

REVIEW ARTICLE

Calcium-dependent physiological processes in trees

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ABSTRACT

Among the various plant nutrients, calcium appears to occupy a unique position, acting as an important regulator in many processes related to both growth and responses to environmental stresses. This applies to stomatal function, cell division, cell wall synthesis, signalling functions in plant defence, repair of damage from biotic and abiotic stress and to the structural chemistry and function of woody tissues. The calcium content in the cambium of poplar was shown to rise transiently by as much as 40% in spring, indicating the significant role that calcium plays in the onset of cambial reactivation. Moreover, during bud flush and the beginning of cell division, calcium was reported to increase significantly in the apical meristem. A reduction in calcium supplies also proved to strongly affect wood formation, as evidenced in the pronounced reduction in wood increment, vessel size and fibre length, as well as in reduced carbonyl and methoxy groups from S-lignin. Induced wounding revealed that calcium acts as an intracellular signal and, furthermore, proved its involvement in long-distance electrical signalling. Environmental stimuli such as cold shock or wounding showed that poplar grown under calcium-starved conditions was incapable of responding to this type of stress. The above evidence highlights the important role of calcium in tree functions, both as a signal in minute physiologically active pools within the cytoplasm, and in higher concentrations for its impact on the structural integrity of cell walls and woody tissues.

INTRODUCTION

In the regulation of physiological and structural processes in plants, calcium has been shown to have a number of important functions. Due to its role as a messenger in different physiological processes and its chemical binding characteristics, Bangerth (1979) considered calcium unique amongst the so-called macronutrients. In plant tissues, at scales ranging from intercellular membranes to the cell walls of tree stems, calcium appears to play a decisive role in enhancing not only stability but also structural integrity of cells. Moreover, regarding both the structure and function of forest ecosystems, McLaughlin & Wimmer (1999) found that calcium supply acts as an important control mechanism for many key plant functions. Calcium is taken up passively *via* the fine roots and is transported acropetally almost exclusively *via* the transpiration stream. Unlike many other nutrients, it is then mainly deposited in the apoplast, where it binds to various cell wall sites, in particular to the carboxyl groups of

pectins within the middle lamella and in the primary cell wall. According to Brett & Waldron (1996) and Guglielmino *et al.* (1997), calcium thus has a stiffening effect on the developing xylem walls in the course of xylem differentiation. During leaf development in *Carya ovata*, Borchert (1990) found excess calcium ions precipitated as calcium oxalate crystals in cell vacuoles, while Fink (1991) observed the same precipitate in intercellular spaces on the outside of mesophyll cells in needles of Norway spruce. Calcium oxalate crystals were also reported in oak and poplar bark, where they were located in thick-walled, chambered lignified cells, adjacent to fibre groups and in sclereids (Trochbrodt 1995).

Cell wall-bound calcium also appears to be essential as a mediating agent in long-term salt adaptation of *Populus euphratica* subjected to salt stress (Ottow *et al.* 2005). Once calcium is bound in the cell wall compartments it is mostly no longer available for further processes in plant metabolism. In contrast to its abundance in the apoplast, calcium is almost non-existent in the symplast. Felle

(1988) and Hirschi (2004) reported free calcium concentrations in the cytoplasm to range from 0.1 to 0.2 μM . Small variations in its concentration enable calcium to act as an effective signal transducer. A number of abiotic or biotic stimuli are capable of triggering calcium signals (Sanders *et al.* 1999; Knight 2000; Anil & Rao 2001; Knight & Knight 2001). White & Broadley (2003) stressed the function of intracellular calcium as a membrane stabilizer, in addition to acting as a messenger. Calcium therefore also has a protective effect against the influx of passive ions, while Plieth (2005) associated calcium with enzyme-activating processes.

Du & Yamamoto (2003) described the role of calcium in the formation of gravistimulated compression wood. As suggested by Westermarck (1982) and Lohrasebi *et al.* (1999), calcium may be essential for the lignification of compression wood, as calcium deficiency may cause a reduction in lignification in the course of tracheid differentiation. Moreover, according to Eklund & Eliasson (1990) and Eklund (1991), low calcium concentrations appear to play a role in reducing wall deposition in spruce hypocotyls. These authors attribute this effect mainly to the inhibition of lignin formation and deposition of non-cellulosic polysaccharide. In old-growth spruce Dünisch & Bauch (1994) observed a positive influence of potassium, calcium and magnesium fertilisation on wood formation. In periods of low precipitation, this effect appeared more pronounced than under conditions where high-soil water contents prevailed.

