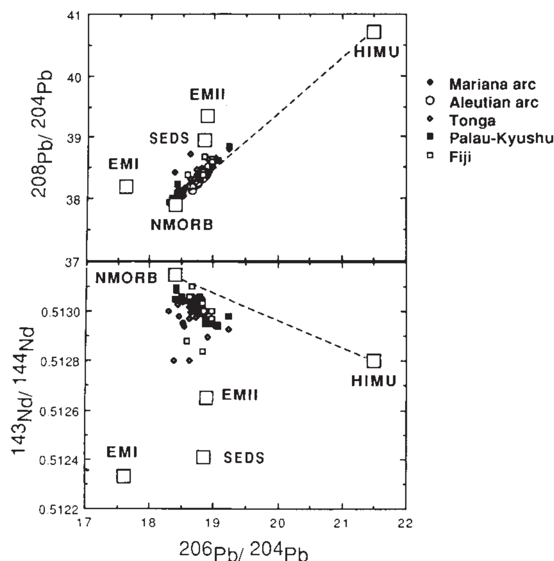

FIG. 4 $^{208}Pb/^{204}Pb$ and $^{143}Nd/^{144}Nd$ plotted against $^{206}Pb/^{204}Pb$ showing relationship of island-arc lavas from the Mariana arc[15,16,32], Fiji[3], the Aleutian arc[2,33], Tonga[14] and the Palau-Kyushu arc[5,17-19,31] to mixtures of NMORB mantle and the HIMU mantle endmember (dashed line). Approximate values for enriched mantle endmembers EMI and EMII[8] and Pacific sediment (SEDS)[15,16,32] are also shown.

elements such as Nb, Zr, La and Nd relative to Rb, Pb, Ba and Sr[28], whereas arc magmas show precisely the opposite pattern. The requisite contribution from HIMU must be small compared with that from other source materials, and/or early melting of the HIMU component during basin magmatism must alter these incompatible element relationships. According to Fig. 4, as much as 86% of the Nd, but only 26% of the Pb in arc magmas comes from the HIMU component rather than NMORB peridotite. Because these two components, as sampled by OIB, have demonstrably the same Pb/Nd ratio[8], their trace element abundances have not been maintained in the sources of island-arc basalts. An additional high-Pb/Nd component, such as fluids expelled from subducted MORB, may complete the picture. □

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Spring phytoplankton blooms in the absence of vertical water column stratification

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THE spring phytoplankton bloom in temperate and boreal waters represents a pulsed source of organic carbon that is important to ecosystem productivity[1] and carbon flux[2] in the world ocean. It is widely accepted that the seasonal development of a thermocline, in combination with increasing solar elevation in spring, is requisite for the development of the bloom in shelf and open ocean environments[3-7]. Here we report results for the offshore waters of the Gulf of Maine which suggest that the spring bloom can precede the onset of vertical water column stability, and may even be a contributing factor in the development of the thermocline. Deep penetration of light in relatively clear, late-winter waters, and weak, or absent, wind-driven vertical mixing, appear to support cell growth rates that overcome the vertical excursion rates in the neutrally stable water column, leading to a bloom. Phytoplankton forms typical of a spring bloom, including gelatinous colonies and chains, may contribute to the cells' ability to maintain a vertical position in a water column lacking stability.

During the winter months in mid- to high-latitude waters, low solar elevations and *in situ* marine light levels, along with deep turbulent vertical mixing of the upper water column, maintain phytoplankton production at its lowest levels of the year. This is despite high concentrations of inorganic nutrients in the surface waters that result from winter convective mixing with deep waters. Many have argued that as the seasonal thermocline develops and phytoplankton cells in the upper mixed layer become isolated above some 'critical depth', phytoplankton photosynthesis exceeds respiration and the bloom commences[3-7]. Field studies have shown that a depth-averaged, vertically integrated irradiance value of about 20.9 W m^{-2} defines this critical depth[4,8-14]. The depth of this critical light intensity increases with solar elevation as spring progresses and, at some point, it intersects with the bottom in inshore waters, or with the depth of the developing upper mixed layer created above the thermocline in deeper offshore waters on the shelf and in the open ocean[3-14].

