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META-TOPOLIN, A HIGHLY ACTIVE AROMATIC CYTOKININ FROM POPLAR LEAVES (*POPULUS* × *CANADENSIS* MOENCH., CV. *ROBUSTA*)

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Key Word Index—*Populus* × *canadensis* Moench., cv. *Robusta*; Salicaceae; aromatic cytokinin; N^6-(*meta*-hydroxybenzyl)adenine; *meta*-topolin.

Abstract—A rapid analytical screening by high-performance liquid chromatography combined with enzyme-linked immunosorbent assay specific for N^6-(*meta*-hydroxybenzyl)adenine and its 9-substituted derivatives revealed several regions of immunoactivity in extracts of mature poplar leaves (*Populus* × *canadensis* Moench., cv. *Robusta*). The identity of the cross-reactive compounds was investigated by UV and mass spectrometry and after permethylation of unknown substances by gas chromatography-mass spectrometry. Physico-chemical analysis indicated the putative cytokinins are N^6-(*meta*-hydroxybenzyl)adenine and its 9-β-D-ribofuranosyl or 9-β-D-glucopyranosyl derivatives. The chemical structure was subsequently confirmed by synthesis. For N^6-(*meta*-hydroxybenzyl)adenine, a highly active aromatic cytokinin, we propose the trivial name '*meta*-topolin'.

INTRODUCTION

Cytokinins, N^6-substituted adenines with potent plant growth regulatory activity, are widespread in plants, animals and microorganisms as the free compound and as a component of *t*RNA [1]. Although there are rapid effects of these phytohormones on transcription, translation and membrane function, the molecular mechanism of cytokinin action remains unknown [2]. Until now, research has concentrated on the members of the 'isoprenoid' class of cytokinins as represented by zeatin, isopentenyladenine and dihydrozeatin. N^6-benzyladenine is still widely regarded as artificial in spite of reports of this compound, or its 2-hydroxylated analogues, in certain plant species [3–8] and tumor galls [9].

We were persuaded by evidence from cytokinin-binding proteins and metabolic studies that aromatic cytokinins must be more widespread and important as natural plant growth regulators than it appears at present. Thus, well authenticated cytokinin-binding proteins (putative receptors) have an unphysiologically low affinity for zeatin, the most active isoprenoid cytokinin, but bind preferentially to N^6-benzyladenine and its analogues [10]. In one case, the induction of cell division in tobacco callus, a classical cytokinin bioassay, the biological activity of various substituted N^6-benzyladenines agreed closely with their relative order of affinity for the binding protein [11]. Also, the levels of cytokinins with an aromatic side chain have been shown to alter in response to changes in the environment, e.g. N^6-(*ortho*-hydroxybenzyl)adenosine following exposure to light [12].

Extracts of poplar leaves (*Populus* × *canadensis* Moench., cv. *Robusta*) have been shown to contain substances immunoreacting with antisera raised against N^6-benzyladenosine-[9R]BAP, N^6-(*ortho*-hydroxybenzyl)adenosine-(oOH)[9R]BAP and N^6-(*meta*-hydroxybenzyl)adenosine-(mOH)[9R]BAP [7, 13]. In standard cytokinin bioassays the activity of these three compounds has been shown to increase in the order: (oOH)[9R]BAP < [9R]BAP < (mOH)[9R]BAP [10, 14]. The cytokinin (oOH)[9R]BAP has been identified in plants [3], as more recently has [9R]BAP [5], formerly regarded as existing only as the synthetic com-