The present review will focus mainly on the interaction of calcium supply and physiological processes such as bud flush, cambial reactivation, wood formation and electrical signalling in poplar.

SEASONAL ACTIVITY

In Europe's temperate climate, tree growth is determined by seasonal variations. Trees endure period unfavourable for growth through periods of dormancy, which Lang (1987) defines as the 'temporary absence of visible growth of any plant structure containing a meristem'. Nevertheless, alongside active growth, dormancy should not merely be considered as a temporary state of inactivity, but also as a process of development. Rohde & Bhalerao (2007) state that trees are capable of shutting down meristem activity and inducing a dormant state in which the meristems are rendered insensitive to signals that would otherwise promote growth. Many interrelated sub-processes are active during different periods of dormancy. Espinosa-Ruiz *et al.* (2004) provide an example for this phenomenon, with the elevation of E2F phosphorylation prior to the transition to dormancy, moreover the hormone ABA is also believed to affect aspects of dormancy. In apical buds, ABA content peaks after growth has ceased and prior to bud setting (Rohde *et al.* 2002). A shortening of day length in temperate latitudes initiates growth cessation, accompanied by autumnal senescence and the shedding of leaves (Keskitalo *et al.* 2005), completion of bud

set (Nitsch 1957; Critchfield 1960) and the ceasing of cambial activity. Once dormancy has set in, drought resistance becomes more pronounced and frost resistance is developed, both of which are considered characteristic sub-processes in buds (Rohde & Boerjan 1991; Ruttink *et al.* 2007) and in the cambium (Chaffey 2001). Eschrich *et al.* (1988) investigated the occurrence and density of minerals in tissue compartments of leaf blade, petiole and subtending stems of beech. It was shown that, prior to leaf shedding in autumn, magnesium, potassium and phosphorus were retrieved from the leaf blade and deposited mainly in the stem, *viz.* in the cortex and pith tissues. As for calcium, a considerable amount was located in the phloem of the green leaf and its level decreased synchronously with leaf preparation for shedding. When leaves turn red-brown, the calcium content in stem tissues rises within the phloem, indicating a retrieval of calcium *via* the phloem. This was unexpected because calcium had been assumed to be absent in sieve tubes (Ziegler 1975). Kauss (1987) offered a potential interpretation of this fact based on a relation to callose deposition in sieve plates in dormant stem sieve tubes due to the activation of β -1,3-glucan synthase. The vanishing chlorophyll colouration in autumn leaves is assumed to be due to a retrieval of organic compartments, *i.e.* of the nitrogen and phosphorus contained therein, confirming the above results. As calcium, potassium and magnesium are also being retrieved, we are presented with a complete picture of the economy of trees.

To date, many studies have dealt with cytological and structural aspects of cambium reactivation, growth and cessation (Iqbal 1990; Catesson 1994; Larson 1994; Chaffey 2001). Biochemical approaches were successfully used to identify some of the key signalling molecules instrumental in these processes, such as plant hormones (Lachaud 1989; Savidge 1996; Sundberg *et al.* 2000; Tanino 2004). As the cambium is responsible for wood formation, studying the transduction of signals conditioned by the seasons (*e.g.* daylength, temperature) that control cambial activity is an important field of future research. Follet-Gueye *et al.* (1998) used ion mass spectrometry in a study of beech during the period of reactivation and reported a strong temporary increase in calcium concentration in both the cambium and phloem. This rise in calcium content is assumed to be related to the regulation of cambial reactivation in spring. However, we do not as yet fully understand the biochemical function of calcium in this context. Arend & Fromm (2000) used energy-dispersive X-ray analysis (EDXA) to show that the calcium content rose by as much as 40% in the cambium of poplar at the time of reactivation. The EDXA technique uses a scanning electron microscope equipped with an energy-dispersive X-ray microanalytical device. This method proved to be suitable for studying changes in various mineral concentrations in different tissues of freeze-dried plant organs. The increase in cambial calcium in spring is immediately followed by a decrease, suggesting that calcium is of particular importance for the onset