The amount of light available for photosynthesis that reaches a particular depth (E_z) is described by

$$E_z = E_0(1-r)\exp\left[\left[\int_0^z -K_z\,dz\right]\right] \quad (1)$$

where E_0 is the solar radiation reaching the sea surface (W m^{-2}), r is the reflectance at the air-sea boundary ($r \approx 0.021$ averaged over the visible spectrum), K_z is the depth-dependent diffuse attenuation coefficient (m^{-1}), and z is the depth (m). As E_0 is the integrated irradiance over the entire visible light spectrum, K_z is expected to change with depth as the ocean water mixture (the combination of pure water and any absorbing particulate and dissolved material) selectively removes some wavelengths near the surface and transmits other wavelengths to greater depths. The depth-dependence of K_z has been described in terms of an arc-tangent model[15]

$$E_z = E_0(1-r)\exp(-k_1 z)[1 - k_2 \tan^{-1}(k_3 z)] \quad (2)$$

where the coefficients k_1, k_2 and k_3 are derived from measured irradiance profiles. The daily irradiance at the sea surface in the

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absence of cloud cover may be expressed as

$$E_0 = \alpha + \beta \sin \omega t \quad (3)$$

where α is the daily irradiance during the winter solstice; β is the difference in daily irradiance between the winter and summer solstice; $\omega = \pi/365\ \mathrm{d}^{-1}$; and t is time (d) past the winter solstice (21 December). For the Gulf of Maine, $\alpha \approx 59.9\ \mathrm{W\,m^{-2}}$ and $\beta \approx 169.4\ \mathrm{W\,m^{-2}}$ (ref. 16). The depth-averaged, vertically integrated irradiance in the sea, E^*, between the ocean surface and the bottom of a surface mixed layer at depth z_m describes the average amount of light experienced by a phytoplankton population within the mixed layer, and is defined as

$$E^* = 1/z_m \int_0^{z_m} E_z\, \mathrm{d}z \quad (4)$$

Vertical light profiles were measured in the offshore Gulf of Maine 21–30 April 1991 using a LiCor submersible spherical radiometer. These data were assumed to represent pre-bloom, clear water conditions in early spring; phytoplankton chlorophyll *a* values at this time were less than $1.0\ \mathrm{mg\,m^{-3}}$. The corresponding k coefficients in equation (2) were derived from irradiance profiles measured at these non-bloom Gulf of Maine stations; $k_1 = 0.089\ \mathrm{m^{-1}}$, $k_2 = 0.381$, $k_3 = 1.72\ \mathrm{m^{-1}}$. E^* was then computed at increments of 1 m bertween the surface and 100 m for each day between the winter solstice (21 December) and the summer solstice (21 June). On each day the critical depth was identified as that for which $E^* = 20.9\ \mathrm{W\,m^{-2}}$. These simulations were then compared with field observations of water column structure during the spring phytoplankton bloom we observed during research cruises in 1990 and 1992.

A spring bloom was observed in offshore Massachusetts Bay in the western Gulf of Maine in March of 1990, which was occurring in the absence of vertical stratification (Fig. 1*a*, *b*). The water column was vertically isopycnal from the surface to 70 m, with no change in density (σ_t) except very near the bottom. The chlorophyll *a* concentrations were $\sim 4\ \mathrm{mg\,m^{-3}}$, and the diffuse attenuation coefficients (K_z) ranged from $\sim 0.4\ \mathrm{m^{-1}}$ near the surface to $0.25\ \mathrm{m^{-1}}$ at 40 m. The light field in early March, based on our calculations for non-blooming Gulf of Maine waters in April of 1991, would dictate a pre-bloom critical depth of about 38 m (where $E^* = 20.9\ \mathrm{W\,m^{-2}}$), but the bloom was progressing despite the lack of any vertical water column stratification shallower than 70 m. The deep chlorophyll fluorescence in Fig. 1*a*, *b* seems to be the result of sinking aggregates of phytoplankton cells, as described earlier[17-21].

