23 Long-Distance Signal Transmission in Trees

Stefano Mancuso, Sergio Mugnai

Abstract Long-distance transmission of signals is a critical event in the life of trees. Many physiological studies have deduced that hormone-like substances together with hydraulic/electrical signals mediate this important function of the plant life. However the nature of the complex network of signalling in trees has remained essentially unexplored. Recent molecular and genetic studies offer new approaches to understanding the mechanisms underlying the transmission of signals.

23.1 Introduction

The ability to sense and respond to environmental parameters is one common feature of living being. This talent is particularly significant in land plants because of their necessity to manage all the environmental information and stimuli without escaping. Among plants, trees, for their necessity to respond in a short time to environmental stimuli despite the often big dimensions, are the most obvious and interesting subjects of study for the long-distance signal transmission.

Trees live in a continuously changing environment and although not all parts of the tree are exposed to the same stimuli at the same time, different parts of it respond in a coordinated fashion, demonstrating the existence of communication between various regions of the tree. For years, researchers have concentrated their efforts on the study of chemical (hormonal) signals in trees, neglecting the fact that plants also use and rely on electrical and hydraulic signals. In addition, it is especially in big plants such as trees that the need for signals other than hormones becomes more important. Considering the large leaf area of a tree, enormous amounts of chemicals would need to be synthesized and transported in order to respond to a signal coming from the roots. In contrast, both electrical and hydraulic signals consume no chemicals in their propagation.

Here, "long distance" will refer to signals running for distances that cannot be covered in reasonable times (a few hours) by diffusion in the aqueous phase, and that often have to cover several metres as in the cases of root-to-shoot communication. For a long time, plant physiologists have presumed that signalling systems in plants must involve transport of "something" through the vascular system, effectively ignoring any other kind of signal

like the electrical and hydraulic ones, whose importance is today increasingly confirmed by experimental results as is widely illustrated in many chapters of this book.

Trees may also transmit a multiplicity of signals to neighbouring organisms. These comprise the myriad of fatty acid derivatives, benzenoids, terpenoids and other scented substances emitted from flowers mainly to attract pollinators (Knudsen et al. 1993), but also the emission of isoprene (Loreto and Velikova 2001) or other volatiles from foliage or other vegetative parts of the trees (Paré and Tumlinson 1999). In the following pages, five different potential mechanisms for long-distance signalling in plants will be discussed:

1. Transmission of chemicals

2. Hydraulic signals

3. Electrical signals

4. Airborne flow of volatile messengers

5. Colour signals

23.2
Transmission of Chemicals

The roots of higher plants comprise a metabolically active and largely unexplored biological frontier. Their prime features include the ability to synthesize a remarkably diverse group of metabolites, and to adjust their metabolic activities in response to different abiotic and biotic stresses. Various experiments have shown that stomatal responses are often more closely linked to soil moisture content than to leaf water status, indicating a likely role of root-sourced chemical signals (e.g. abscisic acid, ABA) in the regulation of stomatal conductance in response to soil drying. Much is known about the role of ABA in closing stomata, as well as its production in dehydrating roots and its circulation in herbaceous species (Chaves et al. 2002). It is unclear, however, whether this is also true in mature trees, where long-distance transport of chemical signals from the roots to the shoots would be required (Jackson et al. 1995). In many instances the dynamics of ABA in trees is linked to changes in stomatal conductance (Blake and Ferrell 1977; Khalil and Grace 1993; Liang et al. 1997; Loewenstein and Pallardy 1998a,b; Maurel et al. 2004), but these results derive mostly from works with potted plants and/or in controlled conditions, and are species-specific (Wartinger et al. 1990; Tenhunen et al. 1994; Correia et al. 1995; Triboulot et al. 1996; Sturm et al. 1998; Niinemets et al. 1999). Particularly important

in much of the root-signal research in trees has been the use of split-root culture, where individual plants are grown with the root system divided among two or more separated soil volumes with independent moisture content. This situation shows that having a portion of the roots in dry soil can trigger strong stomatal closure even when shoot water potential does not decline, strongly supporting the hypothesis of a chemical signal derived from roots triggering stomatal closure (Gowing et al. 1990; Stoll et al. 2000; Augè and Moore 2002; Maurel et al. 2004).

23.2.1
From Where Does ABA Come?

It has been suggested that increased ABA delivery by the fraction of roots growing in the drying soil, rather than an increase in shoot xylem sap ABA concentration, is the signal for stomatal closure. Many studies have shown that, with increasing water stress, ABA is released from root tips into the transpiration stream and transported to the leaves, where it triggers stomatal closure (Khalil and Grace 1993; Triboulot et al. 1996; Fort et al. 1998). However, Fort et al. (1997) reported no increase in ABA delivery to the shoots of *Quercus* seedlings subjected to soil drying even though root xylem sap ABA concentration was increased and stomatal conductance was decreased. The importance of root-originated ABA in stomatal control, as well as the apparent sensitivity of stomatal conductance to root-originated ABA, may vary with genotype, within genotypes as a function of phenotypic plasticity, or with short-term changes in environmental parameters. Furthermore, apparent sensitivity of stomatal conductance to xylem sap ABA concentration decreases with time in water-stressed plants (Correia et al. 1995).

