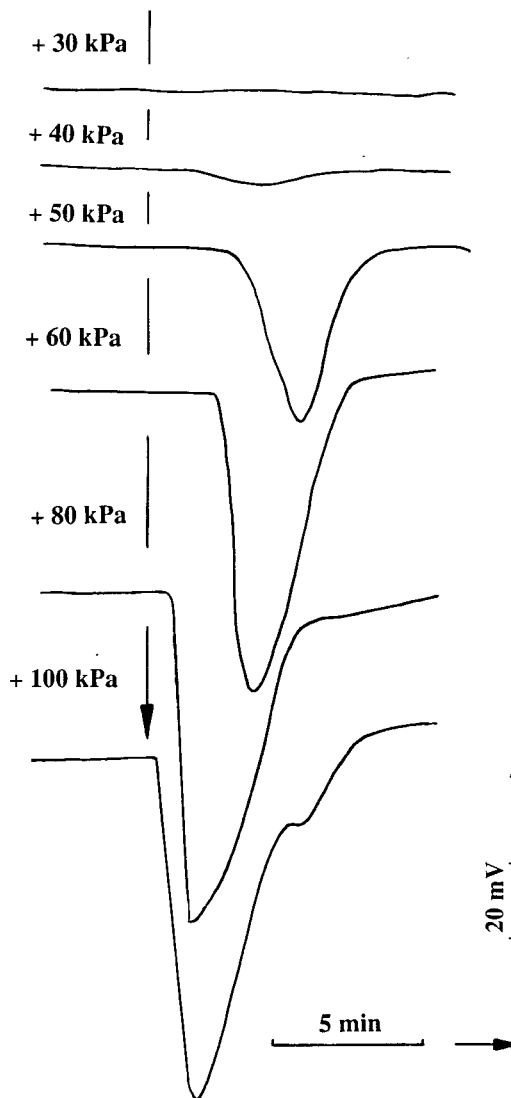


Figure 7. The effect of increasing chamber pressures upon the V_s of the epicotyl surface at a distance of 60 mm from the chamber (position C). Note that there was a minimum value of chamber pressure below which there was no induction of an electric signal. A pressure increase from 50 to 100 kPa doubled the amplitude of the depolarization and reduced the lag time from 150 to 30 s. Eight representative examples are shown out of more than 50 experiments with various chamber pressures.

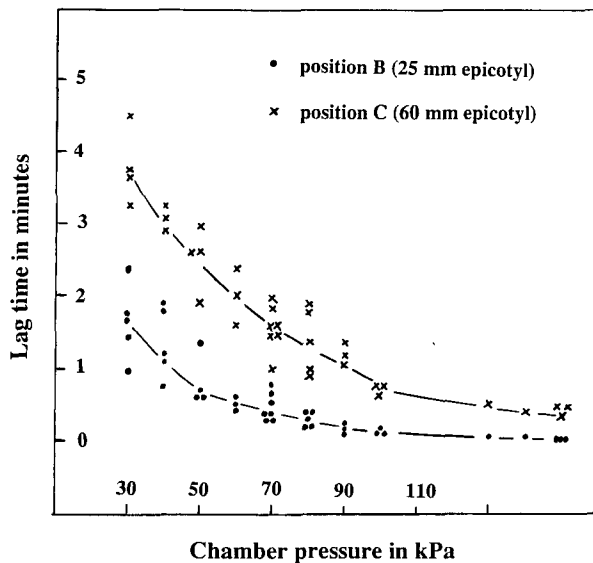


Figure 8. Dependence of the lag times in the transient depolarization of epicotyl cells at positions **B** and **C** on the size of the applied chamber pressure steps. This figure presents the complete set of all defined and measured lag times independent of the size of the induced depolarization. The lag times in both positions increase with decreasing pressure steps. Especially at smaller pressure steps we see an exponential rise in lag times, although the small step of 30 kPa was often insufficient to cause a measurable depolarization with a defined lag phase at either position **C** (see Fig. 7; only 4 of 11 experiments with 30-kPa chamber pressure showed a depolarization with a measurable lag) or at position **B** (6 of 11 experiments with 30 kPa permitted an estimate for this figure). Conditions were as in Figure 3.

