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*Mini-Review*

# Novel Natural Substances Acting in Plant Growth Regulation

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**Abstract.** This review includes novel natural products of microbial and plant origin reported to exert plant growth-regulating activities. The well-known "classic" plant hormones are excluded. The substances described with their biological activities are restricted to those that have been isolated from microbial or plant sources later than 1990 or that have been intensively investigated during the last few years, such as jasmonic acid and brassinosteroids.

Microorganisms and plants possess the capacity to synthesize a large number of organic compounds of an enormous chemical diversity and belonging to quite different chemical classes. Many of these natural products were found to be biologically active either within the organisms producing these metabolites, or they exhibit different biological activities when used in bioassays. To our knowledge more than 300 microbial, and so-called secondary plant products possessing bioregulatory activity in plant systems have been detected and described in the literature.

This review includes natural products of microbial and plant origin connected with plant growth regulatory activities, which are isolated later than 1990 or have been studied in more detail during the last few years. The well-known plant hormones, such as auxins, cytokinins, gibberellins, abscisic acid, and ethylene, have been the subject of numerous recent reviews and monographs and are excluded from this presentation.

The authors are aware of the imbalance in specific knowledge between the various substances reviewed in this article. In contrast to more extensively studied substances, such as jasmonates, brassinosteroids, and salicylic acid, many of the other compounds called *plant growth regulators* are just generally checked in biotests or similar preliminary experiments. Some of them may be excluded later if more specific studies enable us to discriminate real "plant growth regulators" from substances that simply inhibit or reduce plant growth as secondary or tertiary effects. They are grouped in the sections under Stimulators and Inhibitors, where the former compounds are selected in separate sections due to their chemical structures.

This review complements and supplements previously published review articles on this topic (Asakawa 1990, Bearder 1980, Cutler 1991, Gross 1980, 1991, McLaren 1986, Sembdner and Gross 1986, Takahashi 1986). The role of few selected oligosaccharides (acting at very low concentrations and termed *oligosaccharins*) as novel signalling molecules and their effects on plant growth and development was described recently (Aldington and Fry 1993, Darvill et al. 1992, Fry et al. 1993) and therefore are not included in this article. The polyamines have been reviewed by several authors (Galston and Sawhney 1990, Bagni and Torrigiani 1992, Kakkar and Rai 1993) and are also excluded.

## Jasmonates

In recent years probably no other plant-derived compounds came more into the focus of plant biochemists and physiologists than jasmonates or jasmonins, that is, *jasmonic acid* (JA) and related mol-

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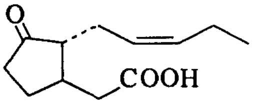
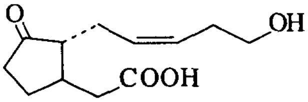
ecules. Following early detection and chemical identification from *Jasminum, Rosmarinum,* and other plants containing fragrant essential oils, jasmonic acid and, in particular, its volatile methyl ester (MJ) have been detected in any plant species investigated so far, even in algae (Sembdner and Parthier 1993, for refs.). The biosynthetic pathway starting with linolenic acid via cyclic intermediates, for example, 12-oxophytodienoic acid, was elucidated (Vick and Zimmerman 1984) and some metabolites are described (Sembdner and Parthier 1993).



(-)-jasmonic acid



tuberonic acid

Several hormone-like aspects and in particular the ubiquitous occurrence of jasmonates in plants was the basis for research on the modes of JA actions in plant growth and development. The impression of a pleiotropic action (Fig. 1), here simply classified as induction, promotion, and inhibition, respectively, might reflect a multiplicity of organ- and cell-specific reactions, however, it could hide a central or basic mode of action at the molecular level as well. The tendency in recent experimental results favors the latter, especially since molecular biological and genetical methods have been successfully used.

Therefore, in addition to the reviews written in the last years (Parthier 1990, 1991, Van den Berg and Ewing 1991, Hamberg and Gardner 1992, Koda 1992, Staswick 1992, Sembdner and Parthier 1993, Wasternack 1994) and due to space limitations, this section on jasmonates refers only to the most recent articles in order to illustrate progress of our knowledge in the mode(s) of action(s) of JA and related structures. Major aspects that will be discussed in more detail are (1) gene expression regulated by jasmonates; (2) jasmonates involved in signal transduction of stress responses; and (3) other jasmonate-mediated physiological processes (tuberization, senescence), and interference with abscisic acid (ABA).

## *Gene Expression Regulation by Jasmonates*

The first detection in our laboratory of jasmonate-induced proteins (JIPs) in barley leaf segments (Weidhase et al. 1987) gave a first hint to specific

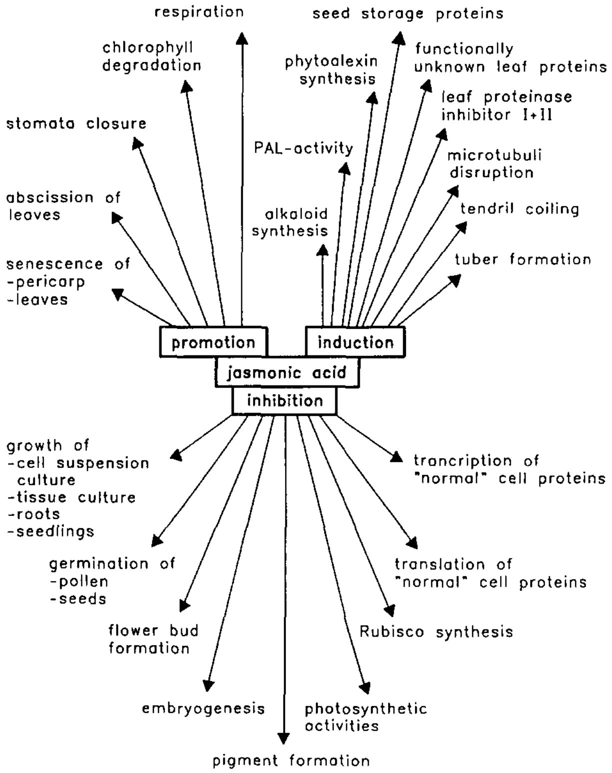


**Fig. 1.** Multiplicity of jasmonate effects in plants (courtesy of Dr. C. Wasternack).

gene expression elicited by jasmonates (Parthier 1990, 1991). Meanwhile, other laboratories reported JA-induced proteins in various species (review: Sembdner and Parthier 1993). Some of these inducible proteins were characterized by molecular sizes, still less by their functions, and, finally, by their gene sequences (Andresen et al. 1992, Becker and Apel 1992). High species-specificity seems to be a peculiarity for JIPs, and, in some cases, specificity is even observed for varieties, for example, of *Hordeum vulgare* (Herrmann et al. 1989). On the other hand, probably the same JIPs in the same plant species are induced by exogenous ABA as well (see below).

Concerning putative functions of JIPs, the observation became important that a set of JIPs can be induced by several but not any stress conditions, in particular, osmotic stress (sorbitol, mannitol), desiccation, or wounding, however, not temperature stress or treatment with salts (Parthier et al. 1992). These data indicate stress-induced JIP formation as a result of stress-mediated increase in endogenous jasmonates as signalling substances, which, in turn, leads to the activation of specific (JIP-) genes. The elevated concentration of endogenous JA is rather due to de novo synthesis from linolenic acid than by remobilization of preexisting jasmonate metabolites like amino acid conjugates, hydroxylated or glucosylated structures (Sembdner and Parthier 1993), although the latter cannot be excluded at present, and even a concomitant de novo synthesis of JA as well as its liberation from metabolites seems to be possible. Additional complication emerges by the observation that metabolized sugars (sucrose, glucose) are likewise JIP-inducible compounds, but not 2-deoxyglucose. Obviously, the increase of endogenous jasmonates is not caused by the osmolality of the carbohydrates as a stress factor (J. Lehmann, personal communication). A coregulation of JA and sugars in vegetative storage protein induction was also suggested (Mason et al. 1992). Altogether, the results available strongly suggest a role of jasmonates in signal transduction towards cellular stress responses (see below).