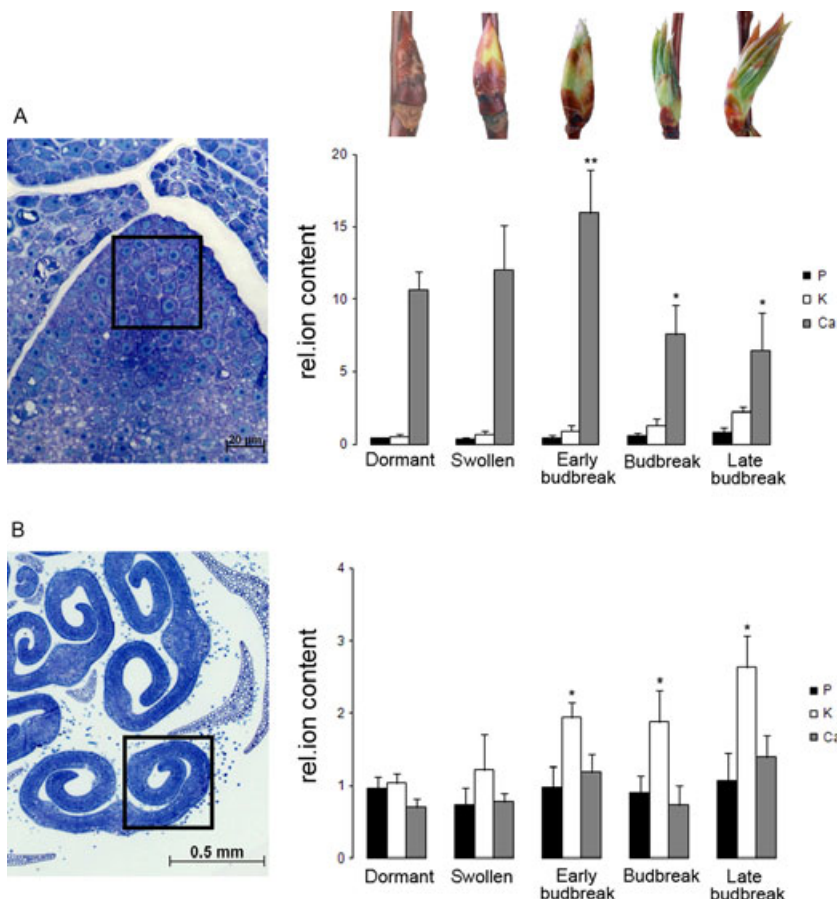


Fig. 1. Relative concentrations of calcium, potassium and phosphorus in poplar buds (*Populus tremula* × *Populus tremuloides*) at different stages of development. A: In the apical meristem at the base of a bud (left, light microscopic image, square represents EDX measuring area as performed with SEM), the calcium content is significantly higher than the potassium and phosphorus content at all developmental stages (right, $P \leq 0.05$). During swelling and early budbreak in spring calcium increases transiently, corresponding to the beginning of cell divisions in the meristematic tissue. Data are means \pm SD, $n = 5$. Asterisks represent statistically significant differences of calcium content (t-test) compared with calcium content during the state of dormancy: * $P \leq 0.05$; ** $P \leq 0.005$. B: In the leaf primordia (left, light microscopic image, square represents EDX measuring area as performed on SEM) of the buds the relative potassium content significantly increases during budbreak and cell elongation (right). Data are means \pm SD, $n = 5$. Asterisks represent statistically significant differences of potassium content (t-test) compared with calcium and phosphorus contents: * $P \leq 0.005$. The scale gives the peak to background ratio of recorded X-ray signals.

of cambial reactivation. In the maintenance of the structure and function of cell membranes, calcium is a major factor, as well as serving as a co-factor in several enzymes, which indicates that its transient increase may play a role in the basic processes of regulation of wood formation. EDXA was also used in our laboratory to show that the calcium level in the apical meristem of dormant buds is very low (Fig. 1A). In spring, however, calcium was observed to gradually rise in the apical meristem during swelling and bud break, suggesting that it may be instrumental in boosting cell division (Fig. 1A). By contrast, the meristematic levels of potassium and phosphorus were found to stay low during bud flush. However, potassium is the dominant ion in leaf primordia. The rise of potassium levels in spring during swelling and bud break is indicative of its involvement in the cell elongation process (Fig. 1B).

To summarize current knowledge of the role of calcium in the course of seasonal changes, it is retrieved from the leaves to the stem at the onset of tree dormancy, with calcium levels in the apical meristem of buds and in dormant cambium becoming very low. In spring, cambial reactivation and bud flushing cause a significant rise in meristem calcium content, correlated to the onset of cell division, suggesting that in the activation of this process calcium plays a significantly promotive role.