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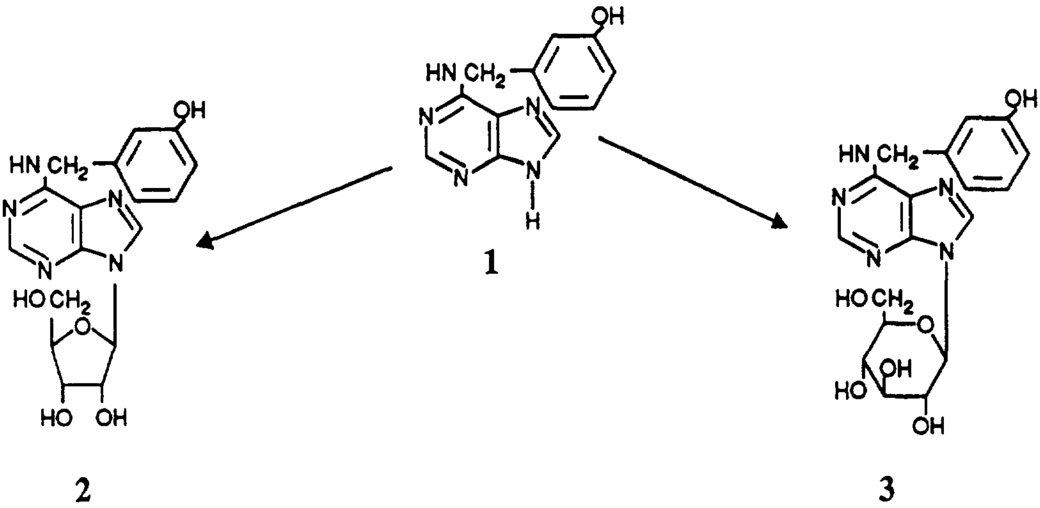

Fig. 1. Structural formulae of: 1; N^6-(*meta*-hydroxybenzyl)adenine-*meta*-topolin, 2; 6-(*meta*-hydroxybenzylamino)-9-β-D-ribofuranosylpurine-*meta*-topolin riboside, 3; 6-(*meta*-hydroxybenzylamino)-9-β-D-glucopyranosylpurine-*meta*-topolin 9-glucoside.

pound. Here we show that N^6-(*meta*-hydroxybenzyl)adenine-(mOH)BAP, for which we propose the name '*meta*-topolin', is a natural constituent of plant tissues, together with its 9-β-D-ribofuranosyl and 9-β-D-glucopyranosyl derivatives. This report reveals the existence in plants of a new and highly active growth substance, '*meta*-topolin', and establishes the fact of a class of natural growth substances, the 'aromatic cytokinins', differing from the isoprenoid cytokinins (zeatin, isopentenyladenine and dihydrozeatin) in biochemistry, receptors and biological activity.

RESULTS AND DISCUSSION

In view of the extremely high activity of synthetic (mOH)BAP and (mOH)[9R]BAP in a number of assays [10, 14–16], a search was made for related compounds in extracts of mature poplar leaves, a tissue known to be a rich source of aromatic cytokinins. Screening was by ELISA of HPLC fractions using antisera raised against (mOH)[9R]BAP (Fig. 1) conjugated to the protein carrier via the ribosyl moiety. The molecular recognition properties of the antibodies, therefore, enable the ELISA to be used to detect the free base, (mOH)BAP (Fig. 1), and 9-substituted derivatives such as riboside and 9-glucoside (Fig. 1) (unpublished data). Assay of HPLC purified extract of *P.* × *Robusta* leaves with the ELISA for (mOH)[9R]BAP detected four different regions containing immunoreactivity (Fig. 2). The major peak of activity co-eluted with authentic (mOH)[9R]BAP. On the basis of their chromatographic behaviour, peaks with retention time 14.2 min and 29.1 min (methanol–triethylammonium acetate (TEAA) gradient, Fig. 2(A) or 7.5 min and 20.4 min (MeCN–TEAA gradient, Fig. 2B) were tentatively identified as the 9-glucoside and free base, respectively. There was insufficient activity in the fourth, non-polar peak to allow further investigation.