Some jasmonate-induced proteins were structurally or functionally identified as molecules involved in stress protection. Proteinase inhibitors were the first enzymes dramatically increasing upon wounding in tomato (Pena-Cortés et al. 1989, 1991, Farmer and Ryan 1992) or after exposition of the plants in an atmosphere containing volatile MJ (Farmer and Ryan 1990). Another candidate was a thionin (JIP-6) accumulating after exogenous treatment of barley leaves with MJ (Andresen et al. 1992). One of the vegetative storage proteins induced by JA (Staswick et al. 1991) was identified as a lipoxygenase (Bell and Mullet 1991, Tranberger et al. 1991, Grimes et al. 1992), a key enzyme in the biosynthetic pathway of jasmonates.

Although most of the barley JIPs await identification of their functions, as stress-responsive elements they might play a role in the protective system of the plant cell against the type of stress in question, for example, desiccation, osmotic changes etc., similar to dehydrin induction in connection with desiccation and ABA-moderated protein induction (Close et al. 1989, Piatkowski et al. 1990, Skriver and Mundy 1990). Nevertheless, the cDNA sequences already elucidated for JIP-23 and JIP-37 do not favor larger sequence homologies with these proteins, and relatedness with late embryogenesis abundant (LEA) proteins may be questionable, too (Wasternack 1994). A very interesting molecule is barley JIP-66. The N-terminal moiety of its sequence (Becker and Apel 1992) has been suggested to be a putative ribosome inactivating protein (RIP) (Reinbothe et al. 1993b, F. Müller-Uri and J. Mundy, personal communication). Its function is likely connected with the jasmonate-induced repression of normal cell proteins (Müller-Uri et al. 1988) in the initiation phase of protein synthesis (Reinbothe et al. 1993a). It can be suggested that JA disintegrates polysome complexes containing mRNA specific for "control" proteins, probably during translation initiation (Reinbothe et al. 1993b). Thus, in addition to the positive control jasmonates exert in the induced expression of JIP genes at the transcript level, the same compounds regulate the amount of "house-keeping" proteins at the translational niveau, if exogenously added jasmonates or stress-induced endogenous jasmonates contact indirectly via RIP the protein synthesizing machinery in normal tissues or cells. In this case, JA should exert a sequential control: first activation of JIP (RIP) genes and transcription/translation to RIP polypeptide; second, the inactivating interaction of RIP with the ribosomal decoding machinery for normal cell proteins, for example, for RuBPCase and other nuclear-encoded plastid constituents (Reinbothe et al. 1993a,c, Roloff et al. 1994). MJ-induced changes in the intermolecular base pairing between RuBPCase mRNA and 16 S rRNA seems to impair RuBPCase translation initiation (Reinbothe et al. 1993c).

### *Jasmonates Involved in Signal Transduction of Stress Responses*

Jasmonates have been proposed as inter- and intracellular signal transducer in cells attacked by herbivores or otherwise wounded tomato plants (Farmer and Ryan 1990, 1992, Pena-Cortés et al. 1991) and in sorbitol-stressed or desiccated leaf tissues of barley as well (Parthier 1991). In both cases the externally stressed tissues or plants respond with a marked increase of endogenous jasmonates prior to the formation of stress proteins—proteinase inhibitor as a defense molecule (Creelman et al. 1992) or other JIPs (Parthier et al. 1992).

The signal transducer hypothesis (Parthier 1991, Ryan 1992) was supported by experiments with plant cell suspension cultures exposed to pathogen attack or treated with elicitor preparations from fungal cell walls. These results suggested the existence of pathogen-responsive genes in various plant species, and these genes coding for certain secondary metabolites are switched on when the endogenous content of (−)JA accumulates 50-fold or more (Gundlach et al. 1992, Kauss et al. 1992). The induction of phytoalexin formation, especially enzymes involved in this pathway (phenylalanine-ammonium lyase, chalcone synthase), is strictly correlated with the increase of endogenous jasmonates or its biosynthetic precursor, 12-oxo-phytodienoic acid (Dittrich et al. 1992), as a result of release of α-linolenic acid, the starting precursor molecule for JA, from the lipid pool of the plant cells (Mueller et al. 1993). It should be mentioned in this connection that a signal function of jasmonates could not be observed in other pathogen–plant interactions, for example, between barley and powdery mildew by *Erysiphe graminis* (Schweizer et al. 1993, C. Wasternack, personal communication). The cyclopentanones did inhibit appressoria differentiation of the fungus and thus protected the barley tissue against infection, however, the induction of pathogenesis-related proteins was not influenced by jasmonates (Schweizer et al. 1993).

Another convincing example in favor of jasmonates (or their octadecanoid precursors) playing a role as signalling substances was demonstrated with coiling tendrils (Weiler 1993). The perception of mechanical touch is vital for winding and climbing plants such as *Bryonia dioica,* the tendrils of which react rapidly to a mechanical stimulus by forming tight but flexible spirals caused by differential flank growth. In order to study the molecular basis of the coiling process the chemical nature of the signals involved between mechanical touch and differential growth reactions was found to be α-linolenic acid (Falkenstein et al. 1991), but MJ appeared to be the most potent inducer, acting in nanogram quantities (Weiler 1993, Weiler et al. 1993). Airborne MJ could completely substitute the tactile stimulus.

In conclusion, there is now sufficient evidence for addressing linolenic acid-derived jasmonates (or intermediate precursors) as participants in inter- and intracellular transduction processes between external stress (herbivore, pathogen, desiccation, mechanical, or osmotic stresses) and macromolecular stress responses in the cells, as a rule, activation of "defense genes." Among the still open questions of this signal transduction chain is the origin of linolenic acid, in spite of indications supporting the release of fatty acids from damaged cell membranes due to the external stress. MJ is most probably the best candidate among signalling molecules that initiates the cellular defense system and, as an inducer of lipoxygenase (Grimes et al. 1992), in sequence controls a cascade process of defense response by the plant or its organs (Farmer and Ryan 1992, Mueller et al. 1993).

### *Other Jasmonate-Mediated Physiological Processes (Senescence, Tuber Induction) and Interference with ABA*

Of the collection of jasmonate effects on different physiological processes (Fig. 1), promotion of leaf senescence was one of the first phenomena described, because of the obvious JA-induced changes from green to yellow colors and other typical senescence-related phenomena (Parthier 1990, for review). The critical question was whether or not the senescence syndrome is directly connected with the induction of new proteins (JIPs). Kinetic studies and various molecular biological evidence provided in the meantime do not suggest a direct or even causal relationship. Yellowing of JA-treated leaf tissues is either a secondary or tertiary consequence of the induction of new JIPs (among them probably degrading enzymes) or of repressed biosynthesis of normal proteins by JA, for example, in plastids, or of these two regulatory functions of jasmonates in protein metabolism together. Such general suggestion should not exclude identical genes which can be activated by both darkness-induced normal senescence and MJ treatment of barley leaves (Becker and Apel 1993).

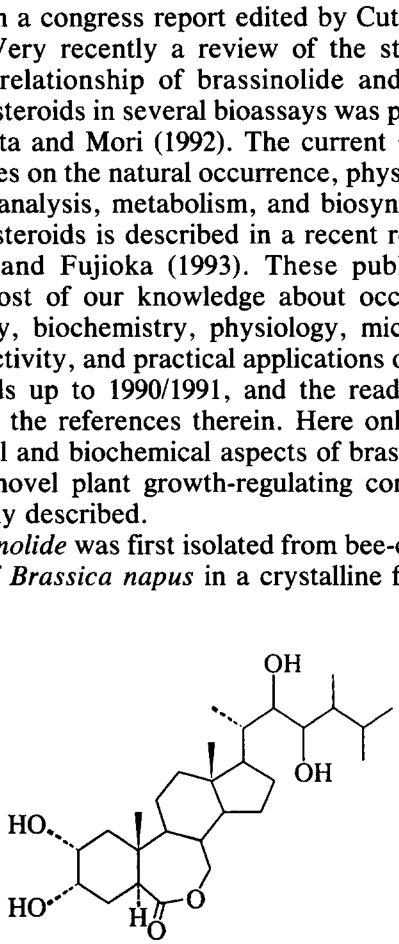
Most interesting is the tuber-inducing effect of jasmonates in general and *tuberonic acid* (12-hydroxylated jasmonic acid) in particular. Tuberonic acid is likewise active and often occurs as its O-glucosylated derivative (Yoshihara et al. 1989, Koda et al. 1991), presumably a transport form of tuberonic acid. Its tuber-inducing capacity was observed with potato and yam stolons in vitro (Koda and Kikuta 1991, Pelacho and Mingo-Castel, 1991), and the molecular level of action was suggested as changes in the microtubuli system of the competent potato cells (Koda 1992, Matsuki et al. 1992).