DISCUSSION

The Pressure Sensitivity of Epicotyl Cells

A transient depolarization can be considered as a normal V_m response of plant cells to a change in P_x and turgor pressure (e.g. Gunar and Kudasova, 1968; Goring et al., 1979; Stahlberg and Polevoy, 1979). Under natural conditions turgor changes are likely to be implemented by a change in P_x pressure rather than in the concentration of intercellular solutes (e.g. Nonami and Boyer, 1990). An increase in P_x converts to a transient turgor pressure increase (Westgate and Steudle, 1985; Malone and Stankovic, 1991; Frensch and Hsiao, 1994) and then results in a transient depolarization. The application of a pressure step of 30 kPa to the root xylem converts to a ΔP_x of only 25 kPa at position **B** of the pea epicotyl, which sufficed to induce a depolarization in the epidermis cells. A chamber pressure step of 100 to 250 kPa was needed, however, to cause detectable, small, and slow turgor changes of about 10 to 25 kPa in epidermal cells of pea epicotyls when measured at the same distance of 30 mm from the pressure chamber (R. Stahlberg and D.J. Cosgrove, unpublished data). At the same distance the turgor change induced by a ΔP_x of 25 kPa would be less than 3 kPa and, hence, undetectable with a pressure probe. We infer that turgor pressure steps as small as 10 kPa cause large depolarizations in epicotyl cells of intact pea seedlings and reveal a surprisingly high hy-

draulic sensitivity of epicotyl cells in intact plants. The small size of the minimal electrogenic ΔP_x (25 kPa) supports the conclusion that SWPs are more likely to occur under natural circumstances of plant life than previously realized (Stahlberg and Cosgrove, 1996).

The Mechanism of SWP Propagation

Three mechanisms were suggested for the propagation of a SWP (see the Introduction). The first possibility was that the SWP reflects the axial transport of a wound-released, electrogenic substance in the xylem. The use of a pressure chamber, minimal chamber pressures, and other evidence (Stahlberg and Cosgrove, 1992, 1996) largely excludes this possibility in pea epicotyls. The second mechanism considered was the electrotonic self-propagation of a depolarizing electric signal. We showed that the SWP passed through a KCN-treated epicotyl position, inducing normal depolarizations before and after, but not in the treated area. A self-propagating electric signal should not be able to pass through an epicotyl section where its generation is suppressed. The third suggestion was that a SWP reflects the axial passage of a hydraulic signal. A SWP with a propagation speed of 20 to 30 mm min^{-1} cannot reflect the axial passage of a pressure wave with a rate of at least 100 mm s^{-1} (as inferred from a GR change that occurred within 1 s of pressure application).

The fourth possibility to consider is that a SWP reflects the radial rather than axial pressure propagation from the xylem to the epidermal cells and the stem surface. Whereas axial pressure propagation in the xylem is very rapid, it takes much more time for radial pressure propagation in the apoplast. This time increases with the distance of the cells from the xylem (Westgate and Steudle, 1985). After a pressure step of 100 kPa, a cell at a distance of 0.8 mm from the xylem took more than a minute to complete its shallow turgor increase, a value that is reasonably close to the range of lag times to the SWP measured in our experiments. We therefore suggest that response times of the turgor increase related to the lag times of the depolarization and that the kinetics of a SWP reflect the slow, radial propagation of ΔP_x in the epicotyl.

Acropetally Increasing Lag Phases of Local Depolarizations Create the Appearance of a Propagating Electric Signal

The leakiness of the epicotyl xylem creates a situation in which any local increase in P_x (due to root pressure, root excision, incision in the epidermis, embolism, or insect bites) will decline with increasing distance and so create a pressure gradient in xylem and intercellular spaces of the pea epicotyl. The acropetally declining size of the P_x change leads the epidermal cells to undergo local depolarizations with increasing lag times and reduced amplitudes. This essentially static scenario has the same appearance as a depolarization propagating along the pea epicotyl. The results show clearly that pea epicotyl responded to a sudden P_x step with an electric signal that was measured both in size and time. Apparently, plants are capable of chang-

Table I. Comparison of induction, propagation, and electric mechanism of APs and SWP