23.2.2
How Much ABA Is Involved in the Response of Trees to Drought?

According to field studies, a threshold response of stomata to xylem sap ABA concentration may exist, above which there are disproportionate increases in stomatal closure with xylem sap ABA concentration. This xylem sap ABA concentration was 500 nM in *Pinus* (Sturm et al. 1998) and *Ceanothus* (Tenhunen et al. 1994) but 200 nM in *Prunus* (Wartinger et al. 1990), indicating the existence of species differences in the stomatal control by ABA. Maximum ABA concentrations were only on the order of 100−150 nM in the study of Triboulot et al. (1996) and reached values of 300−350 nM in *Tilia* and 200–220 nM in *Populus* (Niinemets et al. 1999). Augé et al. (2000) found different values in xylem sap ABA concentration, from 600 to

2,000 nM during the season. The peak xylem sap ABA concentration found by Perks et al. (2002) during a period of severe drought (600 µmol m^{-3}) was of the same order of magnitude as previously reported in mature trees of other conifer species (Wartinger et al. 1990; Triboulot et al. 1996; Sturm et al. 1998), but no significant increase in ABA flux was recorded. Fluxes of ABA remained between 10 and 100 pmol m^{-2} s^{-1} in the work of Augé et al. (2000). Sap flow velocities recorded on a 41 year-old *Pinus* by Perks et al. (2002) are similar to those reported for mature conifer trees of other species (130 cm day^{-1} at 1 m and 240 cm day^{-1} at 9 m in water-stressed plants): data from Milburn (1979) for *Pinus* equate to a rate of 86 cm day^{-1} and data from Köstner et al. (1996) for *P. sylvestris* equate to a rate of 204 cm day^{-1}. During the period of severe drought, Perks et al. (2002) estimated that the time taken for a signal to travel from the roots to the crown increased to more than 6 weeks. These data support the conclusion of Schulze (1991) that "in conifers a root signal transported in the xylem may be too slow to be effective".

23.2.3
ABA and Xylem Sap pH

Some authors have suggested that *g* in herbaceous plants might be regulated by xylem sap pH (Thompson et al. 1997; Wilkinson and Davies 1997) or that stomatal sensitivity to ABA concentration might be modified by xylem sap pH (Jia and Zhang 1997; Zhang et al. 1997): pH gradients in the leaf control ABA distribution in the leaf and ABA concentration at guard cells, and thereby influence stomatal aperture. Results in trees cannot support this hypothesis, as stronger correlations of *g* with ABA concentration than with pH of xylem sap have been observed by Loewenstein and Pallardy (1998a,b). Augé et al. (2000) also found no significant association of *g* values with xylem sap pH.

23.3
Hydraulic Signals

Hydraulic pressure signals are propagating changes in water pressure inside plant tissues (Malone 1996). Plant tissues have plenty of hydraulic connections mainly composed of xylem, and they also provide a pathway for long-distance transmission of hydraulic signals (for an extensive review on hydraulic architecture of trees see Cruiziat et al. 2002). Pressure waves can be relatively quick and fast, as they can diffuse through the plant at the speed of sound (1,500 m s^{-1} in water), but, to be physiologically important,

a hydraulic signal must cause a significant change in turgor pressure inside a cell. As plant cells can be elastic, their turgor will change only when a strong influx (or efflux) of water occurs: the flux is strictly linked with the hydraulic capacitance of the cell. Thus, hydraulic signals must involve significant mass flow of water; for example, to increase the turgor pressure in leaf cells by 1 bar, a net water influx equivalent to 1–5% of the total volume of a leaf must occur (Malone 1996). Clearly, the kinetics of pressure change inside plant tissues; they are correlated to and depend on the magnitude and distribution of hydraulic resistances along the pathway. Leaf hydraulic resistances have been measured for a large number of tree species. Most of the resistance in the aboveground part of a tree is located within the leaf blade. For example, the leaf resistance expressed as a percentage of the total resistance between trunk and leaves is 80–90% for *Quercus* (Tyree et al. 1993a), around 80% for *Juglans* (Tyree et al. 1993b) and less than 50% for *Acer* (Yang and Tyree 1994). Measurements of leaf resistance in young apical and old basal branches of a *Fraxinus* tree have yielded contrasting results (Cochard et al. 1997). Most of the resistance was indeed located in the leaf blade in the apical shoots, but for older shoots, the resistance was mainly in the axis.

In addition, an important factor in hydraulic signal transmission is the hydraulic capacitance of the receiving tissue. There is considerable evidence that trees undergo seasonal and diurnal fluctuations in water content. These fluctuations can be viewed as water going into and out of storage. Water-storage capacity can be defined in different ways (Cruiziat et al. 2002). The relationship between water content and water potential is known as the hydraulic capacitance (Cw) of plant tissue and means the mass of water (ΔMw) that can be extracted per unit change in water potential (ΔΨ) of the tissue: Cw=ΔMw/ΔΨ. In general, hydraulic capacitance is difficult to measure, especially because it is not constant, but varies with the water potential.

The mass flow associated with hydraulic signals can be divided into two components (Malone 1996). The major one, characterized by a long axial pathway (xylem), has a volumetric flow rate approximated by the Hagen–Poiseuille law:

$$J_v \approx \frac{\pi r^4 \Delta P}{8\eta l}, \tag{23.1}$$

where J_v is the volumetric flow rate, r is the tube radius, ΔP is the pressure gradient, η is the kinematic viscosity of the fluid and l is the tube length. The viscosity of water inside xylem vessels varies from negligible values with dilute solutes to considerably higher values when concentrated solutes, like sugars, are present. It is important to note that J_v is proportional to

the fourth power of the capillary (xylem vessel) diameter. This means that a slight increase in vessel diameter causes a considerable increase in conductivity, and thus in hydraulic signal entity, when the other parameters have constant values. The smaller component is defined by a short radial pathway through cells at each end of the flow, which present more hydraulic resistance than the axial pathway.