Authentic standards of these compounds were chemically synthesized using as a basis the condensation of commercially available 6-chloropurine, its 9-β-D-ribofuranoside or its 9-β-D-glucopyranoside, with *meta*-hydroxybenzylamine [17]. The final products were recrystallized from ethanol to constant melting point and purified chromatographically. Pure fractions of both chemically synthesized compounds and material isolated from plants exhibited the following UV spectral characteristics ($\lambda_{\max}^{H_2O}$ nm, pH 2, 7, and 11): (mOH)BAP, 273.4, 269.0 and 269.5, typical for N^6-substituted adenine; (mOH)[9R]BAP, 268.5, 269.5 and 270.5, typical of N^6,9-disubstituted adenine; (mOH)[9G]BAP, 268.5, 267.0, 267.5, i.e. N^6,9-disubstituted adenine. Direct-probe EI-mass spectrometry (70 eV) produced ions for (mOH)BAP at *m/z* (rel. int.) 241 (100), 224(4), 148(5), 135(5), 122(100), 120(22), 107(8), 95(12), 77(19), 65(7); for (mOH)[9R]BAP at *m/z* (rel. int.) 373(17), 284(7), 270(13), 241(100), 224(5), 164(3), 148(8), 135(6), 122(40), 120(8), 107(12), 93(4), 77(6); and for (mOH)[9G]BAP at *m/z* (rel. int.) 403(8), 241(100), 192(16), 164(22), 148(8), 135(6), 122(40), 120(8), 107(12), 93(4), and 77(6). Fast atom bombardment mass spectrometry showed pseudomolecular ions at *m/z*: (mOH)BAP, 242; (mOH)[9R]BAP, 374; (mOH)[9G]BAP, 404. The advantage of this ionization technique is that it offers a more sensitive determination of the structure of unknown cytokinins. The potential of the method is demonstrated in Fig. 3 which shows both the positive ion fast atom bombardment and the electron impact mass spectra of (mOH)BAP.

To establish unambiguously the identity of the three unknown compounds isolated from plants, they were individually permethylated [18, 19], re-isolated by