WOOD FORMATION

Among the numerous mineral nutrients required for tree growth, Eklund & Eliasson (1990) and Dünisch & Bauch (1994) consider calcium essential for basic processes of tree development, such as cell division, cell differentiation and, ultimately, wood formation. In an early study by Davis (1949) on the effects of calcium on xylem development of 1-year-old loblolly pine, a considerable reduction in cross-sectional area due to reduced proportions of primary cortex and pith tissue was found in calcium-deficient trees. Lautner *et al.* (2007) studied poplar (*Populus tremula* L. × *Populus tremuloides* Michx.), grown in hydroponics with different calcium supply regimes, and used EDXA to reveal an increase in calcium in the phloem, cambium and in the xylem expansion zone in response to increasing calcium content. Moreover, under calcium starvation a decrease in vessel size, wood increment and fiber length was revealed by light microscopy studies. Arend & Fromm (2003) used TEM to show that the cambial cells of optimally grown poplar variants possess one large vacuole, with the cytoplasm confined to a narrow peripheral layer along the thin primary cell wall, characteristics known to be typical of active vascular cambium cells in poplar wood. By contrast, a limited cambial zone of only three to five cells in radial direction was

observed in poplar grown under calcium starvation conditions. In these trees, the cell expansion zone was also found to be very narrow. Similar to the ultrastructure of cambial cells in dormancy, as described by Arend & Fromm (2003), the cytoplasm in such cambial cells was very dense, with numerous small vacuoles (Lautner *et al.* 2007). This reduced vacuolation is a possible explanation for the smaller vessel size, based on the fact that cell expansion in poplar wood cells depends on large vacuoles to build up a high osmotic potential (Wind *et al.* 2004).

A potential cause for the observed decrease in cambial growth under calcium deficiency may be a decrease of imported carbon into the cambium. Schulte-Baukloh & Fromm (1993) observed poplar grown under calcium deficiency, which had a lower phloem loading rate in the leaves and a drop in the unloading of photoassimilates from phloem into cambium. Moreover, HPLC analysis of poplar leaves and bark revealed that calcium deficiency caused a considerably rise in sugar concentrations in leaves but a reduction in sugars in the bark (Lautner *et al.* 2007). However, glucose, fructose and sucrose levels increased in the young wood under calcium deficiency, hence the lack of carbon in the bark cannot be considered the cause of anatomical changes, such as smaller vessels and a decreased expansion zone. It can therefore be concluded that calcium appears to have a direct impact on wood structure.

In the course of the year, the chemistry and structure of cambial cell walls are both subject to change. While cells undergo the autumnal transition from an active to a resting state, their cell walls thicken and a cross-linking of acidic pectins by calcium bridges occurs. For the cambium to resume its radial expansion in spring, these calcium bridges must be degraded (Funada & Cateson 1991). During cell division, Golgi vesicles form a cell plate that consists mainly of pectin. Pectin itself consists of partially methylated polygalacturonic acid, with some of the carboxyl groups forming calcium salts. Pectin is the main structural element in the middle lamella, with the formation of the primary and secondary walls occurring successively. Westermark *et al.* (1986) found evidence that pectin is removed in the course of subsequent lignification and calcium ions are used in this process. Westermark (1982) also suggested that a calcium-dependent mechanism brings about the polymerisation of lignin within the cell wall. Peroxidases appear to be key enzymes in the lignification process, converting the hydrophilic gel of the primary wall into a hydrophobic lignin gel. Penel & Greppin (1996) reported a number of apoplastic peroxidases from zucchini and horseradish that are known to bind pectin in their calcium-induced structure. Hence, the pattern of lignin deposition may be subject to changes based on variations in calcium concentration in the cell wall. Lautner *et al.* (2007), using Fourier transform infrared (FTIR) spectroscopy on poplar wood grown under calcium starvation, found direct evidence for the role of calcium in lignification based on the reduction in carbonyl and methoxyl groups from S-lignin. Since the ratio

of S-units and G-units is known to be fairly stable in poplar wood (Hu *et al.* 1999), we assume the above decrease to be indicative of a general drop in lignin concentration.

Both the chemistry and the structure of the various cell types in the xylem are known to have a strong impact on the mechanical properties of wood. Calcium deficiency is considered as one of the factors causing substantial changes in mechanical properties, such as a reduction in tensile strength, in resistance to rupture and in wood elasticity (McLaughlin & Wimmer 1999). It is interesting to note that lignin, calcium and the mechanical properties of wood are related to one another (Wimmer *et al.* 1997). Wimmer & Lucas (1997), in a study on spruce wood, found low calcium content led to a lower lignin proportion, with concomitant alterations in hardness and elasticity of the secondary wall layers. From the perspective of the tree as a whole, a reduction in lignification caused by calcium deficiency is more likely to occur in the crowns of large trees because of greater transport distances and higher competition for calcium within the xylem flow. This was actually confirmed by Wessmann *et al.* (1989), who found foliar lignin content was reduced in the upper canopies of oak–maple and pine forests in the USA. Moreover, in red spruce, McNulty *et al.* (1991) had already shown reduced canopy lignin to be significantly related to increased annual nitrogen deposition, higher soil nitrogen content and lower calcium and magnesium content in the foliage and on the forest floor. These results are indicative of interrelated processes between soil chemistry and canopy chemistry.