In a transpiring plant, the water status of all tissues will firstly approach a dynamic equilibrium with their local xylem, and then with the entire plant. In fact, a change in the flux of water at any site can be transmitted throughout the xylem to any other site of the plant, thus affecting the turgor pressure of living cells. Examples of local changes are, for example, microvariations in the soil matric potential at root level or in light at leaf level (a cloud or wind movements).

The mechanisms by which stomata could sense changes in xylem pressure to adjust g remain largely hypothetical. It seems improbable that xylem pressure itself is the triggering parameter, so a variable correlated to xylem pressure during water stress must be identified. Cavitation is the abrupt change from liquid water under tension to water vapour (Cochard et al. 2002). As water is withdrawn from the cavitated conduit, vapour expands to fill the entire lumen. In a short moment of time (hours or less), air diffuses in and the pressure rises. The vessel then becomes "embolized" (air-blocked). The replacement of water vapour by air is the key point that makes embolism serious since air cannot be dissolved spontaneously in water as can water vapour. It is now clear that drought can induce cavitation and xylem embolism. Xylem cavitation is generally seen as a potentially catastrophic dysfunction of the axial water-conducting system (Salleo et al. 2000), but it may also act as a rapid hydraulic signal initiating the stomatal response, provided that it can be reversed without any major damage to water conduction. Because the onset of cavitation events in leaf blades was correlated with the onset of stomatal closure in *Laurus*, it has been suggested that stomata were responding to hydraulic signals generated by cavitation (Salleo et al. 2000; Nardini et al. 2001). However, in *Juglans* (Cochard et al. 2002), stomatal closure occurred before the onset of cavitation in leaf blades and midribs and only after 70% loss of conductance in the trunk.

23.4
Integration of Chemical and Hydraulic Signals

While it is difficult to reject the strong evidence for positive, root-sourced signals in trees, and the likely presence of ABA as the commonest signals for detecting water stress at soil-root level, it has also been hard not to

consider the leaf water potential (Ψ_l) to explain the full range of responses in stomatal conductance. Recent studies (Salleo et al. 2000) suggest that the stomatal response to drought is the result of the integration of hydraulic and chemical root-generated signals. For example, to link the dosage-response characteristics of the guard cells to ABA with observed xylem imports over a drought sequence, it is often necessary to assume increased sensitivity to ABA at low Ψ_l, an inherent merging of chemical versus hydraulic signalling concepts (Comstock 2002). Numerous reports detail a wide range of different stress treatments in various experiments which are associated with remarkably constant values of Ψ_l when comparing stressed and control plants. This constancy of Ψ_l is often cited as evidence against a hydraulic signal. Such a conclusion, however, implies that the diverse treatments are (1) as a side effect, causing large alterations in hydraulic conductance, (2) that ABA is having an entirely independent effect on stomatal conductance and (3) that these independent effects on hydraulic and stomatal conductance just happen to be so consistently well balanced and produce no measurable perturbation in Ψ_l. This is possible in some cases, but it seems an improbable explanation of such general behaviour. More likely hypotheses would be either that both chemical and hydraulic signals are operative and are integrated at the level of stomatal regulation, or even that hydraulic conductance itself is somehow being actively regulated. As has been pointed out previously (Tardieu and Davies 1993) it is often precisely in those species in which Ψ_l shows the least variation that a component of hydraulic signalling may be most clearly present. Nevertheless, statements that observed homeostatic conservation of Ψ_l during various treatments rules out hydraulic signals are still common in the literature. In describing the method by which leaf hydration controls g in woody plants, Saliendra et al. (1995) noted that both hydroactive and hydropassive processes are likely to be important and would involve both hormonal and hydraulic mechanisms. Correia et al. (1995), Thomas and Eamus (1999) and Augé et al. (2000) also noted the likely interaction of both hormonal and hydraulic influences in modulating g.

23.5
Electrical Signals

The wounding of a leaf or a part of the shoot is known to cause variations in the extracellular electrical potential measured with surface contact electrodes (van Sambeek and Pickard 1976; Shiina and Tazawa 1986; Wildon et al. 1989) or with platinum or silver wires inserted directly into the tissues (Roblin 1985; Zawadzki et al. 1995). Wound- or stimulus-induced electrical phenomena in plants consist of a so-called variation potential (VP) or

"slow-wave", which appears as a wave of negativity with a variable length, shape, amplitude and propagation velocity, capable of passing through dead tissues (Roblin and Bonnemain 1985; Malone 1996; Mancuso 1999) and linked with xylem tension (Mancuso 1999), and briefer and faster signals, called action potentials (AP), considered to be real self-propagated electrical signals (Pickard 1973; Malone and Stankovic 1991; Stankovic et al. 1997). It is also suggested that APs play a major role in intercellular and intracellular communication and for regulation of physiological processes at the molecular and the organism level (Davies 1987). Mancuso (1999) focused on differences between VPs and APs in their mechanisms of propagation. In fact, an AP cannot pass through a dead region of a tissue, is still present in plants at saturating humidity and the amplitude and propagation velocities of APs are fairly constant through the shoots.

Therefore, APs are propagating electrical signals and not merely a local response to a hydraulic dispersal. Though the pathway of APs is not completely clarified, intracellular recordings tend to locate the activity in the phloem parenchyma (Samejima and Sibaoka 1983; Fromm and Spanswick 1993) or in the phloem sieve tubes (Wildon et al. 1992; Fromm and Eschrich 1988a). Numerous papers have been published on the study of VPs and APs. For example, Davies (2004) reviewed the subject, answering to the question "What properties do electrical signals have that chemical signals do not have?" with four terms: *rapidity*, *ubiquity*, *information*, and *transience*.