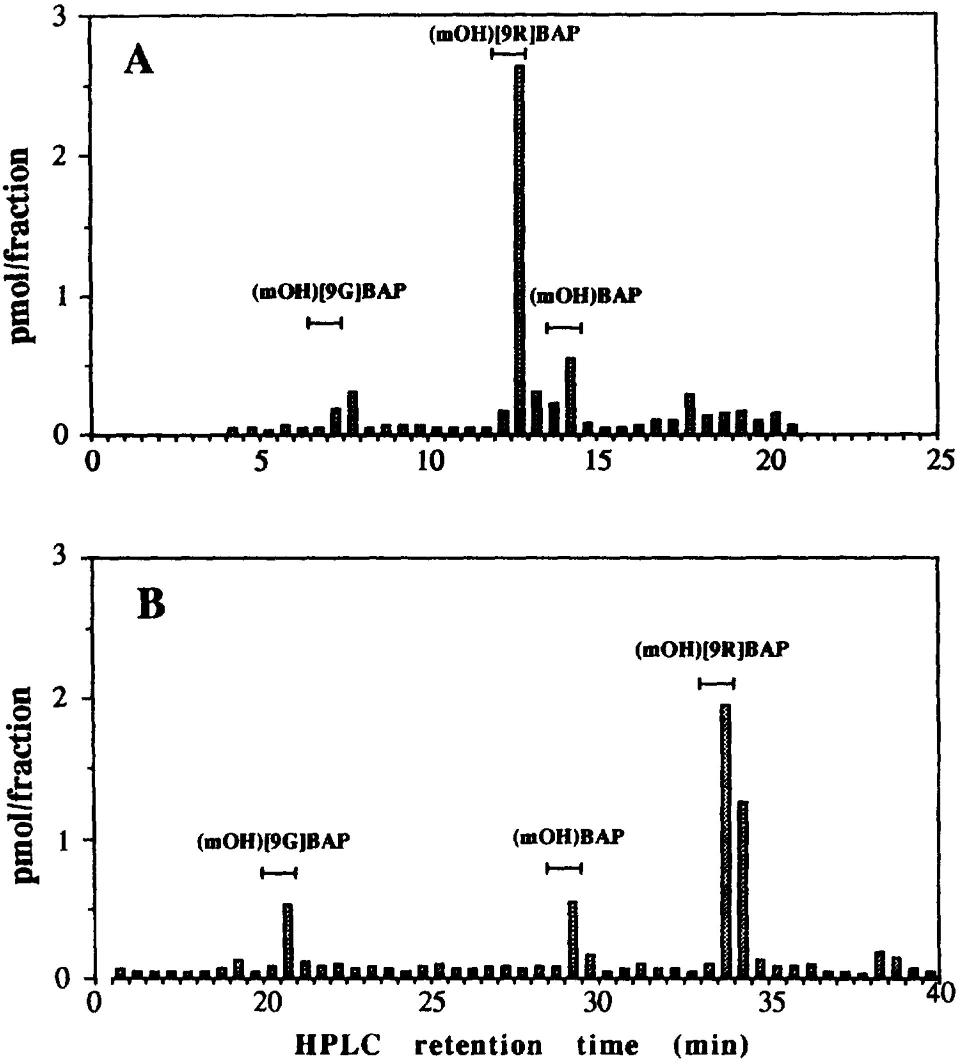

Fig. 2. HPLC–ELISA profiles of *meta*-hydroxylated aromatic cytokinins from mature poplar leaves. A methanolic extract was subjected to *n*-BuOH partitioning, cellulose phosphate chromatography and combined DEAE-cellulose-reversed phase chromatography [7, 27]. The partially purified extract was fractionated by HPLC on a Separon SGX C_{18} column, either (A) in a MeOH-TEAA gradient, at flow rate 1.0 ml min^{-1}, or (B) a MeCN-40 mM TEAA gradient, at flow rate 1.2 ml min^{-1}. Fractions of 0.5 ml (A) or 0.6 ml (B) were dried *in vacuo*, dissolved in 0.5 ml TBS (50 mM Tris–HCl, 10 mM NaCl, 1 mM $MgCl_2$, pH 7.5) and assayed by ELISA using antiserum raised against (mOH)[9R]BAP conjugated to carrier protein via N-9. The retention times of standard cytokinins differed slightly between runs due to varying chromatographic conditions and are indicated by horizontal bars.

HPLC and examined by GC-mass spectrometry. Each of the immunoreactive fractions with HPLC mobility identical to (mOH)BAP, (mOH)[9R]BAP and (mOH)[9G]BAP gave, when permethylated, derivatives that ran as single peaks on HPLC and dual FID-GC. EI-mass spectrometry of these components under GC-mass spectrometry conditions gave the following values for the molecular ion $[M]^+$ and major fragmentation ions at *m/z* (rel. int.): (mOH)BAP, 283(74) $[M]^+$, 268(100), 254(38), 239(4), 224(7), 176(11), 162(89), 150(68), 133(36), 121(21), 107(22); (mOH)[9R]BAP, 443(51) $[M]^+$, 428(3), 298(18), 269(78), 254(86), 240(26), 207(9), 174(7), 150(33), 148(52), 121(51), 101(32); and (mOH)[9G]BAP, 487(28) $[M]^+$, 456(3), 428(1), 298(8), 269(88), 254(64), 240(23), 148(37), 121(38) and 101(60). The fragmentation pattern is consistent with cleavages between the hydroxylated cytokinin side ring, the purine nucleus and a sugar moiety.

Evidence for the position of the side ring hydroxyl group in the compounds isolated from plant material is as follows: a high level of reactivity with antiserum raised against (mOH)[9R]BAP, but negligible reactivity with antiserum, raised against (oOH)[9R]BAP and co-chromatography with the chemically synthesized *meta*-hydroxy isomers in two HPLC systems as underivatized compounds (Fig. 2), and in HPLC, GC and capillary GC systems as the permethylated derivatives (unpublished results).