The identity or at least similarity between the pattern of induced abundant barley JIPs upon exogenous addition of either JA or ABA belong to our earlier observations (Weidhase et al. 1987, Reinbothe et al. 1992), which have been confirmed also in other laboratories (Pena-Cortés et al. 1989, Melan et al. 1990, Hildmann et al. 1992). In tomato leaves ABA seems to be a wounding signal which via jasmonates induce proteinase inhibitor II (Pena-Cortés et al. 1991). Nevertheless, this mode of signalling must not be valid in any plant species (Wasternack 1994), but the assumption that can be made is that JIP formation seems to be always connected with the presence of endogenous jasmonates, since addition of inhibitors of lipoxygenase as one of the key enzyme in jasmonate biosynthesis results in depressed formation of JIPs (Wasternack et al. 1994). However, in the presence of inhibitors of ABA synthesis, or by the use of ABA-deficient mutants, JIP formation takes place in the same order of magnitude as in control or wild-type plants, respectively (Wasternack 1994). These experiments suggest a role of ABA rather auxiliary than basic in the stress signal transduction chain, but it may differ among various species.

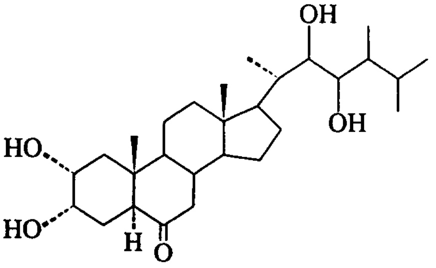
## Brassinosteroids

The brassinosteroids consist of a group of biologically active natural products based on a steroidal structure. They exhibit multiple bioregulatory activities on plant growth and development and are, therefore, considered as a new class of plant hormones. The history and advances in brassinosteroid research is well documented in excellent reviews recently published by Abe (1989), Adam and Petzold (1994), Ikekawa (1991), Mandava (1988), Marquardt and Adam (1991), and Sasse (1991) as well as in a congress report edited by Cutler et al. (1991). Very recently a review of the structure–activity relationship of brassinolide and related brassinosteroids in several bioassays was published by Yokota and Mori (1992). The current status of the studies on the natural occurrence, physiological actions, analysis, metabolism, and biosynthesis of brassinosteroids is described in a recent review of Sakurai and Fujioka (1993). These publications cover most of our knowledge about occurrence, chemistry, biochemistry, physiology, microanalysis, bioactivity, and practical applications of brassinosteroids up to 1990/1991, and the reader is referred to the references therein. Here only recent biological and biochemical aspects of brassinosteroids as novel plant growth-regulating compounds are briefly described.

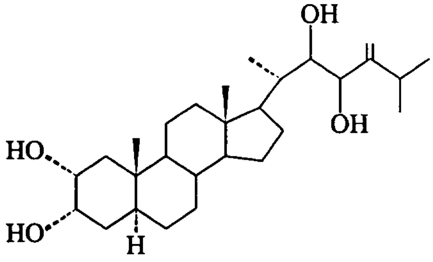
*Brassinolide* was first isolated from bee-collected pollen of *Brassica napus* in a crystalline form and structurally elucidated in 1979 by spectroscopic analysis and X-ray diffraction. It was the first member of a new group of naturally occurring plant growth-regulating substances. Later, a structurally related compound, *castasterone,* was isolated from insect galls of *Castanea crenata* and some other plants. It contains a 6-membered 6-ketonic B-ring instead of the 7-membered 7-oxalactone B-ring of brassinolide. Another structural type of brassinosteroids possessing a nonoxidized B ring is represented by *6-deoxodolichosterone* from immature seeds of *Dolichos lablab.*



brassinolide



castasterone



6-deoxodolichosterone

After the discovery of brassinolide, numerous structurally related plant constituents with plant growth-promoting properties were isolated and identified in different plant sources by using a combination of highly sensitive bioassays and modern microanalysis including GC/MS, GC/SIM, HPLC, and RIA. Naturally occurring brassinosteroids are all 5α-cholestane derivatives and can be grouped into polyhydroxylated $C_{26}$-, $C_{27}$-, and $C_{28}$-steroids. The structural variations of the native members depend on both the B-ring oxidation stage and the kind and orientation of substituents in the cyclic part and also at the side chain linked to C-17.

Nowadays these natural plant growth regulators are assumed to represent a uniform class of plant hormone-like bioregulators commonly termed *brassinosteroids.* Hitherto about 30 fully characterized native brassinosteroids and two brassinosteroid sugar conjugates are known. Brassinosteroids are found through the plant kingdom including gymnosperms, monocotyledons, dicotyledons, and algae. Brassinosteroids can be isolated from most parts of the plant, especially from pollen, immature seeds, and insect galls but also from leaves, stems, shoots, fruit, and other vegetative organs. Both type and level of brassinosteroids vary in different plant tissues, organs, and species. Pollen contains relatively high concentrations (about 100 μg/kg), whereas the content of other plant tissues is in the range of nanograms. Brassinolide and castasterone were found widely distributed and exhibit marked biological activities. Thus, they represent the most important and well-studied native brassinosteroids.

The actions of brassinosteroids were tested in a variety of bioassays and were found to exhibit potent bioregulatory effects at micromolar and lower concentrations. Among them, brassinolide exhibits the highest biological activity for inducing plant growth-promoting effects in various bioassays, for example, in the most sensitive and specific rice lamina inclination assay with a detection limit of $10^{-13}$ M.

Brassinosteroids were reported to exhibit multiple bioregulatory activities and to elicit multiple growth and developmental processes, such as stimulation promotion of plant growth by promoting cell elongation and cell division, increase of crop yields and biomass production, ''antistress'' effects by compensating cold and salt stresses, stimulation of ethylene biosynthesis, interactions with the effects of auxins and abscisic acid, and further, little understood changes of metabolic and growth processes in general.

Some recent communications deal with the following additional biochemical and physiological aspects of brassinosteroids. A radioimmunoassay developed for brassinosteroids seem to be a potent method to determine the amounts of brassinolide and castasterone (Yokota et al. 1990b). This RIA with a detection limit at 0.3 pmol was successfully used to estimate the endogenous brassinosteroid levels in seeds and stems of *Phaseolus vulgaris*. Recently, the co-occurrence of castasterone and 24-epicastasterone has been demonstrated in seeds of *Ornithopus sativus* (Schmidt et al. 1993a). Castasterone and brassinolide were identified in cell lines derived from *Catharanthus roseus* (Choi et al. 1993). 28-Homoteasterone represents a new naturally occurring brassinosteroid which has been identified in *Raphanus sativus* seeds by GC-MS analysis (Schmidt et al. 1991, 1993b). It is accompanied by castasterone, brassinolide, and teasterone. Studies with *Catharanthus roseus* crown gall cells indicated that brassinolide is biosynthesized from castasterone (Yokota et al. 1990a, Fujioka et al. 1992, Suzuki et al. 1993). These studies suggest a biosynthetic pathway: → campestrol → teasterone → typhasterol → castasterone → brassinolide. Experiments on endogenous level and localization of brassinosteroids indicate plastids as important organelles for brassinosteroids (Sasse 1990, Sasse et al. 1992). The stroma may be the site of synthesis, whereas starch granules are assumed as storage sites of these potent growth regulators. Bioactive brassinosteroids were localized in developing and mature pollen of the ryegrass, *Lolium perenne,* by immunocytochemistry (Taylor et al. 1993).

Tomato plants (*Lycopersicon esculentum*) take up and metabolize a tritium-labelled synthetic analogue of brassinolide (Schlagnhaufer and Arteca 1991). Recent experiments on the transport and metabolism of C-24,C-28-tritiated brassinolide, 24-epibrassinolide, and castasterone, respectively, in rice plant have shown that these compounds were translocated from roots to shoots but to a lower extent from leaves to roots (Yokota et al. 1992). The labelled brassinosteroids were mainly metabolized to nonglycosidic water- and to chloroform-soluble metabolites which might be polar sulphate ester-like derivatives of brassinosteroids or of their metabolites. Uptake, translocation, and transformation of $^3$H-labelled brassinolide in paddy rice seedlings was studied (Asano et al. 1993). Foliar uptake was much lower than that of root uptake. 24-Epicastasterone and 24-epibrassinolide, two naturally occurring brassinosteroids, were transformed by the fungus *Cunninghamella echinulata* to give the corresponding 12β-hydroxylated compounds (Voigt et al. 1993a), whereas the fungus *Cochliobolus lunatus* transformed 24-epicastasterone to its 15β-hydroxy derivative (Voigt et al. 1993b). In the rice lamina inclination test, both compounds are less active than 24-epicastasterone and 24-epibrassinolide. This report describes the first microbial biotransformation of native brassinosteroids.