Researchers have rarely focused on woody plants (*Tilia* and *Prunus*, Boari and Malone 1993; *Salix*, Fromm and Spanswick 1993; *Vitis*, Mancuso 1999) although it is in such plants that the need for rapid and efficient signals other than chemicals becomes more obvious. Instead, they have been mainly limited to studying the electrical signals in herbaceous or sensitive plants like *Mimosa pudica* and related species because of their visible response to the stimuli (Ricca 1916; Houwink 1935; Weintraub 1952; Sibaoka 1969; Fromm and Spanswick 1993; Malone 1994b; Koziolek et al. 2004).

Since electrical signals have been shown to be widespread in the plant kingdom (Pickard 1973), it is important to study the physiological processes that might be under their control. Recently, Koziolek et al. (2004) described *M. pudica* responses in light and dark reactions of photosynthesis that indicate electrical signals play an important role in triggering photosynthetic response across long distances within the plant, giving evidence for a link between electrical signalling and photosynthetic response of plants. Electrical signals also regulate assimilate partitioning in *M. pudica* (Fromm and Eschrich 1988b; Fromm 1991), showing that APs trigger sucrose unloading from the pulvinar phloem and cause the turgor-dependent leaf movements.

A strong interaction between APs and hormones has been shown in willow roots by Fromm and Eschrich (1993), with a physiological role in the gas exchange of leaves. So, APs may be evoked by plant hormones. The application of indole acetic acid (IAA) or isopentenyladenine (IPA) in the root medium triggered a propagating AP with an amplitude of more than 80 mV (IAA) or 50 mV (IPA): 3 min later the CO_2 uptake increased and the transpiration rate first slightly decreased and then increased (IAA) or definitely decreased (IPA). In contrast, ABA treatment resulted in a hyperpolarization on the membrane potential, explained by Fromm et al. (1997) assuming that K^+ leaves the cortex cells. Consequently, CO_2 uptake and transpiration decreased sharply after 3 min following stimulation. From these results, ABA-induced stomatal closure seems not to be based on the hormone itself, but on the ABA-induced electrical signal, which by membrane processes causes the stomata to close. Accordingly, Fromm and Eschrich (1993) proposed that information on the soil water content was electrically transmitted to the leaves. With the use of inhibitors of ion channels and energy-dispersive X-ray microanalysis it was demonstrated that influx of Ca^{2+} and efflux of Cl^- and K^+ are responsible for the current flowing during APs in willow roots (Fromm and Spanswick 1993). Efflux of negative ions would reduce the endogenous outward current at the basal elongation zone and enhance the endogenous inward current at the apical elongation.

Grapevine (*Vitis vinifera*) plants exhibit different forms of rapid communication after a stimulus. Following perception of environmental stimuli, hydraulic and electrical signals, travelling for long distances in the plant, are early events in the coordination of the whole plant or some of its organs. The velocity of propagation of the front of the main negative-going signal (VP) was 2.7 mm s^{-1}, while an AP propagated along the shoot with a velocity of about 100 mm s^{-1} (Mancuso 1999). Koziolek et al. (2004) showed that wound-induced electrical signals propagate with a velocity of 4−8 mm s^{-1} within different pinnae of a *M. pudica* leaf. Another type of signal that could be involved in the regulation of photosynthesis after wounding is a chemical signal spreading from the stimulation site through the phloem. The transport velocities in the phloem typically proved to be 50−100 cm h^{-1} (Canny 1975), which is much too slow to account for observed modifications in gas exchange. Also, the possibility of a chemical transport in the xylem can be ruled out because the stimulus was applied upstream within the leaf. Transport through the symplasm might be another pathway for a chemical signal, but the speed of this process (up to 15 µM m s^{-1} in higher plants; Tyree 1970) is even slower than the transport velocity in the phloem.

23.6
Airborne Flow of Volatile Messengers

Gaseous signal transmission in plants, from ethylene to nitric oxide, has a long and established history. The gaseous plant hormone ethylene was described in 1934, but since antiquity the fact that plants emit numerous volatile compounds from flowers, fruits and vegetative parts that exert activity on other organisms has been realized. For example, floral volatiles serve as attractants for species-specific pollinators, whereas the volatiles emitted from vegetative parts, especially those released after herbivore feeding, appear to protect plants by deterring herbivores and by attracting the enemies of herbivores (Kessler and Baldwin 2001; Pichersky and Gershenzon 2002). Leaves normally release small quantities of volatile chemicals, but when a plant is damaged by herbivorous insects, this quantity rapidly increases. An undamaged plant maintains small levels of volatiles as a constitutive chemical reserve, which includes monoterpens, sesquiterpens and aromatics (Markovic et al. 1996, in *Fraxinus*). In contrast, following insect damage, plants release a variety of newly formed volatiles from the damaged site: the composition of the volatile profile changes, because of a de novo synthesis. However, these compounds are not stored in the plant (Paré and Tumlinson 1999), but are quickly released in the surroundings. The metabolic cost of these phytochemical emissions can also be high. In particular, terpenoids are more expensive to manufacture per gram than most other primary and secondary metabolites owing to the need for extensive chemical reduction (Gershenzon 1994). It appears that volatiles need to be judiciously synthesized and safely stored, as increased synthesis can be costly and potentially toxic to the plant. However, decreases in terpene accumulation may make an individual plant more vulnerable to insect pest attacks or temperature stress. In addition to the release of volatiles at the site of herbivore feeding, analysis of volatile emissions from unharmed leaves of insect-damaged plants has established that there is a systemic response. Chemical labelling experiments showed the systemic volatiles are synthesized at the site of release, suggesting that a mobile chemical messenger is transported from the damage location to distal, undamaged leaves to trigger synthesis and volatile release, moving both acropetally (Jones et al. 1993) and basipetally (Davis et al. 1991). The observed signal transduction from sink to source leaves leads to the question of the nature of the systemic signal. Different signal types have been widely proposed, from electrical (Stankovic and Davies 1996), to chemical (Malone et al. 1994; Malone and Alarcon 1995; Rhodes et al. 1999) to hydraulic signals (Alarcon and Malone 1994). Recently, for the first time electrophysiological recordings were performed by Pophof et al. (2005) on single olfactory sensilla of *Cactoblastis cactorum*. Eight volatile organic

