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REVIEW

# The term "caline" in plant developmental biology

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**Abstract**
In the 1930s, Frits Warmolt Went conducted a number of seminal studies on pea seedlings that had been germinated in the dark and assessed their growth when either the apical parts, cotyledons, or roots were cut off or grafted, to assess whether coplant growth factors assisted auxin in the development of these organs. Went assigned the term "calines" to all auxin-assisting substances, specifically rhizocaline, caulocaline, and phyllocaline in root, shoot (and axillary buds) and leaf development, respectively. Those experiments were based exclusively on growth assays, and no supplementary biochemical or physiological analyses were ever conducted, and additional proof was only provided by Went using pea or tomato. The lack of independent reproducibility by other groups, combined with the fact that the hormonal control of these developmental events in plants is now fairly well-studied event, even at the molecular level, suggests that these growth factors that Went observed 80 years ago either do not exist or are known by some other term in modern plant development. The terms related to "calines" should thus no longer be used in plant developmental biology.

**Keywords** Hypothetical substance · Plant growth hormone · Plant hormone · Plant morphogenesis

## History of the discovery of calines

In the mid-1930s, the person who first described the plant growth substance (PGS) auxin (Went 1929), Frits Warmolt Went, hypothesized that a group of substances was responsible for assisting auxin in its various roles in organogenesis, referring to these growth factors (GFs) as "caline" (Went 1938a, b). Using pea (*Pisum sativum* L.) as his model plant, Went claimed that this group of GFs, the "calines," was responsible for root, stem (and axillary bud), and leaf formation, aiding auxin in all cases, specifically by rhizocaline, caulocaline, and phyllocaline, respectively. In all cases, an auxin cofactor or "food factor" was also required: "in order to explain the auxin effect on growth it was necessary to assume a second factor, the food factor" (Went 1938a). Anthocaline, a related term later coined by Van de Sande Bakhuyzen (1947) based on observations on wheat, but inspired by Went's terminology, was a PGS or GF that supposedly induced flowering, referring to it as a florigen that "is probably transferred from the leaves to the growth point." There is, however, a historical challenge to this claim by Went, as stated by Thimann (1977), who attributes the concept to Julius von Sachs: "So we come back to Julius Sachs and his idea of a rhizocaline and a caulocaline." Thimann suggested that auxin was, in fact, acting as a rhizocaline and stated that von Sachs was "close to the mark." Hottes (1932) attributes the concept of organ-specifying signals to von Sachs.

## Formation and storage of calines: proposed mechanisms

Went (1938a, b) stated that calines work as independent PGSs separate from auxin, claiming that a pea seedling with its cotyledons removed has a low level of caulocaline

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but a high level of rhizocaline, that such a plant would not lengthen nor swell when an auxin was added, but instead form an abundance of roots. Went further claimed, after a series of grafting experiments, that caulocaline was formed in roots and in small amounts in cotyledons, but that they were depleted in the latter within a week after removing roots. Went (1938a) described caulocaline as follows: "a special substance is formed in the roots, which moves upwards from cell to cell towards the apical parts of the pea stems where it causes growth in length of the shoot in conjunction with auxin." In addition, "the inhibition of growth of the lateral buds is not a *direct* effect of auxin, but works through diversion of auxin."

Went further claimed that phyllocaline was stored in cotyledons and formed in leaves in light, but was absent in the stem, which he proved by cutting off the cotyledons, thereby halting leaf growth. Went (1938a) described phyllocaline in its relation to auxin as follows: "Auxin regulates midrib and vein growth, but does not influence mesophyll development, which is governed by a special leaf growth substance formed in leaves in the light and stored in pea cotyledons, which I propose to call phyllocaline."

Rhizocaline, Went claimed, was also present in cotyledons as well as in the stem, in considerable quantities in the latter that gradually became reduced 4–6 days after the cotyledon was removed, leaving rhizocaline only in the roots and the stem. Went (1938a) described rhizocaline as "a specific factor coming from the cotyledons which cooperates with auxin." Went (1938a) further stated: "Without this factor no root formation is possible. Low auxin concentrations inside the stem make the rhizocaline move downwards—in the same direction as the polar auxin movement—and cause root formation at the base." Keller and Van Volkenburgh (1997) claimed in a review that caulocaline was a vein GF while phyllocaline was a mesophyll GF, basing their claim on a 1951 book chapter by Went, so it was unclear on what experimental evidence this claim was made. Similar doubts were raised by Njoku (1956), who claimed that "[t]he nature of the complexes of growth factors postulated by Went is, however, still a matter of speculation."