The two auxin antagonists, 2,3,5-triiodobenzoic acid and 2-(p-chlorophenoxy)-2-methyl-propionic acid, inhibit the brassinosteroid-induced ethylene biosynthesis in etiolated mung bean hypocotyl segments at concentrations of 50 and 10 μM, respectively (Arteca et al. 1991). The root growth in seedlings of wheat, mung bean, and maize was inhibited under the influence of the naturally occurring 24-epibrassinolide (Roddick and Ikekawa 1992). Root and shoot development is variably affected by this brassinolide derivative according to species, developmental stage, site of application, and other parameters. Submicromolar concentrations of 24-epibrassinolide supplied to apical and basal regions of excised tomato roots exhibited growth inhibition (Roddick et al. 1993).

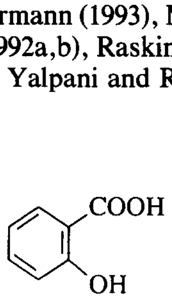
On the other hand, treatment of cuttings of adult Norway spruce, *Picea abies,* with 3, 15, or 60 ppm (22*S*,23*S*)-28-homobrassinolide significantly enhanced the formation of adventitious roots (Rönsch et al. 1993). The homobrassinosteroid was supplied in these studies by direct treatment of cuttings and by pretreatment of clonal stock plants.

The effect of brassinolide on gene expression in elongating soybean epicotyls suggests that the molecular mechanism of brassinolide-induced elongation is likely to be different from that of auxin-induced elongation in this system (Clouse et al. 1992). At submicromolar concentrations brassinolide altered the pattern of gene expression in elongating soybean epicotyls. A synthetic analogue, (22*S*,23*S*)-28-homobrassinolide, caused a stimulating effect on the electrogenic proton pump mechanism in the plasmalemma of *Egeria densa* leaf cells (Dahse et al. 1990). Homobrassinolide, 24-epibrassinolide, $GA_3$ and IAA applied together to leaves of *Vicia faba* enhance $^{14}C$-sucrose uptake by leaf discs (Petzold et al. 1992). An increased transport of the labelled sugar from the treated source region to the apical sink region was observed in brassinolide- and $GA_3$-treated plants after 24 h. A stimulatory effect of brassinolide on the translocation of assimilates in rice plants was also reported (Fuji and Saka 1992). Exogenously applied brassinolide or homobrassinolide promoted tracheary element differentiation of isolated mesophyll cells of *Zinnia elegans* (Iwasaki and Shibaoka 1991). Hypocotyl elongation of *Brassica chinensis* was stimulated by applying 300 ng of a brassinosteroid without change in the mechanical properties of cell walls but with an increase in wall relaxation properties and a passive dilution of the osmotic pressure of the cell sap (Wang et al. 1993). The field application of brassinosteroids in Japan during the last years was comprehended by Takeuchi et al. (1992).

In summary, the various physiological effects described by several laboratories on exogenously applied brassinosteroids or synthetically prepared analogues in plants or plant organs brought about interest observations, few hard facts, and many speculations. Much more experimental and reproducible data are needed, desirably with standardized plant material. At present, the mode of action of brassinosteroids at the molecular level remains unclear and their specific physiological role(s) is still unknown.

## Salicylic Acid

Salicylic acid belongs to the large group of plant phenolics and is probably ubiquitous in higher plants. The highest levels were observed in the inflorescence of thermogenic plants and in plants infected with necrotizing pathogens. Moreover, the exogenous application of salicylic acid to plants has been shown to induce a variety of biological responses, such as floral formation, resistance to phytopathogens, and production of PR proteins. The role of salicylic acid in flowering, in thermogenesis, and in disease resistance of plants was summarized and reviewed by Cutt and Klessig (1992), Dombrowski and Alfermann (1993), Malamy and Klessig (1992), Raskin (1992a,b), Raskin et al. (1992), Ryals et al. (1994), and Yalpani and Raskin (1993).



salicylic acid

Using *Lemna gibba* and other species of Lemnaceae, it was previously shown that salicylic acid possesses flower-inducing activity. However, the induction of flowering is not only triggered by salicylic acid but also by several other organic compounds. Therefore, it is debatable whether salicylic acid really acts in situ as a specific regulator of flowering or not. It was also found that salicylic acid induced potato tuberization in vitro at concentrations $>10^{-5}$ M (Koda et al. 1992). Salicylic acid showed even the strongest activity among the compounds tested, but its activity was markedly less ($10^{-3}$) of that of jasmonic acid (cf. above section on Jasmonates). Thus, these results doubt a specific involvement of salicylic acid in the tuberization process of potato plants.

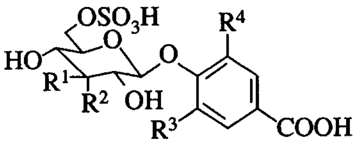
On the other hand, salicylic acid is assumed to be a natural inducer or regulator of heat production during flowering of thermogenic plants, as shown in experiments with *Arum* lilies. The increased temperature in the appendix is responsible for the volatilization of foul-smelling amines and indoles which attract insects as pollinators. The calorigen which is responsible for the heat production of the appendix was isolated from male flowers of *Sauromatum guttatum* and identified as salicylic acid (Raskin et al. 1987, 1989, 1990). On the day preceding the day of blooming, the levels of salicylic acid in the appendix increased almost 100-fold to 1 µg/g fresh weight. It was possible to increase the temperature of as much as 12°C by exogenous application of 0.13 µg/g fresh weight of immature appendix tissue. Among 33 salicylic acid analogues tested, only 2,6-dihydroxybenzoic acid and 2-acetoxybenzoic acid (known as aspirin) possessed thermogenic activity and induced odour production in *S. guttatum*. The structural specificity for salicylic acid to induce the complex process of thermogenes in flowers seems to be very high, however, the mechanism(s) involved and the sequence of biochemical steps are still unknown.

Recent reports denote salicylic acid not only as calorigen but also as an endogenous systemic signalling molecule in the induction chain of disease resistance, in particular, against necrotrophic pathogens, and as an inducer of certain PR proteins synthesized in TMV-infected tobacco and in cucumber after inoculation with *Colletotrichum lagenarium* or *Pseudomonas syringae* pv *syringae* (i.e., Enyedi et al. 1992a, Gaffney et al. 1993, Malamy et al. 1990, 1992, Metraux et al. 1990, Rasmussen et al. 1991, White 1979, Yalpani et al. 1991). In response to acetylsalicylic acid (aspirin) treatment, sunflower plants, *Helianthus annuus,* produce a complete set of PR proteins (Jung et al. 1993). A soluble salicylic acid-binding protein has been identified that may function in a putative signal transduction chain of plant disease-resistance response (Chen and Klessig 1991). Salicylic acid and its acetyl derivative inhibited potato proteinase inhibitor-II by decreasing the enhancer effects of sucrose (Kim et al. 1992). It appears that the interaction of salicylic acid with a receptor molecule is specific.

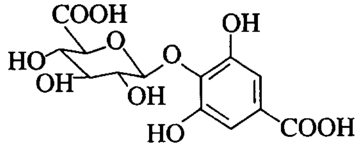
The function of salicylic acid as a component of signal transduction leading to the establishment of systemic acquired resistance and responsible for the induction of PR proteins and other compounds in plants will not discussed here in detail (cf. Cutt and Klessig 1992, Dombrowski and Alfermann 1993, Enyedi et al. 1992b, Gaffney et al. 1993, Malamy and Klessig 1992, Raskin 1992a,b, Raskin et al. 1992, Ryals et al. 1994, Yalpani and Raskin 1993, and references therein).