compounds emitted by *Opuntia stricta*, a host plant of *C. cactorum*, were identified using gas chromatography–mass spectrometry, *β*-caryophyllene being the major compound. Five compounds identified by gas chromatography in the headspace of *O. stricta* elicited responses in olfactory receptor cells of *C. cactorum*, nonanal being the most active compound and therefore a candidate attractant of *C. cactorum*.

23.7
Colour Signals

Colour change and colour pattern are powerful tools in plant–animal communication. The functional and evolutionary importance of colour signalling in animals has received great consideration in zoology, resulting in numerous theories and wide experimentation (Majerus 1998). In contrast, with the exclusion of studies on the colour importance for the attraction of pollinators to flowers (Chittka et al. 1999) and frugivors to fruit (Ridley 1930), the biological relevance of colour has been extensively underestimated in plant sciences. Yet, visual signals sent to animals are usually more efficient than olfactory signals on long-distance signalling, owing to the great influence of the environment on the diffusion of volatiles (Dobson 1994; Anderson and Dobson 2003).

One the most exciting colour signals produced by plants is the bright autumn coloration displayed by many deciduous trees. Why some tree species make this spectacular exhibition of colour is one of the most puzzling questions in tree biology. The usual explanation is that autumn colours are simply a secondary and mere side effect of leaf senescence. In autumn the degeneration of chloroplasts and the degradation of chlorophyll pigments in colourless low molecular products allows the red and yellow pigments (carotenoids and flavonoids) to appear from the background (Sanger 1971; Goodwin and Mercer 1983). This point of view, however, overlooks two important facts: many trees do not show any bright colouration in autumn and, more important, there are numerous pieces of evidence that colour change is also due to the synthesis of new pigments (Chang et al. 1989; Matile et al. 1992).

Two recent papers have challenged this interpretation by suggesting that these red and yellow leaf colours are an honest signal of tree's ability to defend itself against potential insect pests (Archetti 2000; Hamilton and Brown 2001). Hamilton and Brown's theory explains that the bright colour of autumn foliage is not just a side effect of chlorophyll reabsorption but acts as a signal, for aphids that are looking for places to lay their eggs, to indicate that the tree has invested heavily in chemical defence, and it is, therefore, not suitable for aphids. Hamilton and Brown (2001) predicted

that tree species which suffer greater insect damage invest more in autumn colour than less troubled species. Maples, for example, which exhibit one of the most impressive autumn displays, are some of the most heavily aphid infested species (Blackman and Eastop 1994).

Hagen et al. (2003) explored experimentally Hamilton and Brown's autumn signalling hypothesis in *Betula*. As predicted by the theory, early autumn colour change (i.e. more colourful trees in autumn) results in less insect damage the following spring. In addition, from an index of tree conditions (fluctuating asymmetry), they found a positive relationship between tree condition and colour signal intensity. Recently, Archetti and Leather (2005) published the first direct observation of a key assumption of the theory, that parasites avoid bright colours. By monitoring the colonization of the aphid *Rhopalosiphum padi* on individual tress of *Prunus padus* in autumn they were able to observe a strong preference of aphids for trees with green leaves and to demonstrate that aphids colonizing trees with green leaves develop better in spring than aphids colonizing trees with bright autumn colours, which is consistent with the main assumption of the theory.

23.8
Conclusions and Future Prospects

In the past year several exciting reports have suggested new models for the production and transmission of long-distance signals in physiological and developmental controls of trees. Nevertheless, we still have a long way to go to fully understand the complex roles of the different mechanisms. For example, the findings described in this review mark only the beginning of an interesting challenge to elucidate the complex regulatory network of chemical, hydraulic and electrical signalling and responses. Continuing advances in genomics, especially in the availability of mutants and genome sequences, along with developments in chip microarray technology, should cause rapid progress in this field. In addition, speaking about trees, we cannot forget to mention that grafting has been an essential technique in the discovery of long-distance signal pathways (e.g. root-to-shoot communication). We think that a refined grafting technique, also today, could be the key for allowing identification of alterations in gene expression which would give insights into long-distance signal transduction and gene functions.