In early April of 1992 the spring bloom was underway throughout most of the Gulf of Maine, and was occurring at stations with little or no vertical stratification. Density differences in the upper water column ($\Delta\sigma_t$)were $0.04\ \mathrm{kg\,m^{-3}}$ from 0 to 100 m at the stations in Fig. 2*a* and *b*, whereas the calculated critical depth in these waters for this date was about 43 m. The chlorophyll *a* concentrations exceeded $2.5\ \mathrm{mg\,m^{-3}}$. Not all stations were neutrally stable, and the bloom was also underway at stations with salinity stratification at depths near, or less than, the critical depth, as shown in Fig. 2*c*. The deep extension of the chlorophyll fluorescence in Fig. 2*a* and *b* also shows evidence of sinking aggregates of cells.

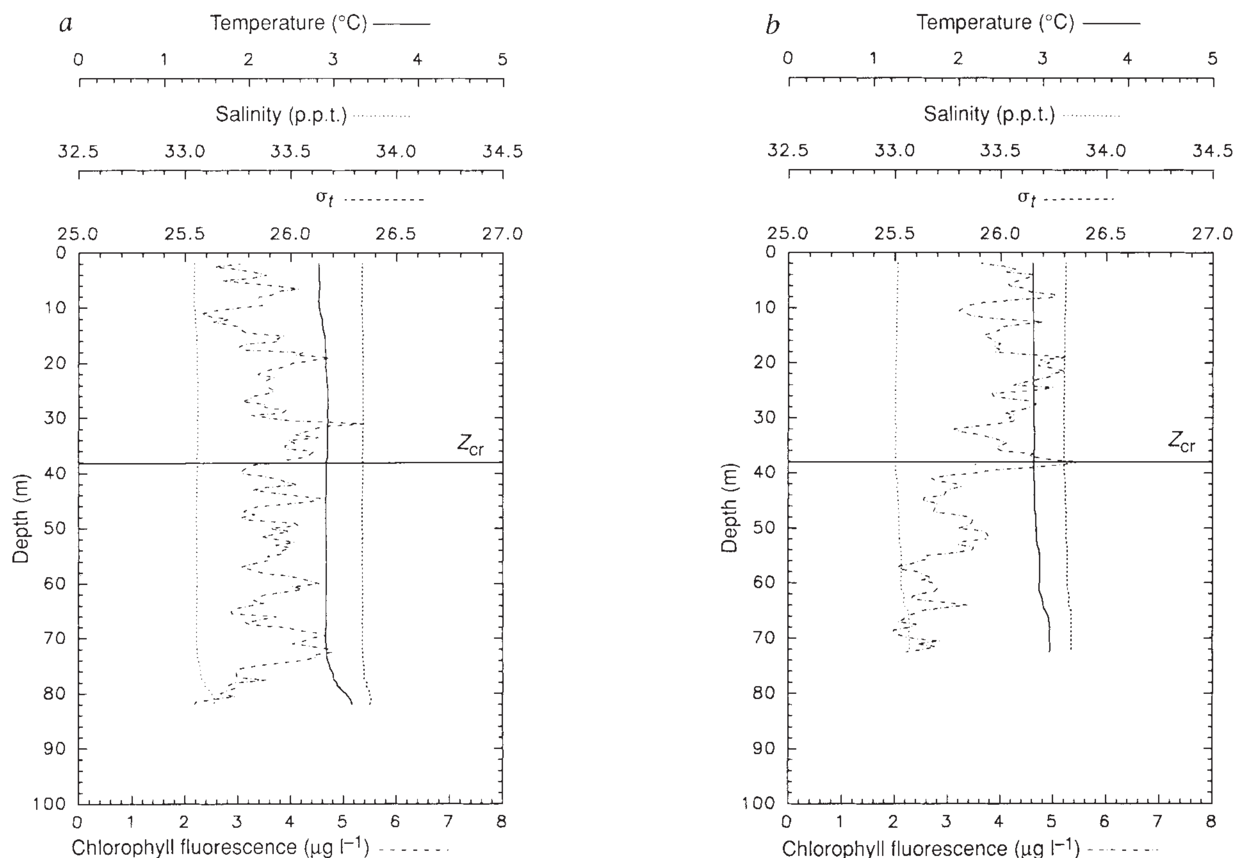

FIG. 1 Vertical profiles showing bloom levels of chlorophyll in the absence of vertical stratification and a critical depth (Z_{Cr}) of 38 m. Temperature (°C), salinity (p.p.t.), density (σ_t kg m^{-3}) and *in situ* chlorophyll