## Turgorins

The well-known phenomenon that certain plants can react by autonomous movement triggered by different physical stimuli such as temperature, contact, shock, light, etc., is based on turgor changes in the cells concerned. The signals that induce nastic movements in plants are called *turgorins.* In 1981 the first turgorin isolated from the nyctinastically reacting *Acacia karoo* was structurally elucidated as 4-O-(6'-O-sulpho)glucoside of gallic acid (Schildknecht and Schumacher 1981). Later, this compound and several structurally related turgorins were found in *Mimosa pudica* and some other species of the Fabaceae, Oxalidaceae, Malvaceae, Vitaceae, and Portulacaceae (see Schildknecht 1986, Kallas et al. 1989, and references therein). The turgorins I-VI are shown to be 4-O-glycosides of gallic acid, protocatechuic acid, and p-hydroxybenzoic acid, respectively; in each case the 6-hydroxy group of the glucosyl moiety is esterified with sulphuric acid. Turgorin VII contains glucuronic acid instead of glucose.



| | $R^1$ | $R^2$ | $R^3$ | $R^4$ |
|---|---|---|---|---|
| turgorin I | OH | H | OH | OH |
| turgorin II | $OSO_3H$ | H | OH | OH |
| turgorin III | OH | H | H | OH |
| turgorin IV | OH | H | H | H |
| turgorin V | OH | H | H | $OCH_3$ |
| turgorin VI | H | OH | OH | OH |

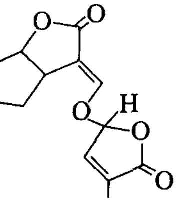


turgorin VII

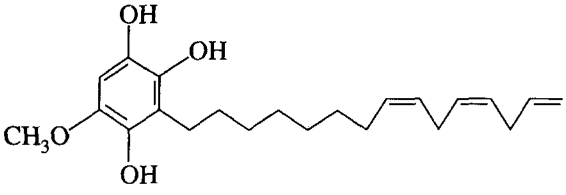
The turgorins are known to promote leaf movement at hormonal concentrations ($10^{-5}$ to $10^{-7}$ M). The nastic activity of these endogenous plant constituents was determined using a special bioassay, estimation of the leaf movement reaction after exogenous application of the corresponding turgorin to the sensitive plant *Mimosa pudica.* This plant contains binding sites for turgorin I on plasma membranes (Kallas et al. 1990). Turgorins are signalling molecules, but their mode of action in the mechanism(s) of signal transduction remain(s) to be clarified.

## Strigol and Related Germination Stimulants

A very potent stimulant of seed germination, *(+)-strigol,* was first isolated from root exudates of cotton, *Gossypium hirsutum* (Cook et al. 1966). It was structurally identified as a sesquiterpene lactone (Cook et al. 1972, Coggon et al. 1973, Brooks et al. 1985). Strigol stimulated seed germination of the harmful semiparasitic weed, *Striga lutea,* which damages numerous leguminous and gramineous crops including sorghum, millet, corn, and sugarcane. Its seed germination-stimulating activity was also demonstrated in other root-parasitic flowering plants of the genera Striga, Orobanche, and Alectra, for example, in *Striga asiatica, S. hermonthica, S. gesnerioides, Alectra vogelii*, and *Orobanche aegyptica*. Seed germination of these plants requires stimulation by chemical substances which are exuded from the host plants. The concentrations of strigol causing 50% germination of *Striga* seeds are as low as $10^{-12}$ to $10^{-16}$ M. Although *Gossypium hirsutum* is a "false host" which is not attacked by the parasitic plants, strigol exuded from cotton roots stimulates the seed germination of *Striga* species.



strigol

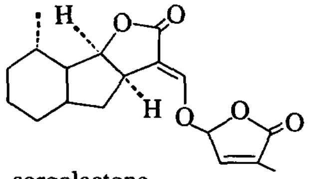


sorgoleon

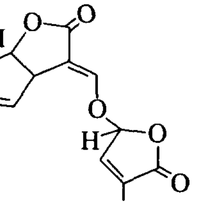
Another *Striga* seed germination stimulant, *sorgoleon*, was isolated from root exudates of another host plant, *Sorghum bicolor* (Chang et al. 1986, Netzly et al. 1988). The compound was identified as p-hydroquinone substituted with a hydroxy and a methoxy group and an unsaturated $C_{15}$ side chain which is responsible for the hydrophobic character of the substance.

The synthesis of this compound has also been reported (Sargent and Wangchareontrakul 1990). Sorgoleon was shown to stimulate germination of *Striga asiatica* and *S. hermonthica* seeds at concentrations of $10^{-7}$ M. In agar, *Striga asiatica* seeds germinated in high percentages within a distance of 5 mm of a sorghum host root surface, no germination was observed at distances >1 cm (Fate et al. 1990). The studies established an apparent steady-state concentration gradient of sorgoleon around the sorghum root.

A second germination stimulant, *sorgolactone*, was recently isolated from root exudates of *S. bicolor*. Based on spectroscopic data, its chemical structure was proposed to be closely related to (+)-strigol (Hauck et al. 1992). The germination of the seeds of *Striga asiatica* and *S. hermonthica* is promoted at concentrations down to $10^{-12}$ M. Both sorgoleon and sorgolactone are the first natural seed germination stimulants isolated from a genuine host plant.



sorgolactone

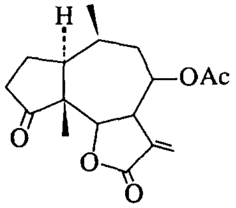


alectrol

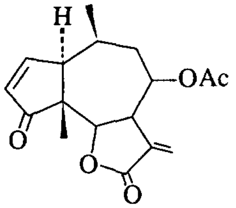
*Alectrol* detected recently in root exudates of the leguminous plant, *Vigna unguiculata*, was found to be a potent germination stimulant for the seeds of *Alectra vogelii* and *Striga gesnerioides* (Müller et al. 1992). Its proposed structure is closely related to strigol and sorgolactone. Alectrol stimulates 50% of the seeds of *A. vogelii* and *S. gesnerioides* at concentrations down to $10^{-12}$ M and is more active than strigol in seed germination of these angiospermous root parasites.

There are some new published data dealing with different aspects of these novel bioactive natural compounds, for example, synthesis and bioactivity of strigol and its synthetic analogues (Berlage et al. 1987a,b, Bradow et al. 1990, Mangnus and Zwanenburgh 1992a,b, Mangnus et al. 1992a,b, Samson et al. 1991), configurational assignment at C-2′ of some strigol analogues (Frischmuth et al. 1993), separation of racemic strigol into its enantiomers and their biological activity (Hauck and Schildknecht 1990), biosynthesis (Vail et al. 1990), standardized bioassay (Mangnus et al. 1992c), and studies on structure–activity of sesquiterpene lactones (Fischer et al. 1990). The field application of strigol or an efficient analogue could serve as a basis of a novel method for controlling parasitic weed pests.

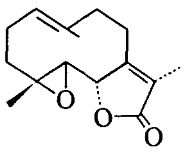
The endogenous sesquiterpene lactones, *confertiflorin* from *Ambrosia confertiflora, parthenin* from *Parthenium hysterophorus* and *11,13-dihydroparthenolide* from *A. artemisiifolia* significantly increased germination of witchweed, *Striga asiatica* (Fischer et al. 1989). Their activity is comparable to the activity of strigol and its synthetic analogues. It is not yet known whether these native plant constituents play a role as plant growth regulators in situ.



confertiflorin



parthenin



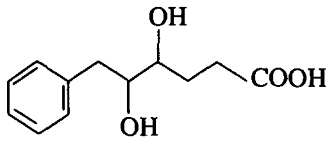
11,13-dihydroparthenolide

The novel plant products strigol, alectrol, sorgolactone, and sorgoleon are discussed as a new class of plant hormones. They act at very low levels as chemical signal molecules by which dormant seeds of *Striga asiatica* and related species recognize their correct host plants and trigger germination. Therefore, seed germination of these root parasites is only initiated by these highly specific natural germination stimulants which are exuded by the host root and break the seed dormancy of the root-parasitic plants. The molecular basis of the host–parasite relationship and the biochemical link of the chemical communication between the root of a host plant and the seed of its root parasite are still unknown.