A resynthesized summary of the location of biosynthesis of rhizocaline, caulocaline and phyllocaline, based on Went (1938a), is shown in Fig. 1.

In summary, Went believed, based on trials using a single ('Alaska' in Went (1938a)) or several (Went 1938b) cultivars of pea, that stem elongation, lateral bud growth, root formation and leaf growth all required the presence of auxin, but not alone, and that in the absence of rhizocaline, caulocaline, and phyllocaline, such processes were not possible. This was clearly asserted by Went (1938a), who stated: "Independently of any previous theoretical considerations it has been shown in this paper that it is not the presence of auxin which determines whether elongation, swelling, or root formation will take place in a pea stem, but rather more specific, independent factors, which have been named 'calines.' Their existence so far has not been directly proven, but enough evidence has been collected to make their existence highly probable."

Very importantly, even though Went (1938a) referred to these substances as GFs, he also referred to them as a "hormone-like factor," and a "new group of plant hormones," potentially confusing the readership. While

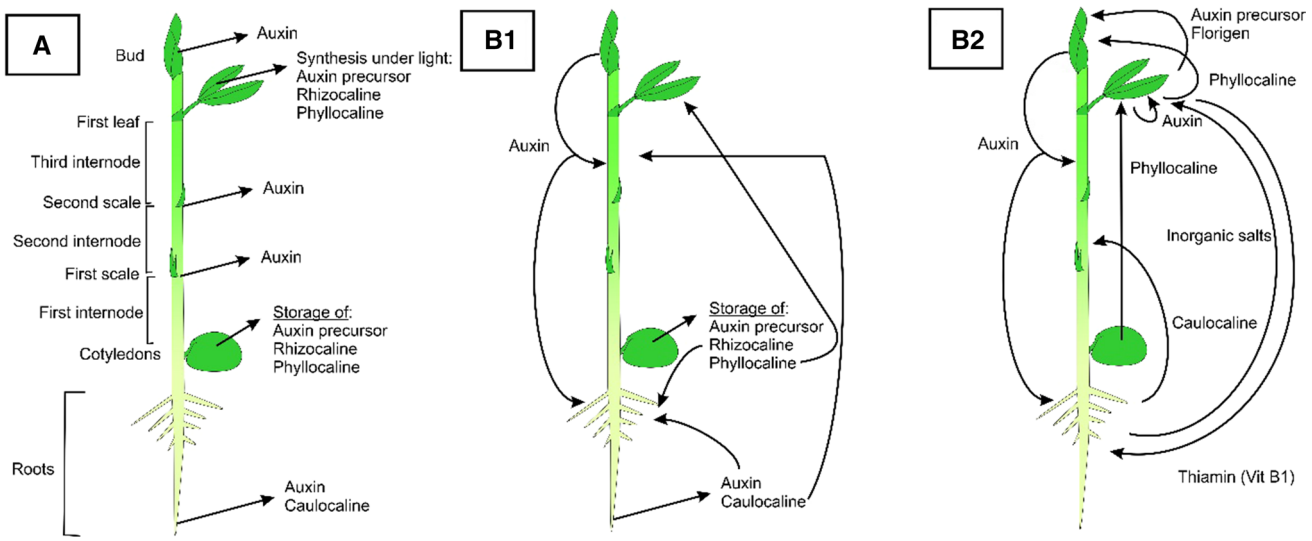


**Fig. 1** Organ-specific locations in a pea seedlings where different forms of caline are biosynthesized and stored according to Went (1938a) (**A**), as well as the biosynthesis, translocation, and storage pathways according to Smith and Kersten (1942) of peas germinated in the dark (**B1**) or light (**B2**). Picture A was inspired from figure 6 of Went (1938a), and B was inspired from this Fig. 1 and 2 of Smith and Kersten (1942)