fluorescence (mg chlorophyll *a* m^{-3}) were measured at stations in Massachusetts Bay in the western Gulf of Maine on 6 March 1990 using a Neil Brown Mark III CTD with a Sea Tech *in situ* fluorometer. The error in the *in situ* chlorophyll fluorescence was about ±1 mg m^{-3} chlorophyll *a*, based on acetone extractions of water samples. *a*, Measurements taken at 42° 19.9′N, 70° 25.8′W, about 20 nautical miles west of Boston, bottom depth 86 m, and *b*, at 42° 18.4′N, 70° 32.9′W, about 18 nautical miles west of Boston, bottom depth 74 m. The dominant phytoplankton species at these two stations, determined from microscopic examinations of water samples, were *Detonula confervacea*, *Thalassiosira pseudonana* and *Chaetoceros socialis*[27]. The spiked fluorescence traces are apparently the result of flocculated cells, which can occur at densities of ~10 per litre (ref. 21). The horizontal lines at 38 m (Z_{Cr}) indicate the critical depth.

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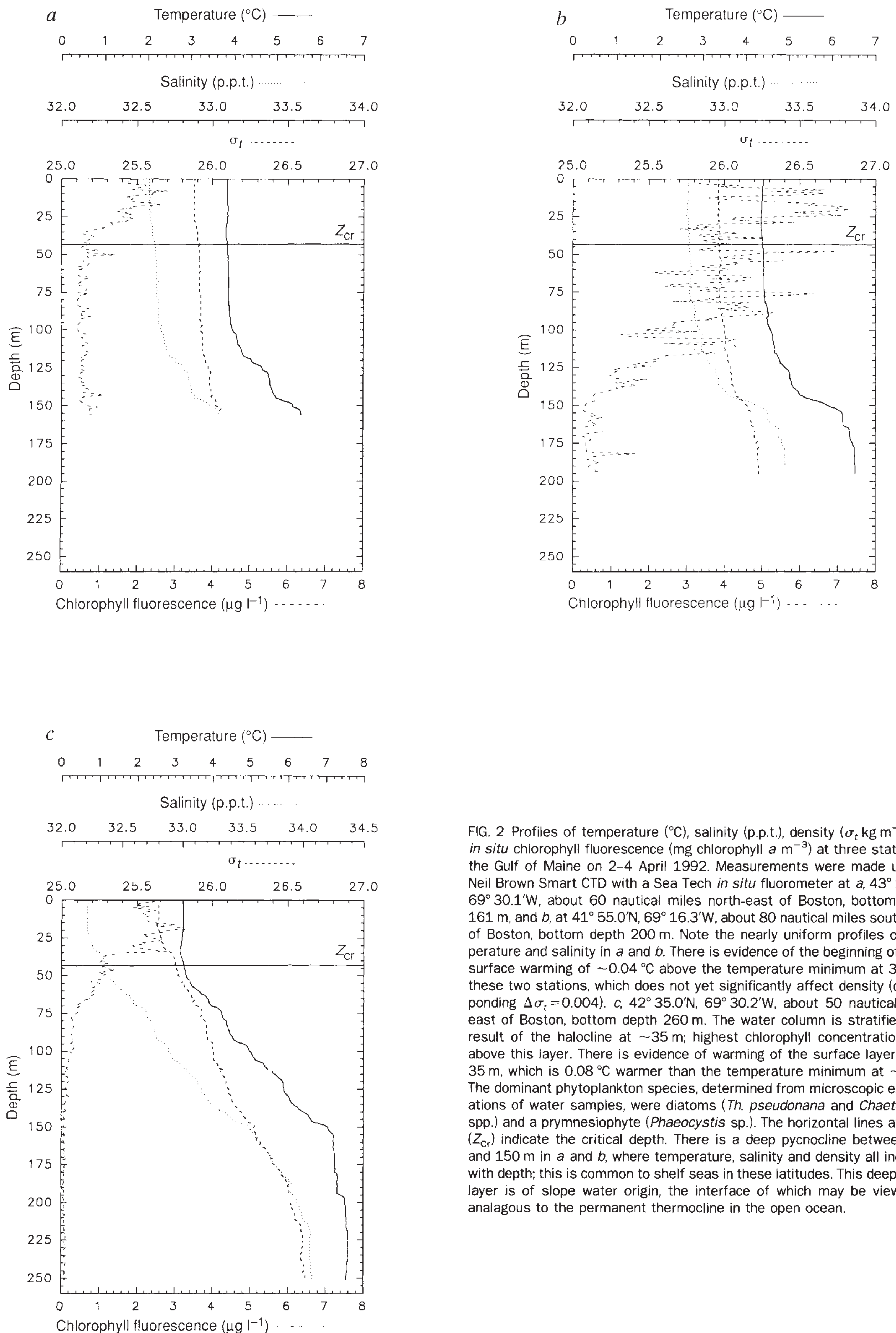