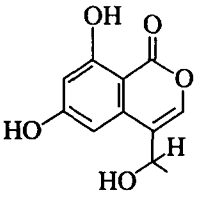
### Stimulators of Seed Germination and Plant Growth

There are some novel natural products both of microbial and plant origin that have been recently reported to exhibit root growth activity at concentrations $<10^{-4}$ M when tested in certain bioassay systems. As shown below, these plant growth-regulating substances belong to quite different chemical groups.

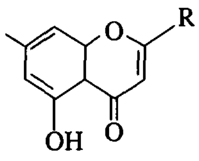
Root growth-stimulating activity has been demonstrated, for example, for *4,5-dihydroxy-6-phenylhexanoic acid* from the bacterium *Erwinia quercina* (Wright et al. 1989), the isocoumarin derivative *sescandelin* from the culture filtrate of the fungus *Sesquicillium candelabrum* (Kimura et al. 1990), the *altechromones A* and *B* from *Alternaria* species (Kimura et al. 1992a), *dihydroampullicin* from the *Ampulliferina*-like fungus sp. No. 27 (Kimura et al. 1993b), *3-(hydroxyacetyl)indole* from the Oregon red alga *Prionitis lanceolata* (Bernart and Gerwick 1990), and the Br-containing *α-O-methyllanosol* from the marine algae *Odonthalia washingtoniensis* and *O. floccosa* (Kubo 1989, Kubo et al. 1990).



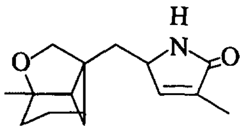
4,5-dihydroxy-6-phenylhexanoic acid



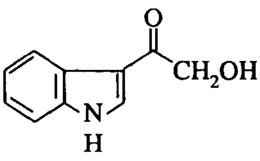
sescandelin



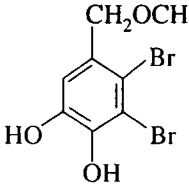
altechromone A R=$CH_3$
altechromone B R=$CH_2COCH_3$



dihydroampullicin

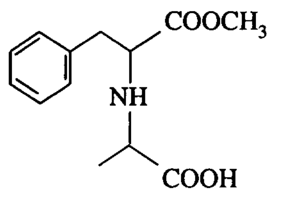


3-(hydroxyacetyl)indole

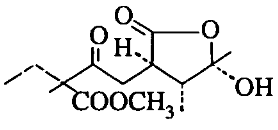


α-O-methyllanosol

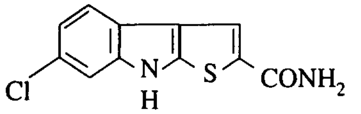
The structure of a new plant growth regulator produced by the fungus, *Botrytis squamosa*, was elucidated to be *1-methyl hydrogen 3-phenyl-2(S),2'(S)-iminodipropionate* (Kimura et al. 1993a, Nakashima et al. 1993). At concentration of 300 ppm it promoted root growth of lettuce seedlings by about 220% compared to that of the control.



methyl hydrogen
3-phenyl-2,2′-iminodipropionate



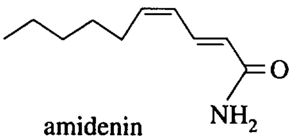
spicifernin



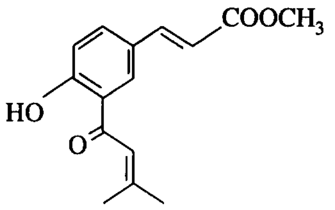
thienodolin

The phytopathogenic fungus, *Cochliobolus spicifer*, was found to produce a plant growth-regulating metabolite, *spicifernin*, that promoted root and shoot elongation of rice seedlings (Nakajima et al. 1990). The γ-hydroxy-δ-lactone part found in spicifernin is rare among fungal metabolites. The biosynthesis of spicifernin was elucidated recently (Nakajima et al. 1992a). It should be noted that other secondary metabolites produced by *C. spicifer* simultaneously and termed *spiciferones A, B, and C* and *spiciferinone*, have been found to act phytotoxic (c.f. section on inhibitors). Recently a tricyclic sulphur-containing indole derivative, *thienodolin*, was isolated from the fermentation broth of *Streptomyces albogriseus* (Kanbe et al. 1993a,c). Depending on the concentration used it showed growth-promoting and -inhibiting activity against rice seedlings. *Amidenin* (2*E*,4*Z*-decadienamide) was found as a new plant growth-regulating substance in the fermentation broth of a *Amycolatopsis* sp. (Kanbe et al. 1993b).

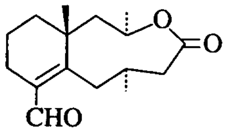
Some potent root growth stimulating substances have also been isolated from higher plants, such as the cinnamic acid-derived *capillarol* from *Artemisia capillaris* (Ueda 1989), or the sesquiterpene lactones *isoalantodiene* from the roots of *Inula racemosa* (Kalsi et al. 1989), *saussureal* from *Saussurea lappa* (Talwar et al. 1992, Singh et al. 1992) or several *nagilactones* from *Podocarpus nagi* (Kubo et al. 1991).



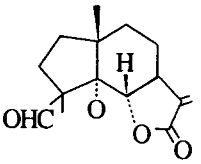
amidenin



capillarol

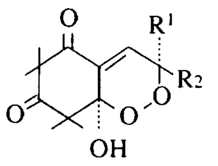


isoalantodiene



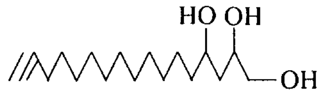
saussureal

Previously isolated plant growth regulators termed *G-inhibitors* occurring in adult leaves of *Eucalyptus grandis* and other Myrtaceae and stimulating rooting of mung bean cuttings, are reported to be prepared by chemical syntheses (Kalsi et al. 1987, Baltas et al. 1992). *1,2,4-Trihydroxy-n-heptadeca-16-yne* is the most active compound of the nonauxinic rooting promoters previously isolated from avocado, *Persea americana* (Raviv et al. 1986) and shows to possess 2*R*,4*R* configuration (Becker et al. 1990).



G-inhibitors

|  | $R^1$ | $R^2$ |
|---|---|---|
| $G_1$ | $CH_3$ | $C_2H_5$ |
| $G_2$ | $C_2H_5$ | $CH_3$ |
| $G_3$ | $CH_3$ | $CH_3$ |



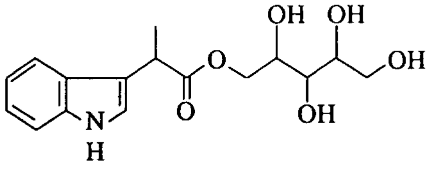
1,2,4-trihydroxy-n-heptadeca-16-yne

The long-chain alcohol, 1-*triacontanol* [$CH_3$-$(CH_2)_{28}$-$CH_2OH$], occurs as common constituent of plant waxes and seems to play a role in plant growth regulation (cf. review of Ries 1991). Exogenously applied, it stimulates growth and yield of important annual vegetable and crop species. Triacontanol is used commercially as a plant growth regulator, particularly in Asia. Moreover, the effect of triacontanol on the growth of *Artemisia annua,* on its level of the sesquiterpene lactone artemisinin and the content of gibberellins and abscisic acid was studied recently (Shukla et al. 1992). In other experiments triacontanol effects growth, photosynthesis, and alkaloid content of *Papaver somniferum* (Srivastava and Sharma 1990) and the content of essential oil in *Cymbopogon flexuosus* (Misra and Srivastava 1991). Triacontanol predominantly stimulates plant growth and other metabolic functions of rice seedlings at nanomolar concentrations in concert with *octacosanol* [$CH_3$-$(CH_2)_{26}$-$CH_2OH$] which inhibits the activity of triacontanol at equimolar concentrations (Ries and Wert 1988). Both alcohols were shown to elicit formation or release of two second messengers. One of them was found to possess potent plant growth-regulating properties and was identified as *9-β-L(+)-adenosine* (Ries et al. 1990, Ries 1991, 1992). This adenosine enantiomer in which L(+)-ribose is linked to the adenine residue has not been reported previously as native natural product. It stimulated the growth of several species at picomolar concentrations. Recently, its influence on malate dehydrogenase activity in rice was studied (Savithiry et al. 1992). Foliar application of picomole quantities of 9-β-L(+)-adenosine increased the $Ca^{2+}$, $Mg^{2+}$, and $K^+$ concentration in tomato, cucumber, and maize plants (Ries et al. 1993). It was concluded that 9-β-L(+)-adenosine acts by eliciting a rapidly propagated signal that increases the concentration of several ions in the apoplast. The response of maize and rice to 9-β-L(+)-adenosine applied under different environmental conditions has also been studied (Ries and Wert 1992). On the basis of these experiments, 9-β-L(+)-adenosine is assumed to be a new naturally occurring plant growth substance.