Signal	APs	Reference	SWPs	Reference
Direction	Depolarization		Depolarization	
Duration	Short spikes (<10 s)	Davies (1987); Davies et al. (1991); Hodick and Sievers (1988); Houwinck (1935); Opritov (1978); Stahlberg and Cosgrove (1994); Umrath (1959); Wildon et al. (1992); Zimmerman and Beckers (1978)	Long transients (10 s to several min)	Alarcon and Malone (1994); Boari and Malone (1993); Houwinck (1935); Julien et al. (1991); Kawano (1955); Malone (1992); Sibaoka (1953); Stahlberg and Cosgrove (1992, 1995); Umrath (1959)
Induction				
	Turgor pressure change	Wendler et al. (1983); Zimmerman and Beckers (1978)	Rise in turgor pressure after positive hydraulic signal	Malone and Stankovic (1991); Stahlberg and Cosgrove (1995, 1996)
Chemicals (?)	Depolarization Unidentified	Sibaoka and Tabata (1981) Umrath (1959)	Raw extract (?), systemin, cholate	Cheeseman and Pickard (1977a); Moyen and Johannes (1996); Stahlberg and Cosgrove (1996)
Environmental factors	Light; wounding, cold + heat treatment	Cheeseman and Pickard (1977b); Davies et al. (1991); Opritov (1978); Opritov and Retivin (1982); Stahlberg and Cosgrove (1994); Wildon et al. (1992)	Insect bites, wounding, bending embolism, heat treatment	Alarcon and Malone (1994); Boari and Malone (1993); Davies et al. (1991); Frachisse et al. (1985); Houwinck (1935); Julien et al. (1991); Kawano (1955); Malone (1992); Malone and Stankovic (1991); Roblin and Bonnemain (1985); Stahlberg and Cosgrove (1992, 1995); Tsaplev and Zatssepina (1980); Umrath (1959)
Propagation				
Mode	Electrotonic	Opritov and Retivin (1982); Sibaoka and Tabata (1981); Tabata and Sibaoka (1987)	Nonelectrotonic	This paper
Path	In phloem	Fromm and Bauer (1994); Opritov (1978); Opritov and Retivin (1982)	In xylem and apoplast	Stahlberg and Cosgrove (1992, 1995)
Rates	10 to 70 mm s ⁻¹	Fromm and Bauer (1994); Stahlberg and Cosgrove (1994); Tabata and Sibaoka (1987); Umrath (1959); Wildon et al. (1992)	0.1 to 10 mm s ⁻¹	Roblin and Bonnemain (1985); Sibaoka (1953); Stahlberg and Cosgrove (1992, 1994, 1996)
In same species	Faster than SWP	Davies et al. (1991); Houwinck (1935); Roblin and Bonnemain (1985); Sibaoka (1953)	Slower than AP	Davies et al. (1991); Houwinck (1935); Roblin and Bonnemain (1985); Sibaoka (1953)
Mechanism	Activation of Ca ²⁺ , Cl ⁻ , and K ⁺ channels	Hodick and Sievers (1988); Kourie (1994); Lunevsky et al. (1983); Wayne (1994); Zimmermann and Beckers (1978)	Inactivation of H ⁺ pumps	Julien et al. (1991); Stahlberg and Cosgrove (1992, 1996)

ing electric fields in a spatial, timely, well-coordinated manner, the importance of which is completely unknown.

Propagation Rates in Other Plants

The application of modest chamber pressures around 60 kPa created a pressure gradient in the pea epicotyl that optimized the time separation of the depolarization between the electrode positions. Under such conditions pea

seedlings generate SWPs with the relatively slow, apparent rate of 15 to 30 mm min⁻¹, which allowed us to conduct this kinetic study on the mechanism of their propagation. SWP rates reported from other plants are generally higher, e.g. 1 to 4 mm s⁻¹ in *Tradescantia* (Tsaplev and Zatssepina, 1980) and tomato seedlings (Wildon et al., 1992). SWPs induced by heat stimulation in wheat leaves spread so quickly that they developed simultaneously at all positions

along the leaves, which made it impossible to determine a distinguishable rate of travel (Malone, 1992). Burning an adjoining leaf or applying 5 bars external pressure produced similar changes in turgor pressure (Malone and Stankovic, 1991), which indicates that the high speed of the SWP in wheat leaves was due to the appearance of considerably higher pressure steps than occurred in our experiments.

APs and SWPs Follow Different Mechanisms

Turgor pressure changes may cause APs as well SWPs (e.g. Zimmermann and Beckers, 1978; Wendler et al., 1983; Stahlberg and Cosgrove, 1994). With perhaps few exceptions (Gradmann, 1976; Wildon et al., 1992), most APs are based upon activity changes of Cl^- , K^- , and Ca^{2+} ion channels (e.g. Hodick and Sievers, 1988; Fromm and Bauer, 1994; Kourie, 1994; Wayne, 1994), whereas SWPs follow an activity change of H^+ pumps (Stahlberg and Cosgrove, 1996). The signals differ also in their mode of propagation. Whereas APs show an electrotonic mechanism (Sibaoka, 1953; Sibaoka and Tabata, 1981) and use the phloem to propagate (Opritov, 1978; Opritov and Retivin, 1982; Fromm and Bauer, 1994), at least for the experiments and materials reported in this paper, SWPs are spread by a pressure change in the xylem. The quantitative description of the hydraulic induction as well as the identification of the mechanism of SWP propagation represents considerable progress in our understanding of this signal and allows, to our knowledge, the first mechanistic comparison with APs (Table I). The characterization of SWPs and APs as two distinct types of electric long-distance signals provides new testable criteria for the identification of propagating electric signals.

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