FIG. 2 Profiles of temperature (°C), salinity (p.p.t.), density (σ_t kg m^{-3}) and *in situ* chlorophyll fluorescence (mg chlorophyll *a* m^{-3}) at three stations in the Gulf of Maine on 2–4 April 1992. Measurements were made using a Neil Brown Smart CTD with a Sea Tech *in situ* fluorometer at *a*, 43° 20.0′N, 69° 30.1′W, about 60 nautical miles north-east of Boston, bottom depth 161 m, and *b*, at 41° 55.0′N, 69° 16.3′W, about 80 nautical miles south-east of Boston, bottom depth 200 m. Note the nearly uniform profiles of temperature and salinity in *a* and *b*. There is evidence of the beginning of slight surface warming of ~0.04 °C above the temperature minimum at 30 m at these two stations, which does not yet significantly affect density (corresponding $\Delta\sigma_t = 0.004$). *c*, 42° 35.0′N, 69° 30.2′W, about 50 nautical miles east of Boston, bottom depth 260 m. The water column is stratified as a result of the halocline at ~35 m; highest chlorophyll concentrations are above this layer. There is evidence of warming of the surface layer above 35 m, which is 0.08 °C warmer than the temperature minimum at ~35 m. The dominant phytoplankton species, determined from microscopic examinations of water samples, were diatoms (*Th. pseudonana* and *Chaetoceros* spp.) and a prymnesiophyte (*Phaeocystis* sp.). The horizontal lines at 43 m (Z_{cr}) indicate the critical depth. There is a deep pycnocline between 125 and 150 m in *a* and *b*, where temperature, salinity and density all increase with depth; this is common to shelf seas in these latitudes. This deep-water layer is of slope water origin, the interface of which may be viewed as analagous to the permanent thermocline in the open ocean.