References

Anderson S, Dobson HEM (2003) Behavioural foraging responses by the butterfly *Heliconius melpamene* to *Lantana camara* floral scent. J Chem Ecol 29:2303–2318

Alarcon JJ, Malone M (1994) Substantial hydraulic signals are triggered by leaf-biting insects in tomato. J Exp Bot 45:953–957

Archetti M (2000) The origin of autumn colour by coevolution. J Theor Biol 205:625–630

Archetti M, Leather SR (2005) A test of the coevolution theory of autumn colours: colour preference of *Rhopalosiphum padi* on *Prunus padus*. Oikos 110:339–343

Augé RM, Moore JL (2002) Stomatal response to nonhydraulic root-to-shoot communication of partial soil drying in relation to foliar dehydration tolerance. Environ Exp Bot 47:217–229

Augé RM, Green CD, Stodola A, Saxton A, Olinick JB, Evans RM (2000) Correlations of stomatal conductance with hydraulic and chemical factors in several deciduous tree species in a natural habitat. New Phytol 145:483–500

Blackman RL, Eastop VF (1994) Aphids on the world's trees. CABI, Wallingford, UK

Blake J, Ferrell WK (1977) The association between soil and xylem water potential, leaf resistance and abscisic acid content in droughted seedlings of Douglas-fir (*Pseudotsuga menziesii*). Physiol Plant 39:106–109

Boari F, Malone M (1993) Wound-induced hydraulic signals: survey of occurrence in a range of species. J Exp Bot 44:741–746

Canny MJP (1975) Mass transfer. In: Zimmermann HM, Milburn JA (eds) Encyclopedia of plant physiology. Springer, Berlin Heidelberg, New York, pp 139–153

Chang KG, Fechner GH, Schroeder HA (1989) Anthocyanins in autumn leaves of quaking aspen in Colorado (USA). For Sci 35:229–236

Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osòrio ML, Carvalho I, Faria T, Pinheiro C (2002) How plants cope with water stress in the field. Photosynthesis and growth. Ann Bot 89:907–916

Chittka L, Thomson JD, Waser NM (1999) Flower constancy, insect psychology, and plant evolution. Naturwissenschaften 86:361–377

Cochard H, Peiffer M, Le Gall K, Granier A (1997) Developmental control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L.: impacts on water relations. J Exp Bot 48:655–663

Cochard H, Coll L, Le Roux X, Améglio T (2002) Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut. Plant Physiol 128:282–290

Comstock JP (2002) Hydraulic and chemical signalling in the control of stomatal conductance and transpiration. J Exp Bot 53:195–200

Correia MJ, Pereira JS, Chaves MM, Rodrigues ML, Pacheco CA (1995) ABA xylem concentrations determine maximum daily leaf conductance of field-grown *Vitis vinifera* plants. Plant Cell Environ 18:511–521

Cruiziat P, Cochard H, Améglio T (2002) Hydraulic architecture of trees: main concepts and results. Ann For Sci 59:723–752

Davies E (1987) Action potentials as multifunctional signals in plants: a unifying hypothesis to explain apparently disparate wound response. Plant Cell Environ 10:623–631

Davies E (2004) New functions for electrical signals in plants. New Phytol 161:607–610

Davis JM, Gordon MP, Smit BA (1991) Assimilate movement dictates remote sites of wound-induced gene expression in poplar leaves. Proc Natl Acad Sci USA 88:2393–2396

Dobson H (1994) Floral volatiles in insect biology. In: Bernays EA (ed) Insect–plant interactions. CRC, Boca Raton, pp 47–81

Fort C, Fauveau ML, Muller F, Label P, Granier A, Dreyer E (1997) Stomatal conductance, growth and root signalling in young oak seedlings subjected to partial soil drying. Tree Physiol 17:281–289

Fort C, Muller F, Label P, Granier A, Dreyer E (1998) Stomatal conductance, growth and root signalling in *Betula pendula* seedlings subjected to partial soil drying. Tree Physiol 18:769–776

Fromm J (1991) Control of phloem unloading by action potentials in *Mimosa*. Physiol Plant 83:529–533

Fromm J, Eschrich W (1988a) Transport processes in stimulated and non-stimulated leaves of *Mimosa pudica*. Trees 2:18–24

Fromm J, Eschrich W (1988b) Transport processes in stimulated and non-stimulated leaves of *Mimosa pudica*. I: The movement of ^{14}C-labelled photoassimilates. Trees 2:2–17

Fromm J, Eschrich W (1993) Electric signals released from roots of willow (*Salix viminalis* L.) change transpiration and photosynthesis. J Plant Physiol 141:673–680

Fromm J, Spanswick R (1993) Characteristics of action potentials in willow (*Salix viminalis* L.). J Exp Bot 44:1119–1125

Fromm J, Meyer AJ, Weisenseel MH (1997) Growth, membrane potential and endogenous ion currents of willow (*Salix viminalis* L.) roots are all affected by abscisic acid and spermine. Physiol Plant 99:529–537

Gershenzon J (1994) Metabolic costs of terpenoid accumulation in higher plants. J Chem Ecol 20:1281–1328

Goodwin TW, Mercer EI (1983) Introduction to plant biochemistry, 2nd edn. Pergamon, New York

Gowing DJG, Jones HG, Davies WJ (1993) Xylem-transported abscisic acid: the relative importance of its mass and its concentration in the control of stomatal aperture. Plant Cell Environ 16:453–459

Hagen SB, Folstad I, Jakobsen SW (2003) Autumn colouration and herbivore resistance in mountain birch (*Betula pubescens*). Ecol Lett 6:807–811

Hamilton WD, Brown SP (2001) Autumn tree colours as a handicap signal. Proc R Soc Lond 268:1489–1493

Houwink AL (1935) The conduction of excitation in *Mimosa pudica* L. Rec Tav Bot Neerl 32:51–91

Jackson GE, Irvine J, Grace J, Khalil AM (1995) Abscisic acid concentrations and fluxes in droughted conifer saplings. Plant Cell Environ 18:13–22