natural substances that control plant growth are now referred to as (phyto)hormones or PGSs, synthetic substances are referred to as plant growth regulators, or PGRs (Macháčková et al. 2008), thereby annulling these ambiguous terms introduced by Went. Several of these terms that Went introduced in 1938 in international plant science journals appear to have already been used in earlier English and German publications between 1934 and 1936, including in his 1928 PhD thesis, as evidenced by the reference list in Went (1938a). However, these publications are impossible to access, given their local and restricted nature, so an assumption is made in this paper that the terms caline and its derivatives appeared in the international plant developmental literature in 1938. Most importantly, the evidence presented by Went (1938a, 1938b) experiments used seedling growth and a single plant species (pea), and no biochemical, physiological or other methods were used to assess the presence of these GFs. Went (1943a), in a continued series of trials related to grafting experiments involving peas, once again claiming that "the growth rate of the scion is limited by the supply of growth factors from the seed and not by the rate of translocation through stem or graft union," "the growth rate of the scions is determined by a growth factor other than auxin, coming from the stock," and that root growth and scion growth were correlated caused by "rhizocaline [which] also moves across a graft union, perhaps slightly lagging behind caulocaline, and that a continuous supply from the stock is needed to keep up the ability of scions to root," attributing the action to caulocaline and attributed the rooting of the scion to rhizocaline. Hayward and Went (1939) felt that caline-type GFs moved between stock and scion during grafting "under pressure" even when before the formation of vascular elements between them.

Additional experiments by Went and Bonner (1943) and Went (1943b) on tomato reinforced the notion that caulocaline produced in the roots was necessary for stem growth, but only when auxin and sugar were also provided. Howell and Skoog (1955), using pea, showed how adenine sulfate promoted the growth of in vitro epicotyls, not only reversing the inhibitory effect of IAA, but in fact being enhanced by the presence of IAA.

Went also attributed leaf size to the action of phyllocaline: "Leaf size of the scions apparently was determined by different amounts of stored phyllocaline in the cotyledons of the stocks" (Went 1974); "It is concluded that the cotyledons store a specific leaf growth substance, phyllocaline, which formed in leaves in the light" (Went 1938b); "Now it is possible that stipule growth requires the same factor (phyllocaline), and that in some way the distribution of the available phyllocaline over leaf and stipule is affected by the stock. […] the hypothesis of a special stipule-caline is premature, but in either case we need the assumption of a specific effect coming from the cotyledons" (Went 1938b).

According to schematics by Van de Sande Bakhuyzen (1947), all calines (the original term used was "caline substances") are produced in the same biosynthetic path as the vernalization regulator, vernaline (Fig. 2). According to Van de Sande Bakhuyzen, vernalase, the enzyme supposedly catalyzing vernaline biosynthesis from protocaline functions optimally in response to cold, vernaline synthesis is optimal under warm temperatures and short days, while anthocaline synthesis is optimal under warm temperatures and long days. Van de Sande Bakhuyzen also stated that anthocaline was transported from the leaves, where it was also formed, to the axil of the bractene. These earlier descriptions of the GFs related to flowering are somewhat confusing and crude, and a better understanding of the process now exists (see some later descriptions in this paper).

Even though Nešković (1967) claimed that the existence of caulocaline was confirmed by de Ropp (1946) in rye, an analysis of de Ropp's paper revealed no such claim, confounding the accuracy of the published literature on this topic.

## Current state of the existence of calines

Additional experiments by Went (Bonner et al. 1939) in pea suggested that the phyllocaline he had described for his earlier experiments might have been adenine (I) and hypoxanthine (III). Until the present, no further experiments were conducted to report the existence, analyze the chemical structures, or even to explain the signaling process by calines