For accurate quantitation of the amounts of these

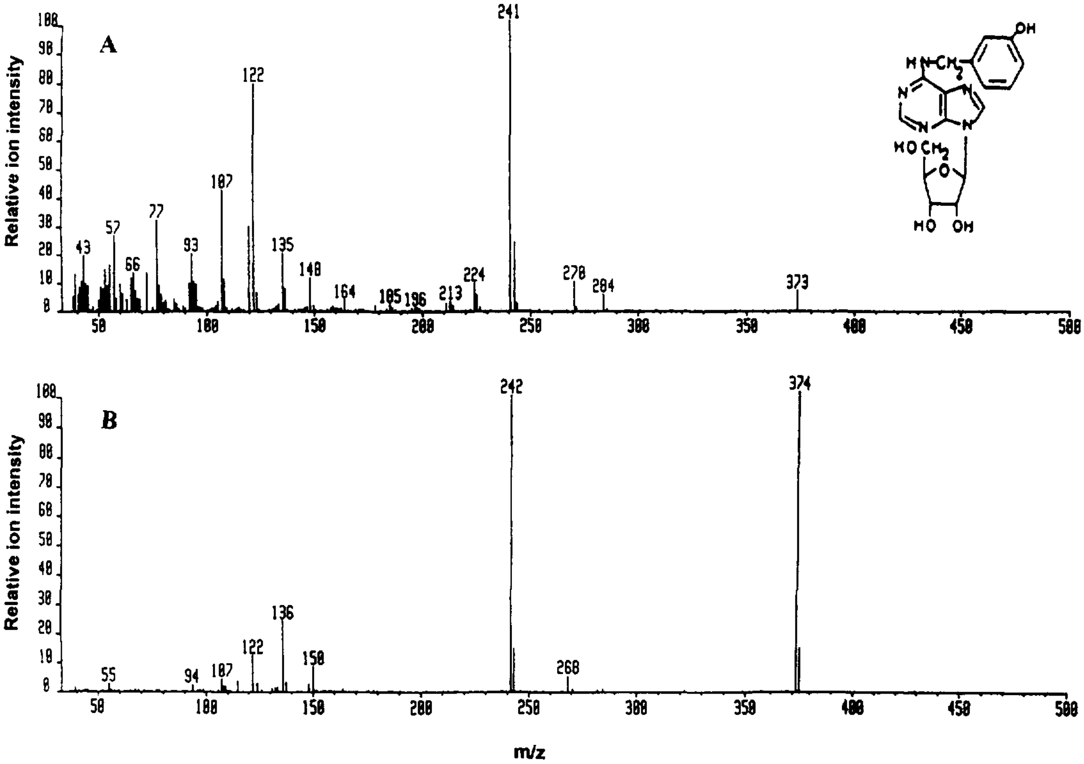

Fig. 3. Identification of N^6-(*meta*-hydroxybenzyl)adenosine by direct-probe (A) electron impact and (B) fast atom bombardment mass spectrometry. See text for details.

new cytokinins in poplar leaves, high specific radioactivity (approx. 1.0 TBq mmol^{-1}) [2-^{3}H](mOH)BAP and [2-^{3}H](mOH)[9R]BAP were synthesized and used as recovery markers, enabling measurements made by HPLC–ELISA to be validated by an internal standardization procedure. The endogenous levels in poplar leaves were determined as 22 ± 5 pmol g^{-1} fr. wt of (mOH)BAP, 37 ± 6 pmol g^{-1} fr. wt of (mOH)[9R]BAP, and 13 ± 3 pmol g^{-1} fr. wt of (mOH)[9G]BAP. These concentrations are at least two orders of magnitude lower than those reported for (oOH)[9R]BAP in mature poplar leaves [4].