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Although our results are from a continental shelf sea, it is important to note that upper water column physical processes over deep shelf waters are the same as in the open ocean, where there are anecdotal accounts of similar phytoplankton blooms in the absence of vertical stratification. Earlier workers in the North Atlantic have observed spring phytoplankton blooms that apparently began before the development of the thermocline, prompting the suggestion of transient thermoclines[22-24]. One study reported that a top-to-bottom temperature difference of as little as 0.2 °C in shelf waters apparently provided sufficient stabilization of the water column to allow the bloom to commence[11]. In the Gulf of Maine, a density difference of 0.1–0.2 $\Delta\sigma_t$ in the top 30 m has been assumed to be required for the initiation of the spring bloom[5]. None of these earlier studies provide conclusive evidence that the development of the thermocline or water column stability preceded the onset of the bloom, though examples do exist. Our results suggest that vertical water column stability may not be a prerequisite to maintain phytoplankton cells above the critical depth. The deepening penetration of light in the clear winter waters during the spring months, in conjunction with absent, or weak, vertical wind mixing, could maintain cell growth rates that overcome the vertical excursion rates in the neutrally stable water column, thus leading to a bloom. Once begun, the bloom may enhance the warming of the surface waters (Fig. 2) by virtue of the light scattering and absorption properties of the phytoplankton particles[25,26]. Thus, in some instances, the development of the thermocline may be initiated by, rather than serve as a prerequisite for, the spring phytoplankton bloom. □

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Electrical signalling and systemic proteinase inhibitor induction in the wounded plant

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THE wound response of several plant species involves the activation of proteinase inhibitor (*pin*) genes and the accumulation of *pin* proteins at the local site of injury and systemically throughout the unwounded aerial regions of the plant[1,2]. It has been suggested that a mobile chemical signal is the causal agent linking the local wound stimulus to the distant systemic response, and candidates such as oligosaccharides[3], abscisic acid[4] and a polypeptide[5,6] have been put forward. But the speed of transmission is high for the transport of a chemical signal in the phloem. The wound response of tomato plants can be inhibited by salicylic acid[7] and agents like fusicoccin that affect ion transport[8], and wounding by heat[9] or physical injury produces electrical activity that has similarities to the epithelial conduction system[10] used to transmit a stimulus in the defence responses of some lower animals[11]. Here we design experiments to distinguish between a phloem-transmissible chemical signal and a physically propagated signal based on electrical activity. We show that translocation in the phloem of tomato seedlings can be completely inhibited without effect on the systemic accumulation of *pin* transcripts and *pin* activity, and without hindrance to propagated electrical signals.

Mechanical damage applied to the lamina of one of the cotyledons of a tomato seedling with one expanded leaf (Fig. 1*a*) leads to electrical activity (Fig. 1*b*) which can be detected by extracellular electrodes placed on the stem and on the petiole of leaf 1, morphologically the lowest (first-formed) leaf (Fig. 1*a*). The electrical activity propagates beyond the cotyledon and through the plant at a speed of between 1 and 4 mm s^{-1}. We refer to this activity as a systemic electrical signal. Chilling the petiole of the wounded cotyledon to 3 °C has little effect on the electrical signal recorded on the petiole of leaf 1 (Fig. 1*c*), a result that is consistent with observations on action potential conduction at low temperature in cold-blooded animals[12] and plants[13]. Chilling a petiole is, however, a recognized means of inhibiting phloem transport[14]. In these experiments chilling is necessary, given that the maximum reported speeds of phloem transport[15] (35–250 mm min^{-1}) are such that a chemical signal might exit the wounded cotyledon in a time comparable to that for an electrical signal. As the effects of chilling and their duration are dependent on plant species[14], we analysed the effect of the treatment on tomato seedlings. As shown in Fig. 2, chilling of the cotyledonary petiole to 4 °C completely stops translocation of ^{11}C-labelled photosynthate through the chilled region for a period of at least ten minutes before a spontaneous recovery. Chilling the cotyledonary petiole to 0.5 °C extends the time for spontaneous recovery to about 25 minutes. Similar results are obtained on chilling the petiole of leaf 1 to 3 °C, except that translocation is inhibited for at least 20 minutes. Given the spontaneous recovery of the petiole tissue from chilling, it was necessary to excise the wounded cotyledon within the period in which phloem transport is inhibited in order to prevent any delayed movement of a chemical signal from the wound-site through the phloem. Leaf excision alone has little effect on *pin* induction in tomato plants[7].

In the experiments shown in Table 1, *pin* activity was assayed by the inhibitory effect of leaf extracts on chymotrypsin activity (Table 1 legend). Untreated tomato seedlings (line 1) contain negligible *pin* activity and the chymotrypsin is not inhibited.

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