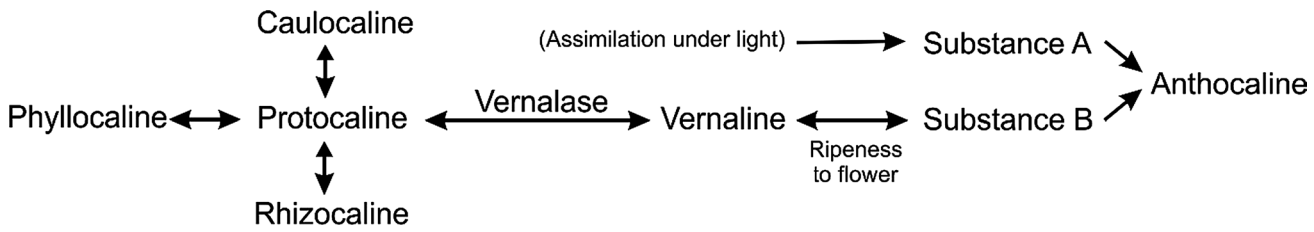


**Fig. 2** Caline–vernaline biosynthesis, according to Van de Sande Bakhuyzen (1947, p. 154, p. 156). Chouard (1960) referred to substance B as "florigen" B

initially proposed by Went and to a lesser extent by Van de Sande Bakhuyzen. Mendel (1992) stated that subsequent research rendered the term calines obsolete, a position we wish to reiterate in this paper.

Bouillene and Bouillene-Walrand (1952 *c.* Bastin 1966) proposed that rhizocaline is the product of a reaction catalyzed by an oxidase enzyme between auxin (indole-3-acetic acid or IAA) and an *o*-diphenol, i.e., an auxin-phenolic conjugate, but Bastin curiously failed to acknowledge the seminal work done by Went, while the experimental evidence provided by Bouillene and Bouillene-Walrand (1955) was shot down by Wilson and van Staden (1990) in a review as being insufficient and unsupportive of the conclusions drawn: "the existence of rhizocaline depends on whether these two classes of substances [IAA and phenolics] react together in vivo. The work of Bouillenne and Bouillenne-Walrand (1955) evidently does not demonstrate this." Thus far, there is no strong evidence to show that auxin-phenolic conjugates occur naturally in plants nor that they have roles in the formation of adventitious roots, i.e., that these may be rhizocaline (Wilson and van Staden 1990). Also, if IAA and rhizocaline are synergistic, the diphenolic compound that is hypothetically part of rhizocaline is actually a competitive inhibitor of IAA oxidase (Bastin 1966). Some researchers doubted the hormone-like nature of rhizocaline, a term that Kawase (1964) claimed was coined in Bouillenne and Went (1933), claiming that it might be a non-specific nitrogenous or carbohydrate compound such as the combination of sucrose and ammonium sulfate or arginine (Doak 1940 *c.* Kawase 1964; van Overbeek et al. 1946). Unlike the claim made by Kawase, Wilson and van Staden (1990) claimed that the term rhizocaline was coined by Went in 1929 (Went 1929), but there is no way to independently verify either claim given the lack of access to that literature. Skoog (1944) claimed that caulocaline was not needed for the initiation or growth of stems in hybrid tobacco tissue cultures, reinforcing disagreements by Skoog et al. (1942) with Went that as the cultures were kept actively growing in liquid medium, they grew to 30–50 mm, some even developing branched systems, i.e., without the need for caulocaline, while tobacco cultures also developed branched roots, suggesting that rhizocaline was not needed (Skoog 1944).

Reid et al. (1969), using tomato, stated that gibberellic acid ($GA_3$) is homologous to Went's (1938a) caulocaline. Hayes (1978) claimed that Went and Thimann (1937), a text that could not be accessed, "postulated two basic kinds of leaf growth factors: (a) caulocalines, such as IAA, which were identified as vein growth factors, and (b) phyllocalines, such as adenine, which are mesophyll growth factors." However, this statement appears to contradict the definitions provided by Went in 1938 (Went 1938a, 1938b) in which caulocalines complemented the activity of auxins and were not themselves auxins.

Similar to another hypothetical PGS coined by Chaïlakhyan (1937 *c.* Chaïlakhyan 1975), referred to as "florigen," the physiological nature of anthocaline continues to remain elusive. Florigen is only briefly discussed in this paper. According to Chaïlakhyan, "florigen" is synthesized in leaves, the same location that Van de Sande Bakhuyzen (1947) described as the place for anthocaline synthesis.