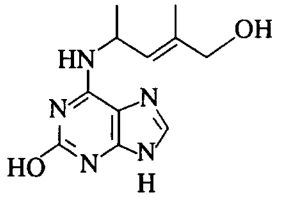
## Inhibitors of Seed Germination and Plant Growth

A number of microbial metabolites predominantly of fungal origin and of plant constituents inhibit plant growth. For older literature, the reader is referred to reviews mentioned in the Introduction. The following compounds represent newly described growth inhibitors.

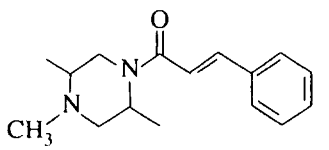
*Acremoauxin A,* produced by the fungus, *Acremonium roseum,* strongly inhibits the growth of Chinese cabbage at concentrations of 2 ppm (Sassa et al. 1989). It was identified as D-arabitol ester of 3-indolylpropionic acid. The synthesis of this naturally occurring indole derivative was also described (Yoshida and Sassa 1990).



acremoauxin A



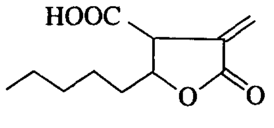
2-hydroxy-1′-methyl-zeatin



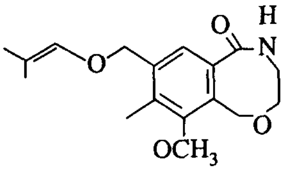
N-methyl-trans-2,5-dimethyl-N′-cinnamoylpiperazine

The pathogenic fungus, *Alternaria brassicae,* produces three plant growth-inhibiting substances of different chemical structures, *2-hydroxy-1′-methyl-zeatin, N-methyl-trans-2,5-dimethyl-N′-cinnamoyl-piperazine,* and *3-carboxy-2-methylene-4-pentyl-*

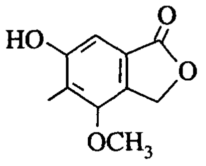
*butenolide,* respectively (Dahiya and Tewari 1991). *Porritoxin* and *porriolide* are produced by *Alternaria porri* and were found to inhibit root elongation both of lettuce and stone-leek seedlings at concentrations between 10 and 400 ppm (Suemitsu et al. 1992, 1993).



3-carboxy-2-methylene-4-pentyl-butenolide

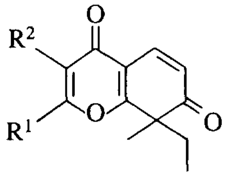


porritoxin

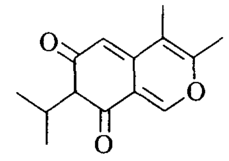


porriolide

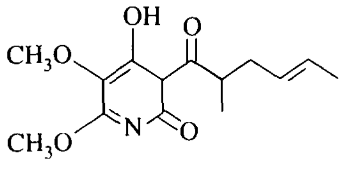
Another phytopathogenic fungus, a strain of *Cochliobolus spicifer,* is capable of producing several phytotoxic compounds named *spiciferone A, B,* and *C* and *spiciferinone* (Nakajima et al. 1989, 1990, 1991, 1992b). These fungal metabolites represent a new structural type—they contain a bicyclic ring system composed of a γ-pyrone and a cyclohexadienone. Among these compounds, spiciferinone was shown to be the most potent one. It is remarkable that this fungus also produces the plant growth-promotor spicifernin (c.f. section on Stimulators). *Harzianopyridone* from *Trichoderma harzianum* inhibited the growth of wheat coleoptiles at concentrations of $10^{-5}$M (Cutler and Jacyno 1991). Only the (−)-form showed biological activity.



spiciferone A $R^1=R^2=CH_3$
spiciferone B $R^1=CH_2OH$; $R^2=CH_3$
spiciferone C $R^1=CH_3$; $R^2=CH_2OH$



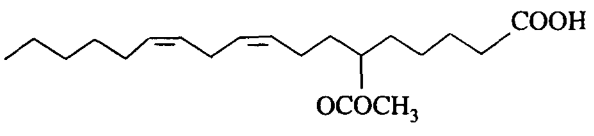
spiciferinone



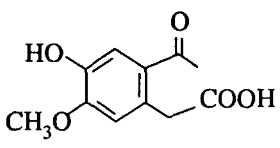
harzianopyridone

Two 18- and 22-membered macrolide plant growth inhibitors, *kaimonolide A* and *B,* were isolated from a *Streptomyces* strain and their structures elucidated (Hirota et al. 1989a,b, 1990). Very recently, *rotihibin A* was isolated from *Streptomyces* sp. The substance suppresses root growth of lettuce seedlings at a dose of 1–2 ppm (Fukuchi et al. 1992). Rotihibin A is built up from seven amino acid-like residues. *Tricolorin A* ($C_{50}H_{86}O_{21}$) was isolated from *Ipomoea tricolor* as a potent inhibitor of plant growth and was identified as a linear tetraglycoside of jalapinolic acid (Pereda-Miranda et al. 1993).

Furthermore, the natural occurrence of pollen germination inhibitors has also been reported. A substance inhibiting tea pollen growth was isolated from the marine alga *Spatoglossum pacificum* (Tazaki et al. 1991). It was structurally elucidated as *6-acetoxylinoleic acid.* The acetoxy group was found to be essential for the biological activity of this compound.

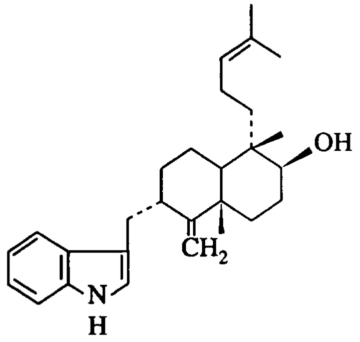


6-acetoxylinoleic acid

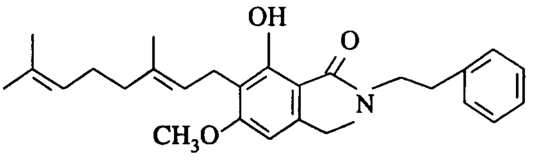


vulculic acid

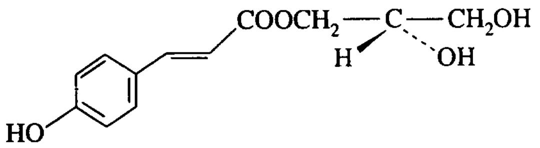
*Pinus* pollen germination is inhibited by *vulculic acid* which is produced by a species of *Penicillum* and represents a naturally occurring derivative of phenylacetic acid (Kimura et al. 1991a). The indole diterpene *(−)-emeniveol* isolated from the culture filtrate of the fungus, *Emericella nivea*, and structurally elucidated, inhibited pine and tea pollen growth (Kimura et al. 1992b). The total synthesis of this pollen-growth inhibitor was published recently (Shimokawa and Smith 1993). Another pollen growth inhibitor, named *hericerin*, has been found in the mushroom, *Hericium erinaceum* (Kimura et al. 1991b). It represents an unusual isoindolinone derivative.



emeniveol



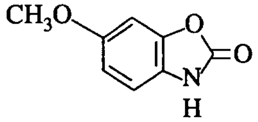
hericerin



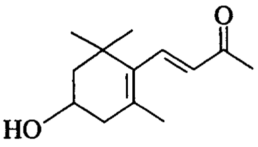
1-(*E*-p-coumaroyl)-glycerol

Several novel plant constituents isolated and structural elucidated during the last years, have also been demonstrated to exhibit plant growth-inhibiting properties.

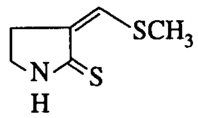
Sesquiterpene lactones, such as *artemisinin* extracted from leaves of *Artemisia annua*, inhibited seed germination and seedling growth (Chen and Leather 1990). A molluscicidial sesquiterpene lactone, *podoandin* from *Podocarpus andina*, completely inhibited the germination of lettuce seeds at 100 ppm (Kubo et al. 1992). *1-(E-p-Coumaroyl)glycerol* from immature seeds of corn suppressed root elongation of Chinese cabbage seedlings (Ikeda et al. 1989). A novel cholestane glycoside, *helojaposide* ($C_{43}H_{66}O_{16}$), from *Heloniopsis japonica*, was described to exhibit significant inhibitor activity if the root elongation of rice was tested (Shingu et al. 1992). Light-grown maize shoots contain a growth-inhibiting substance, which was structurally elucidated as *6-methoxy-2-benzoxazolinone* and shown to be a potent antiauxin (Hasegawa et al. 1992).