The Aberystwyth group has referred to 6-(*ortho*-hydroxybenzylamino)purinyl compounds as 'populins' [4]. In recognition of their pioneering work in the discovery of aromatic cytokinins, we would have liked to adopt this name as a generic term for the natural hydroxybenzyladenines [20]. Sadly, this is not practical because 'populin' had already been used for salicin benzoate [21] a hundred years or so before it was adopted for (oOH)[9R]BAP. To avoid all confusion with salicin benzoate, a substance still in current use [22], we would like to propose instead the name 'topolins', derived from 'topol', the Czech word for a poplar, as the trivial name describing the N^6-(hydroxybenzyl)adenines. Further, we propose here the trivial names '*meta*-topolin' for N^6-(*meta*-hydroxybenzyl)adenine, '*meta*-topolin riboside' for 6-(*meta*-hydroxybenzylamino)-9-β-D-ribofuranosylpurine, and '*meta*-topolin 9-glucoside' for 6-(*meta*-hydroxybenzylamino)-9-β-D-glucopyranosylpurine. Appropriate abbreviations following Letham's system [23] would be 'mT', '[9R]mT' and '[9G]mT', respectively. It follows that it would be consistent to adopt the trivial name '*ortho*-topolin riboside' ([9R]oT) as the trivial name for 6-(*ortho*-hydroxybenzylamino)-9-β-D-ribofuranosylpurine, the aromatic cytokinin discovered by the Aberystwyth group [3, 4].

These three cytokinins were re-tested for biological activity in three different bioassays: stimulation of tobacco callus growth, inhibition of wheat leaf senescence, and dark induction of betacyanin synthesis in *Amaranthus* cotyledons (unpublished results). The high activity of *meta*-topolin and *meta*-topolin riboside, comparable to that of the most active isoprenoid cytokinin, zeatin, in these bioassays was confirmed. Glucosylation at N-9 decreased activity by at least 10-fold. The relative activity of different aromatic cytokinins seems to differ for different bioassays. While *ortho*-hydroxylated benzyladenosine was much less active than the unsubstituted benzyladenosine in the stimulation of soybean callus growth, the two cytokinins delayed the onset of radish leaf disc senescence to much the same extent [4]. In the stimulation of expansion of radish leaf discs, activity increased in the order *meta*-hydroxy < *ortho*-hydroxy < unsubstituted benzyladenine [16], in marked contrast to the results obtained more recently with other assays [10, 14, 15]. Differences in the biological activity of exogenous substances may well be comparatively trivial consequences of differences in transport or metabolism, but could indicate specialization of function for individual aromatic cytokinins.

The discovery that *meta*-hydroxybenzyladenines are natural components of plants adds a third, and active, member to what becomes thereby a class of natural plant growth substances, the aromatic cytokinins. To what extent the functions of the aromatic cytokinins in plants are distinct from those of the isoprenoid cytokinins remains to be discovered. Receptor studies [10] suggest that there is clear discrimination between aromatic and isoprenoid cytokinins at the earliest stage in the response to these compounds. It is interesting to note that *meta*-topolin is more active than zeatin and benzyladenine in the promotion of shoot formation in plant tissue cultures [24, 25].

EXPERIMENTAL

Plant material. The expanded, fully developed and photosynthetically active leaves were harvested for cytokinin analysis from poplar trees (*Populus* × *canadensis* Moench., cv. *Robusta*) growing in the field to the west of Olomouc, Czech Republic. Detached leaves were frozen immediately with liquid nitrogen and then extracted or stored at -70° until use.

Cytokinins and other reagents. Unlabeled cytokinins were from Apex Organics (Leicester, U.K.); isopentenyladenosine, isopentenyladenine, zeatin, zeatin riboside, dihydrozeatin, dihydrozeatin riboside, kinetin, N^6-benzyladenosine, N^6-benzyladenine, and N,N′-diphenylurea were from Sigma (St Louis, MO, U.S.A.); 6-(*ortho*-hydroxybenzylamino)-9-β-D-glucopyranosylpurine, 6-(*meta*-hydroxybenzylamino)-9-β-D-glucopyranosylpurine, [2-^{3}H]N^6-benzyladenine, [2-^{3}H]N^6-benzyladenosine, [2-^{3}H]N^6-(*meta*-hydroxybenzyl)adenine and [2-^{3}H]N^6-(*meta*-hydroxybenzyl)adenosine (specific activity approx. 1.0 TBq mmol^{-1}) were prepd (unpublished results) from 6-chloropurine, 6-chloro-9-β-D-ribofuranosylpurine, 2,6-dichloro-9-β-D-ribofuranosylpurine and 6-chloro-9-β-D-glucopyranosylpurine (Sigma, St Louis, MO, U.S.A.). *Meta*-hydroxybenzylamine was prepared as previously described [25]. All other chemicals were obtained from Lachema (Brno, Czech Republic) or have been cited in ref. [26].