## Current models to explain the chemical control of plant growth and development

### Phytohormones in organ development

The discovery of cytokinins (CKs) in the 1950s as agents that promote cell division (Miller 1955a; b), as well as a study on tobacco growth and organ development in in vitro tissue culture (Skoog and Miller, 1957), began to show that the growth and development of different plant organs are primarily regulated by the balance of CKs and auxins. Later, the discovery of other phytohormones such as ethylene (Gane 1934), abscisic acid (Cornforth et al. 1965), gibberellins (MacMillan and Suter 1958), brassinosteroids (Grove et al. 1979), and jasmonates (Demole et al. 1962), and their roles in plant physiology and development, proved that they integrate different environmental and endogenous signals and thereby regulate different physiological and developmental processes (Weyers and Paterson 2001).

Current knowledge and models confirm what was basically hypothesized by Went, namely that in plants, the regulation of growth and development differs from that of animals. In animals, the regulation of physiological and developmental processes occurs by specific effect induced by a hormone, the classical "synthesis–transport–action" model in which a process is stimulated or inhibited, but in plants, such processes are regulated by multiple phytohormones or chemical signals whose ratio determines the morphogenic response (Weyers and Paterson 2001). Processes related to growth and developmental in plants are regulated instead by the balance, as well as spatial and temporal changes of theses chemical signals, including phytohormones (reviewed in Weyers and Paterson 2001), making the classical animal model of hormone action inapplicable to plants.

CKs are considered to be the main controllers and regulators of growth and development in plants, together with other phytohormones. The main site of CK biosynthesis is the root tip in intact plants, but they can also be biosynthesized in other tissues, such as cambial tissues, the shoot apex, or mature embryos (Kakimoto 2003). The biologically most active forms of CKs are the free bases (nucleobases), while their ribosides and ribotides, in which β-D-ribose or β-D-ribose-5′-phosphate are attached at the $N^9$-position, respectively, have lower activity but they are the major

transport forms. Transport within the plant occurs both by selective transport systems and diffusion (Sakakibara 2006). CKs play important and decisive roles in the regulation of the cell cycle, and they stimulate cell division, morphogenesis, the development and maturation of chloroplasts, shoot development, flower induction and seed development and maintain meristematic competence for growth (Werner et al. 2001; Kulaeva et al. 2002; Van Staden et al. 2008; Rijavec and Dermastia 2010; Cortleven et al. 2011; Ding et al. 2013). Plant growth, development and morphogenesis are mainly directed by the balance of auxins and CKs. A high ratio of auxins to CKs results in root formation from cuttings (Van Staden et al. 2008). In addition, as the auxin to CK ratio decreases, the morphogenetic pathway changes, through callus initiation in monocots, embryogenesis induction, adventitious root formation from callus, callus initiation in dicots, adventitious shoot formation to axillary shoot proliferation at the highest CK to auxin ratio (Van Staden et al. 2008; Fig. 3).

The CK signaling pathway occurs in multiple-step phosphorelays, including transmembrane histidine kinases (hybrid-type sensor kinases, AHKs; CK receptors), nuclear response regulators (ARRs; types A and -B), and histidine phosphotransfer proteins (AHPs) which transfer the signal from the CK receptors localized in the membrane (AHKs) to the ARRs in the nucleus. ARRs act as transcriptional modulators of primary response genes, or as modulators of other responses (nutrition, stress, light) (Ferreira and Kieber 2005; Rijavec and Dermastia 2010). In the model of auxin-mediated transcription activation during auxin signaling, auxin response factors (ARFs) have specialized functions, since auxin-regulated genes in plants are regulated via ARFs.

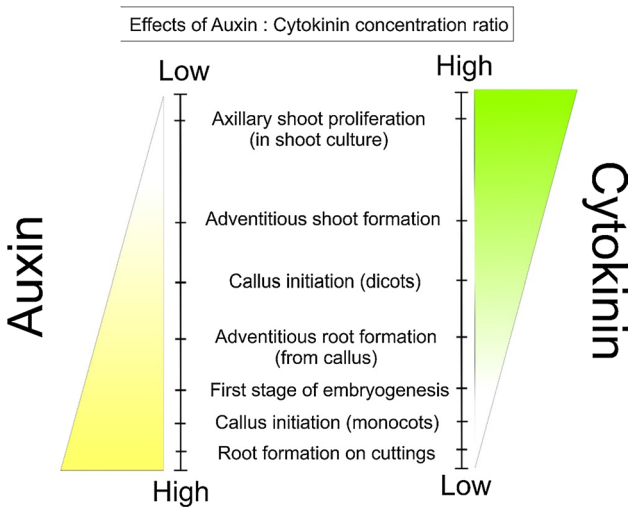


**Fig. 3** Relative auxin/cytokinin ratio determines the morphogenic outcome, according to and redrawn and modified from Van Staden et al. (2008, p. 220)

Degradation of the Aux/IAA repressor is a crucial step that allows the activity of ARF transcription factors and thus the auxin response by changing gene expression (Chapman and Estelle 2009; Fig. 4).