In summary, calcium supply rates in trees have an impact on wood formation by causing significant changes in wood structure and chemistry. Various authors report the particular significance of calcium in the cross-linking of carboxyl groups within the pectin layer and, furthermore, in secondary wall synthesis and lignification. Also, the role of calcium in xylogenesis is being investigated more intensively, involving molecular studies of calcium channels, calcium-mediated enzymes and xylem receptors, to obtain a better understanding of calcium regulation in trees.

LONG-DISTANCE ELECTRICAL SIGNALLING IN RESPONSE TO STRESS

The sensitivity of plant cells in response to environmental and physical stimuli is a well established fact. This kind of stress is known to produce calcium impulses and, moreover, to trigger calcium-dependent electrical signals within the plant (Fromm & Spanswick 1993; Trewavas 2000; Felle & Zimmermann 2007). The past two decades have seen the development of new calcium-specific reporter molecules, which have made temporal and spatial sequences measurable at the intracellular level. Novel concepts have been developed regarding the generation and transmission of calcium-induced signals in plants and their potential physiological functions (Trewavas & Malho

1997; McAinsh & Hetherington 1998; Fromm & Lautner 2007). With regard to overall plant physiology, calcium signals may be triggered by various external stimuli, which, upon recognition by internal receptors, elicit corresponding responses. McAinsh & Hetherington (1998) state that some signals may take the form of oscillations with specific frequencies and amplitudes that are capable of controlling the activation levels of enzymes *via* rates of phosphorylation and dephosphorylation. Roberts & Harmon (1992), on the other hand, identified a number of calcium-activated proteins involved in calcium-generated responses in plants.

In the generation of electrical signals capable of bridging long distances in trees *via* the phloem, the increase in intracellular calcium is also a major element (Davies 1987). Fromm & Spanswick (1993) report the generation of electrically induced action potentials in willow by initial calcium influx into the cytoplasm, and also potassium and chloride efflux into the apoplast. Voltage-dependent anion channels in plants are known to require elevated cytoplasmic levels of calcium and hence Hedrich & Becker (1994) assume that the activation of calcium-permeable channels signifies the first step within an action potential. Fromm *et al.* (1997) used a vibrating electrode in combination with a micro-electrode to assess the apparent efflux of anions and cations of 200–700 pmol·cm⁻² per action potential in willow roots. Distances of up to 2 m were thus found to be bridged, suggesting that these types of rapid signal (at a rate of 2–20 mm·s⁻¹) are capable of coordinating physiological activities in trees. From the results of two-dimensional imaging analyses of chlorophyll fluorescence, combined with gas exchange measurements in poplar, Lautner *et al.* (2005) deduced that wound-triggered electrical signals are able to travel over long distances and to modify photosynthesis in distant leaves. In trees grown under calcium deficiency, phloem cell excitability was totally blocked after leaf wounding. Nor was there any significant response in gas exchange in calcium-deficient trees upon wounding. These results suggest that calcium channels are involved in the induction of long-distance electrical signals. They also confirm observations by Trewavas (2000) that a complex calcium signalling network exists based on calcium channels and transducers. Taken together, in the environmental stress response, calcium plays an essential signalling role. Electrical signalling makes the rapid transmission of information possible in trees where, due to their very large size, rapid communication within the tree system is vital. It was shown that these signals trigger specific responses in the photosynthesis of distant leaves and are furthermore part of a mechanism in plant defence and in the repair of damage from biotic and abiotic stress.

Future research needs to focus on the molecular control points of calcium signalling, which are essential for a better understanding of tree physiology. Knowledge in this field will also be useful in practical applications, *i.e.* utilisation of poplar in the development of intensive

forestry in short-rotation plantations. Poplar plantations may prove useful in the mitigation of atmospheric gas accumulation, the removal of soil and surface water contaminants (phytoremediation) and, based on their high growth rates, for the production of wood for uses such as a construction material, energy resource and in the paper industry.

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