Jia W, Zhang J (1997) Comparison of exportation and metabolism of xylem-delivered ABA in maize leaves at different water status and xylem sap pH. Plant Growth Regul 21:43–49

Jones CG, Hopper RF, Coleman JS, Krischik VA (1993) Control of systematically induced herbivore resistance by plant vascular architecture. Oecologia 93:452–456

Kessler A, Baldwin IT (2001) Defensive function of herbivore-induced plant volatile emissions in nature. Science 291:2141–2144

Khalil AAM, Grace J (1993) Does xylem sap ABA control the stomatal behaviour of water-stressed sycamore (*Acer pseudoplatanus* L.) seedlings. J Exp Bot 44:1127–1134

Knudsen JT, Tollsten L, Bergstrom LG (1993) Floral scents, a checklist of volatile compounds isolated by head-space techniques. Phytochemistry 33:253–280

Köstner B, Biron P, Siegwolf R, Granier A (1996) Estimates of water vapour flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods. Theor App Clim 53:105–113

Koziolek C, Grams TEE, Schreiber U, Matyssek R, Fromm J (2004) Transient knockout of photosynthesis mediated by electrical signals. New Phytol 161:715–722

Liang J, Zhang J, Wong MH (1997) How do roots control xylem sap ABA concentration in response to soil drying? Plant Cell Physiol 38:10–16

Loewenstein NJ, Pallardy SG (1998a) Drought tolerance, xylem sap abscisic acid and stomatal conductance during soil drying: a comparison of young plants of four temperate deciduous angiosperms. Tree Physiol 18:421–430

Loewenstein NJ, Pallardy SG (1998b) Drought tolerance, xylem sap abscisic acid and stomatal conductance during soil drying: a comparison of canopy trees of three temperate deciduous angiosperms. Tree Physiol 18:431–439

Loreto F, Velikova V (2001) Isoprene produced by leaves protects the photosynthetic apparatus against ozone damage, quenches ozone products, and reduces lipid peroxidation of cellular membranes. Plant Physiol 127:1781–1787

Majerus MEN (1998) Melanism. Evolution in action. Oxford University Press, Oxford

Malone M (1994a) Rapid inhibition of leaf growth by root cooling in wheat: kinetics and mechanisms. J Exp Bot 44:1663–1669

Malone M (1994b) Wound-induced hydraulic signals and stimulus transmission in *Mimosa pudica* L. New Phytol 128:49–56

Malone M (1996) Rapid, long-distance signal transmission in higher plants. Adv Bot Res 22:163–217

Malone M, Alarcon JJ (1995) Only xylem-borne factors can account for systemic wound signalling in the tomato plant. Planta 196:740–746

Malone M, Alarcon JJ, Palumbo L (1994) An hydraulic interpretation of rapid, long-distance wound signalling in the tomato. Planta 193:181–185

Malone M, Stankovic B (1991) Surface potentials and hydraulic signals in wheat leaves following localised wounding by heat. Plant Cell Environ 14:431–436

Mancuso S (1999) Hydraulic and electrical transmission of wound-induced signals in *Vitis vinifera*. Aust J Plant Physiol 26:55–61

Markovic I, Norris DM, Phillips JK, Webster FX (1996) Volatiles involved in the nonhost rejection of *Fraxinus pennsylvanica* by *Lymantria dispar* larvae. J Agric Food Chem 44:929–935

Matile P, Flach BMP, Eller BM (1992) Autumn leaves of *Ginkgo biloba*: optical properties, pigments and optical brightners. Bot Acta 105:13–17

Maurel M, Robin C, Simonneau T, Loustau D, Dreyer E, Desprez-Loustau ML (2004) Stomatal conductance and root-to-shoot signalling in chestnut saplings exposed to *Phytophtora cinnamomi* or partial soil drying. Funct Plant Biol 31:41–51

Milburn JA (1979) Water flow in plants. Longman, London, pp 81–103

Nardini A, Tyree MT, Salleo S (2001) Xylem cavitation in the leaf of *Prunus laurocerasus* and its impact on leaf hydraulics. Plant Physiol 125:1700–1709

Niinemets Ü, Söber A, Kull O, Hartung W, Tenhunen JD (1999) Apparent controls of leaf conductance by soil water availability and via light-acclimation of foliage structural and physiological properties in a mixed deciduous, temperate forest. Int J Plant Sci 160:707–721

Paré PW, Tumlinson JH (1999) Plant volatiles as a defense against insect herbivores. Plant Physiol 121:325–331

Perks MP, Irvine J, Grace J (2002) Canopy stomatal conductance and xylem sap abscisic acid (ABA) in mature Scots pine during a gradually imposed drought. Tree Physiol 22:877–883

Pichersky E, Gershenzon J (2002) The formation and the function of plant volatiles: perfumes for pollinator attraction and defense. Curr Opin Plant Biol 5:237–243

Pickard B (1973) Action potentials in higher plants. Bot Rev 39:172–201

Pophof B, StangeG, Abrell L (2005) Volatile organic compounds as signals in a plant–herbivore system: electrophysiological responses in olfactory sensilla of the moth *Cactoblastis cactorum*. Chem Senses 30:51–68

Rhodes JD, Thain JF, Wildon DC (1999) Evidence for physically distinct systemic signalling pathways in the wounded tomato plant. Ann Bot 84:109–116

Ricca U (1916) Soluzione di un problema di fisiologia: la propagazione di stimolo nella 'Mimosa'. Nuovo G Bot Ital 23:51–51

Ridley HN (1930) The dispersal of plants throughout the world. Reeve, UK

Roblin G (1985) Analysis of the variation potentials induced by wounding in plants. Plant Cell Physiol 26:455–461