Extraction, purification and estimation of cytokinins. A methanolic extract of fully developed poplar leaves (100 g fr. wt) was subjected to *n*-BuOH partitioning, cellulose phosphate chromatography and combined DEAE-cellulose–reversed phase chromatography [7, 27], in that order. High specific radioactivity (approx. 1.0 TBq mol^{-1}) [2-^{3}H](mOH)BAP and [2-^{3}H](mOH)[9R]BAP were synthesized and used as recovery markers during purification and fractionation of extracts.

The partially purified extract was fractionated by HPLC on a Separon SGX C_{18} (Tessek, Prague, Czech Republic) column, either (A) in a MeOH–TEAA soln gradient at flow rate 1.0 ml min^{-1} [7, 27], or (B) an MeCN $-$ 40 mM MeOH–TEAA soln gradient at flow rate of 1.2 ml min^{-1}. Frs of 0.5 ml (A) or 0.6 ml (B) were dried *in vacuo*, dissolved in 0.5 ml TBS (50 mM Tris–HCl, 10 mM NaCl, 1 mM $MgCl_2$ pH 7.5) and assayed by ELISA using polyclonal antibodies raised against (mOH)[9R]BAP. The assay was performed using a modification of the ELISA protocol previously described [7, 27]. The cytokinin value obtained by the ELISA of the frs containing [2-^{3}H] labelled cytokinin was corrected by the appropriate cross-reactivity and recovery values to obtain estimates of cytokinin levels in plant tissue (expressed as (mOH)[9R]BAP equivalent). If there was any spread of radioactivity into a second fraction, the cytokinin content was estimated from the fractions containing radioactivity. Levels of 9-glucosides were calculated from immunoactivity (in the appropriate ELISA) of frs collected at the retention time of authentic standards and on the assumption that recovery for these cytokinins was the same as the recovery of [2-^{3}H]ribosides.

Derivatization and identification. Methanolic solns of chemically synthesized compounds, or HPLC frs containing immunoreactive material isolated from poplar leaves, were evapd in 1-ml hypovials (Pierce, Chester, U.K.) and dried *in vacuo* over P_2O_5. The residues were permethylated by reaction with MeI in the presence of an excess of dimethylsulphinyl carbanion in DMSO [18, 19]. The reaction was terminated by addition of an equal volume of H_2O and partitioned into 100 μl $CHCl_3$, and dried in a stream of N_2 gas. The purity of permethylated compounds was checked by dual FID-GC: 3 m × 0.4 cm i.d. glass column, packed with 3% OV-1 on Diatomite C (Pye Unicam, Cambridge, U.K.); He carrier gas, flow rate 45 ml min^{-1}; 200° for 3 min, then to 300° at 8° min^{-1}. Permethylated standards and samples were purified by HPLC: 150 × 4 mm i.d., 5 μm Microsorb C_{18} (Rainin Instr., Woburn, U.S.A.), mobile phase: 30 min linear gradient of 10–50% MeCN in 40 mM TEAA soln, pH 3.35, flow rate 1 ml min^{-1}. UV absorbing frs were dried under N_2 stream, dissolved in $CHCl_3$ and subsequently analyzed by GC-MS: 15 m × 0.32 mm, i.d. quartz capillary column, 0.5 mm polydimethylsiloxane; He carrier gas, flow rate 2 ml min^{-1}, from 100° at 15° min^{-1} to 320° and 320° for 10 min. Mass spectrometry was by electron impact ionization at 70 eV, on a VG Masslab Model 12–253 quadrupole, using 1.1 second cyclical scans from 33 to 900 amu. FAB measurements were made with a VG ZAB-E instrument using 8 kV xenon atoms.

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