## Phloem-mobile chemical signals

Grafting experiments and molecular studies in recent decades (Wang et al. 2017; Ko and Helariutta 2017) have proved that classic phytohormones as well as other phloem mobile chemical signals that serve as regulators of growth and development also play a role in the signaling and regulation of growth and development and in communication between different plant organs. These signaling substances can be transported over a short or a long distance. Short-distance transport occurs via plasmodesmata, while the phloem plays an active role in the long-distance transport of these chemical signals (Ham and Lucas 2017; Kehr and Kragler 2018). Mobile RNAs, such as messenger (mRNA), silencing (siRNA), and micro-(miRNA) RNAs, play a role in signaling and regulation of gene expression and even in mediating epigenetic transgenerational memory in plants (Liang et al. 2011; Molnar et al. 2011; Pattanayak et al. 2013; Spiegelman et al. 2013; Kehr and Kragler 2018; Tamiru et al. 2017). They have a proven effect on the development of leaves, roots, tubers and flowering, their delivery is a well-regulated process, and RNA-binding proteins, which act as chaperons, protect RNAs from degradation and ensure their transport (Spiegelman et al. 2013). Besides mobile RNAs, different peptides delivered by the phloem, or even sucrose itself, may act as long-distance messengers and signaling molecules (Ko and Helariutta 2017).

## What is the nature of florigen?

Molecular genetic studies rendered probable that "florigen," i.e., the floral formation agent, is the product of *FLOWERING LOCUS T (FT)* mRNA or protein (Aksenova et al. 2006). Later studies (Shalit et al. 2009; Turnbull 2011; Kher and Kragler 2018) proved that FT is a phloem-mobile protein (and at a low concentration, also phloem-mobile *FT* mRNA), serving as a universal signal for flowering in addition to its other roles such as dormancy, tuberization, or meristem determination. Gibberellin or CKs, as the mediators of environmental signals, can induce flowering, depending on the plant species. Gibberellin in shoot tips may act as a direct transcriptional activator by activating a transcription factor which can bind to the *LEAFY* promoter, thereby activating the expression of *LEAFY* (Turnbull 2011). Moreover, gibberellin regulates *FT* by increasing its expression (Turnbull 2011). Although the direct action of a CK in shoot tips is highly probable, this has not been proved yet. However, CK can activate an *FT* homologue (*TSF*) (Turnbull 2011).