Roblin G, Bonnemain JL (1985) Propagation in *Vicia faba* stem of potential variation induced by wounding. Plant Cell Physiol 26:1273–1282

Saliendra NZ, Sperry JS, Comstock JP (1995) Influence of leaf water status on stomatal response to humidity, hydraulic conductance and soil drought in *Betula occidentalis*. Planta 196:357–366

Salleo S, Nardini A, Pitt F, and Lo Gullo MA (2000) Xylem cavitation and hydraulic control of stomatal conductance in laurel (*Laurus nobilis* L.). Plant Cell Environ 23:71–79

van Sambeek JW, Pickard BG (1976) Mediation of a rapid electrical, metabolic, transpirational and photosynthetic changes by factors released from wounds. I. Variation potentials and putative action potentials in intact plants. Can J Bot 54:2642–2650

Samejima M, Sibaoka T (1983) Identification of the excitable cells in the petiole of *Mimosa pudica* by intracellular injection of procion yellow. Plant Cell Physiol 24:33–39

Sanger JE (1971) Quantitative investigations of leaf pigments from their inception in buds through autumn coloration to decomposition in falling leaves. Ecology 52:1075–1089

Schulze ED (1991) Water and nutrient interactions with plant water stress. In: Mooney HA, Winner WE, Pell EJ (eds) Response of plants to multiple stresses. Academic, New York, p 89

Shiina T, Tazawa M (1986) Action potentials in *Luffa cylindrical* and its effects on elongation growth. Plant Cell Physiol 27:1081–1089

Sibaoka T (1969) Physiology of rapid movements in higher plants. Annu Rev Plant Physiol 20:165–184

Stoll M, Loveys B, Dry P (2000) Hormonal changes induced by partial rootzone drying of irrigated grapevine. J Exp Bot 51:1627–1634

Stankovic B, Davies E (1996) Both action potentials and variation potentials induce proteinase inhibitor gene expression in tomato. FEBS Lett 390:275–279

Stankovic B, Zawadzki T, Davies E (1997) Characterization of the variation potential in sunflower. Plant Physiol 115:1083–1088

Sturm N, Köstner B, Hartung W, Tenhunen JD (1998) Environmental and endogenous controls on leaf- and stand-level water conductance in a Scots pine plantation. Ann Sci For 55:237–253

Tardieu F, Davies WJ (1993) Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. Plant Cell Environ 16:341–349

Tenhunen JD, Hanano R, Abril M, Weiler EW, Hartung W (1994) Above- and below-ground environmental influences on leaf conductance of *Ceanothus thyrsiflorus* growing in a chaparral environment: drought response and the role of abscisic acid. Oecologia 99:306–314

Thomas DS, Eamus D (1999) The influence of predawn leaf water potential on stomatal responses to atmospheric water content at constant C_i and on stem hydraulic conductance and foliar ABA concentrations. J Exp Bot 50:243–251

Thompson DS, Wilkinson S, Bacon MA, Davies WJ (1997) Multiple signals and mechanisms that regulate leaf growth and stomatal behaviour during water deficit. Physiol Plant 100:303–313

Triboulot MB, Fauveau ML, Brèda N, Label P, Dreyer E (1996) Stomatal conductance and xylem sap abscisic acid (ABA) in adult oak trees during a gradually imposed drought. Ann Sci For 53:207–220

Tyree MT (1970) Symplast concept: a general theory of symplastic transport according to thermodynamics of irreversible processes. J Theor Biol 26:181–214

Tyree MT, Sinclair B, Lu P, Granier A (1993a) Whole shoot hydraulic resistance in *Quercus* species measured with a new high-pressure flowmeter. Ann Sci For 50:417–423

Tyree MT, Cochard H, Cruiziat P, Sinclair B, Ameglio T (1993b) Drought-induced leaf shedding in walnut. Evidence for vulnerability segmentation. Plant Cell Environ 16:879–882

Yang S, Tyree MY (1994) Hydraulic architecture of *Acer saccharum* and *Acer rubrum*: comparison of branches to whole trees and the contribution of leaves to hydraulic resistance. J Exp Bot 45:179–186

Wartinger A, Heilmeier H, Hartung W, Schulze ED (1990) Daily and seasonal courses of leaf conductance and abscisic acid in the xylem sap of almond trees (*Prunus dulcis*) under desert conditions. New Phytol 78:821–825

Weintraub M (1952) Leaf movements in *Mimosa pudica* L. New Phytol 50:357–382

Wildon DC, Doherty HM, Eagles G, Bowles DJ, Thain GF (1989) Systemic responses arising from localised heat stimuli in tomato plants. Ann Bot 64:691–695

Wildon DC, Thain JF, Minchin PEH, Gubb IR, Reilly AJ, Skipper YD, Doherty HM, O'Donnell PJ, Bowles DJ (1992) Electrical signalling and systemic proteinase inhibitor induction in the wounded plant. Nature 360:62–65

Wilkinson S, Davies WJ (1997) Xylem sap pH increase: a drought signal received at the apoplastic face of the guard cell that involves the suppression of saturable abscisic acid uptake by the epidermal symplast. Plant Physiol 113:559–573

Zawadzki T, Dziubinska H, Davies E (1995) Characteristics of action potentials generated spontaneously in *Helianthus annuus*. Physiol Plant 93:291–297

Zhang J, Jia W, Zhang DP (1997) Effect of leaf water status and xylem pH on metabolism of xylem-transported abscisic acid. Plant Growth Regul 21:51–58