6-methoxy-2-benzoxazolinone



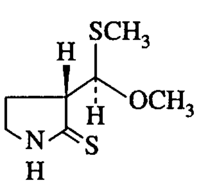
3-hydroxy-β-ionone



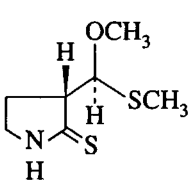
3-(methylthio)methylene-pyrrolidine-2-thione

A potent growth inhibitor, *R-(−)-3-hydroxy-β-ionone*, was isolated from light-grown shoots of a dwarf cultivar of *Phaseolus vulgaris* (Kato-Noguchi 1992, 1993, Kato-Noguchi et al. 1993). This compound has been detected previously in tobacco plants and quince fruits and was found to inhibit the growth of hypocotyls of lettuce and dwarf bean seedlings at concentrations greater than 0.03 μM.

It has previously reported that light-grown radish (*Raphanus sativus*) seedlings contain several growth-inhibiting compounds, such as the raphanusols A and B, raphanusamide, the raphanusanins, and 2-thioxothiazolidine-4-carboxylic acid. In addition, a structurally related compound, 3-(*E*)-methylthio)methylene-pyrrolidine-2-thione, was isolated as a new endogenous plant growth substance from light-grown radish seedlings, and inhibitor of hypocotyl growth in cress seedlings (Sakoda et al. 1990).



raphanusanin A



raphanusanin B

The structures of the *raphanusanins A* and *B* were revised by X-ray crystallographic structure analysis and shown to be (3*R*,6*R*)- and (3*R*,6*S*)-3-[methoxy-(methylthio)methyl]-pyrrolidine-2-thione, respectively (Harada et al. 1991). Thus raphanusanin A is the stereoisomer of raphanusanin B. The raphanusanins found to be widespread in the genus *Raphanus* cause light-growth inhibition or phototropism in illuminated radish hypocotyls (Sakoda et al. 1991, 1992). Structure–activity relationships of the raphanusanins and their analogues were studied using the growth inhibition of lettuce hypocotyls and *Amaranthus* roots (Sakoda et al. 1993). It was established that the active sites of these compounds were the thioamide moiety at C-2 of the skeleton and a methylthiomethylene group or a structurally related substituent in the C-3 position of the side chain.

## Conclusions

Growth and development of plants or their organs are regulated by a multiplicity of exogenous and endogenous factors. Some new of them, those of chemical nature, are compiled in this review. It contains a heterologous collection of structures (known by chemical identification), but probably still more diversity rules their putative modes of actions within the biological matter. Here we are still at the beginning of detailed research with increasing difficulties. The more sophisticated the test system used, the more complex a seemingly simple process like seedling growth stimulation or inhibition in bioassay will become. The natural products exerting either inhibitory or stimulatory effects when applied to plants or plant organs at concentrations of $<10^{-5}$ M on an average may influence probably various physiological processes, since rooting, flowering, senescence, organogenesis, or growth can be monitored by different bioassays.

Therefore, the depth of knowledge about jasmonate action and a few other groups of substances differs markedly from those of manifold "inhibitor" or "stimulator" molecules detailed in the sections on Stimulators and Inhibitors. Few of them may be of specific value after further elucidation of their mode of actions, most of them might not withstand deeper proof and will be abolished. Few compounds, such as jasmonic acid or salicylic acid, are suggested to be plant-specific signal transmitter substances involved in different growth and developmental processes. Therefore, these biologically active compounds are now under intensive investigation in order to understand their precise role in plant growth regulation as well as their physiological and molecular modes of action.

Microbial and plant-derived compounds with bioregulatory activity represent a large pool of chemical structures that can be used as templates for the development of novel agrochemical compounds with optimized or altered properties. Some important aspects of this strategy were discussed recently by Fugmann et al. (1991, 1992). It is to hope that some of the substances listed in this review will be successfully used as bioregulators in future agriculture.

## Note Added in Proof

*(−)-Jasmonic acid* (JA), *(R)-mellein,* and a new compound, designated *theobroxide* [3(*S*),6(*R*)-dihydroxy-4(*R*),5(*S*)-epoxy-1-methylcyclohex-1-ene], have been isolated from the fungus, *Lasiodiplodia theobromae,* as potato tuber-inducing substances (Nakamori et al. 1994). Four tuber-forming substances in *Helianthus tuberosus* were isolated and structurally elucidated as *JA, methyl β-D-glucopyranosyl tuberonate,* and the new polyacetylene compounds, *β-D-glucopyranosyl helianthenate A* and *B* (Matsuura et al. 1993).

Seeds of sugar beet, *Beta vulgaris,* contain the brassinosteroids *castasterone* and *24-epicastasterone* (Schmidt et al. 1994). *Teasterone-3-myristate* has been found to occur naturally in *Lilium longiflorum* anthers (Asakawa et al. 1994). Structurally related brassinolide metabolites, *3,24-bisepibrassinolide-3-laurate, -3-myristate,* and *-3-palmitate,* respectively, have been isolated after application of 24-epibrassinolide to cell suspension cultures of *Ornithopus sativus* (A. Kolbe and B. Schneider, personal communication). Such brassinosteroids esterified at the C-3 hydroxyl group with unsaturated fatty acids represent a new type of brassinosteroid conjugates occurring either as native plant constituents or as products of biotransformation. In addition a catabolic side-chain degradation of exogenously applied 24-epicastasterone and 24-epibrassinolide was also shown. The two metabolites were identified as the corresponding 20-keto compounds (Kolbe et al. 1994). Contrary, suspension cultures of *Lycopersicon esculentum* transformed exogenously applied 24-epibrassinolide to another type of conjugate which was structurally elucidated as *25-β-D-glucosyloxy-24-epibrassinolide* (Schneider et al. 1994). It represents the first naturally occurring brassinosteroid with a (glucosylated) hydroxy group at C-25. The introduction of a lactone group into the brassinosteroids typhasterol and teasterol promotes the specific effect found by the rice lamina inclination bioassay (Abe et al. 1992).

In healthy and virus-inoculated tobacco *salicylic acid* was found to be biosynthesized from cinnamic acid via benzoic acid (Yalpani et al. 1993). Tobacco leaves were also used to study the role of *salicylic acid* β*-glucoside* in pathogenesis. This glucoside is rapidly hydrolyzed to salicylic acid suggesting a possible role of the endogenous glucosyl conjugate in the induction of systemic resistance (Hennig et al., 1993). The function of active oxygen in the salicylic acid-induced plant systemic acquired resistance was studied. Salicylic acid specifically inhibited the catalase activity in vitro and induced an increase of $H_2O_2$ concentration in vivo. The action of salicylic acid is likely mediated by elevated amounts of $H_2O_2$ (Chen et al. 1993).

*Botcinolide* represents a new hydroxylated nonalactone esterified with 4-hydroxy-2-octenoic acid (Cutler et al. 1993). It was isolated from *Botrytis cinerea* and found to inhibit etiolated wheat coleoptile growth. The ketone function an C-7 and the methyl group at C-2 of *spiciferone A* produced by the fungus *Cochliobolus spicifer* are essential to its phytotoxicity (Nakajima et al. 1993). Aerial parts of *Tithonia diversifolia* contain the sesquiterpene lactones *tagitinin A* and *C* and the flavone *hispidulin* as germination and growth inhibitory substances (Baruah et al. 1994). *4-Methoxy-6-phenethyl-2H-pyran-2-one* (dihydro-5,6-dehydrokawain) was isolated from *Alpinia speciosa* leaves (Fujita et al. 1994). It was found to possess plant growth inhibiting activities. *Azalein* (5-O-methylquercetin-3α-rhamnoside), (+)*-catechin* and (−)*-epicatechin* from *Rhododendron mucronatum* have been found to promote pollen tube growth (Ozawa et al. 1993).

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