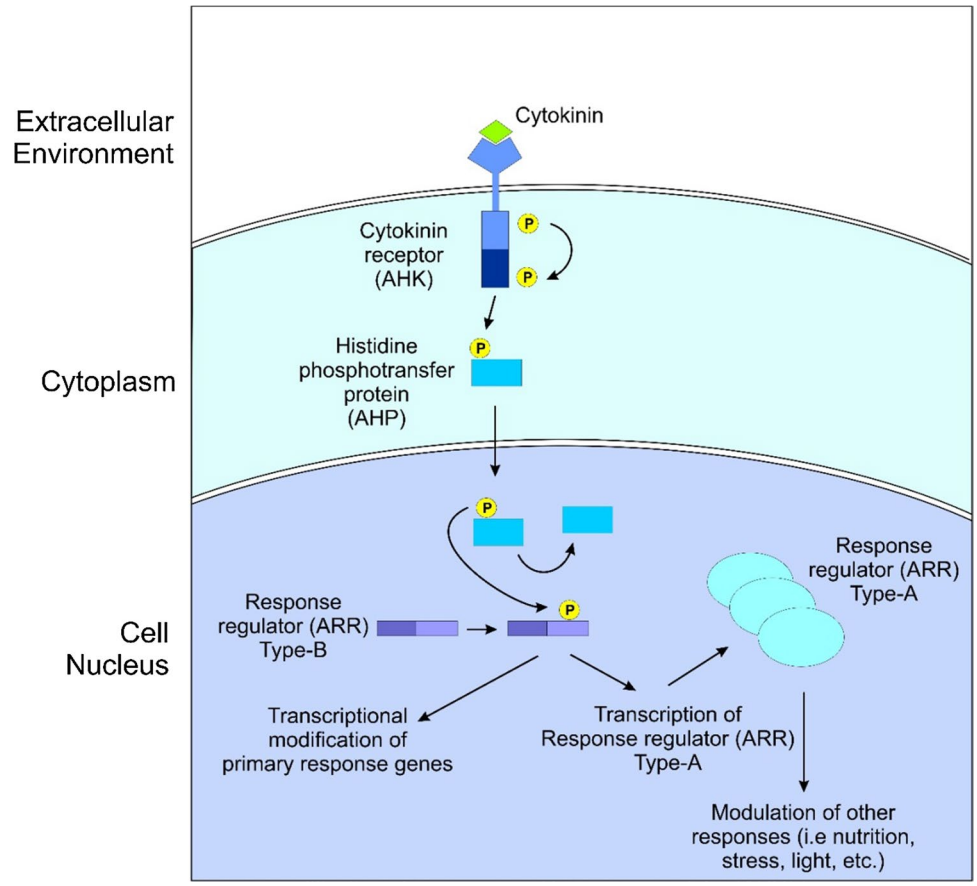


**Fig. 4** Multistep phosphorelays of cytokinin signaling pathways in plants, according to Schmülling et al. (1997), Ferreira and Kieber (2005), Hwang and Sakakibara (2006), and Rijavec and Dermastia (2010). Cytokinin receptors (AHK; transmembrane histidine kinases) in the plasmalemma in the presence of the signal (cytokinin) dimerize, and autophosphorylation occurs in the histidine parts of the kinase. In the second step, the phosphorylation of histidine phosphotransfer protein (AHP) in the cytoplasm is initiated by the phosphorylated AHK, which enters into the nucleus and transfers the phosphoryl group to the nuclear response regulators (ARRs; types A and B). The phosphorylated ARRs (ARR, type B) act as transcriptional modulators of primary response genes causing the activation of expression of the primary cytokinin response genes (type A ARRs). The type A ARRs then can partly regulate the cytokinin response (by negative feedback, mainly) and participate in other responses (like light or nutrition)

Phloem-mobile mRNA and protein from *ATC* (*CENTRORADIALIS*) is induced by short days and is a negative regulator of flowering, as it reduces the activity of FT (Kher and Kragler 2018).

## Conclusions for future biology

Calines are supposedly a currently existing group of chemicals, such as of PGSs, hormones or phloem-mobile mRNAs and proteins. In current models, chemical signals such as different phytohormones and mobile RNAs or peptides, involved in the regulation or formation of different organs, have now been discovered and identified. Apart from early proposals made by Went, no additional experimental evidence has emerged to support the existence of "calines," or to validate that the continued use of the term. We therefore propose the permanent retirement of these terms (caline, rhizocaline, caulocaline, phyllocaline, anthocaline) in the light of a fairly robust literature on the hormone-based regulation and functioning of PGSs and their signals associated with callus, root, stem, leaf and flower formation, respectively. Despite this posturing, the importance of such terms needs to be emphasized within a historical context in which terms evolve as experimental evidence sheds light at that time in history. The fact that bioactive root-initiating peptides, phytosulphokines, can also promote the formation of adventitious roots (Yamakawa et al. 1998) while auxin has not always been a fail-safe mechanism to induce adventitious roots in the stems of many deciduous e.g., *Salix pseudolasiogyne* (Park et al. 2008), *Salix sachalinensis* or *Morus alba* (Kärkönen et al. 1999) or herbaceous e.g., *Solanum tuberosum* (Kaur et al. 2015; Mohapatra and Batra 2017) plants, in which rooting was successful without the supply

of auxins, suggests that basic knowledge related to auxin signaling might still be lacking or evolving.

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## Declarations

**Conflict of interest** The authors declare no conflicts of interest of relevance to this paper.

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