The role of plant growth regulators in the development and germination of the desiccation-sensitive (recalcitrant) seeds of *Avicennia marina*

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Abstract

The contents of the cytokinins zeatin (Z), zeatin riboside (ZR), and isopentenyladenine (IPA), the combined contents of gibberellins, A3 (GA), and the contents of indoleacetic acid (IAA) and abscisic acid (ABA) were measured during the development of the desiccation-sensitive seeds of *Avicennia marina* (Forssk.) Vierh. During the stage of histodifferentiation the amounts of these plant growth regulators (PGRs) were measured on whole fruits. During the phase of seed growth and reserve accumulation measurements were made on the embryonic axis, cotyledons and pericarp separately. Patterns in the amounts of PGRs present during histodifferentiation were similar to those reported for desiccation-tolerant seeds and it suggested that this process is under similar 'hormonal' control in *A. marina* as in orthodox seeds. Very high contents of cytokinins, particularly ZR, were present in both axes and cotyledons during reserve accumulation. This is thought to be related to the nature of the reserves accumulated (soluble sugars), rather than to the phenomenon of desiccation sensitivity. With the exception of ABA, embryonic contents of PGRs were relatively high at seed shedding, consistent with the rapid germination of this highly recalcitrant seed. ABA contents in the embryo were low during reserve accumulation, but concentrations in the pericarp increased throughout this development stage. ABA in the pericarp could act to prevent precocious germination. The low concentrations of ABA in the embryo could be related to the desiccation-sensitivity of the seeds of *A. marina*.

Keywords: ABA, *Avicennia marina*, cytokinins, desiccation tolerance/sensitivity, plant growth regulators, recalcitrant, seed development

Introduction

The differences in post-shedding behaviour between desiccation-tolerant (orthodox) and desiccation-sensitive (recalcitrant) seeds have been well characterized (Chin and Roberts, 1980; Berjak et al., 1989). On shedding, desiccation-tolerant seeds have a low water content and are metabolically quiescent. Because these seeds are tolerant of desiccation and chilling they can be successfully stored by maintenance of the desiccated state at sub-zero temperatures (Roberts, 1973). Desiccation-sensitive seeds have a high moisture content and are intolerant of drying. Such seeds are metabolically active and in general, will initiate germination upon or shortly after shedding and consequently storage lifespan is severely curtailed (Farrant et al., 1988; 1989; Berjak et al., 1989).

The differences between these seed types must arise as a consequence of differences in their pre-shedding development. While considerable research has been conducted on various aspects of a variety of

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Abbreviations: ABA = abscisic acid; DAFS = days after fruit set; DAS = days after shedding; GA = gibberellin; IAA = indoleacetic acid; IPA = isopentenyladenine; PGR = plant growth regulator; Z = zeatin; ZR = zeatin riboside
desiccation-tolerant seeds, with the exception of studies on *Quercus robur* L. (Finch-Savage, 1992; Finch-Savage et al., 1992; Grange and Finch-Savage, 1992), little systematic work has been reported on the development of desiccation-sensitive types. The present contribution is part of a comprehensive study on the development of the desiccation-sensitive seeds of the mangrove *Avicennia marina* (Forssk.) Vierh. It examines the types of changes in each of the major types of plant growth regulators (PGRs) during development and germination of seeds of this species. This study was undertaken in order to: (1) ascertain how PGRs might be involved in the developmental processes of this highly desiccation-sensitive seed, and (2) to identify if, and how, the PGR trends differ from those occurring during the development and germination of desiccation-tolerant seeds.

From a survey of the literature it has become apparent that, although there are individual differences between species, the general trends in PGR status during the development of desiccation-tolerant seeds can be represented schematically as shown in Fig. 1. In most cases it is PGR contents of whole seeds that have been reported and in very few instances have PGRs been measured in different components of the seed.

The contents of cytokinins, gibberellins (GAs) and the auxin, indoleacetic acid (IAA) are generally elevated during histodifferentiation, and decline at the completion of that stage or shortly thereafter (reviewed for example by van Staden et al., 1982; Khan, 1982; Pharis and King, 1985; Reinecke and Bandurski, 1987; Roberts and Hooley, 1988). Cytokinins, and in some instances gibberellins (Cionini et al., 1976; Yeung and Sussex, 1979), have been implicated in the processes of cell division during embryogenesis (van Staden et al., 1982). Gibberellins and IAA are thought to be involved in the control of differentiation and initial growth of the embryonic structures (Pharis and King, 1985; Sandberg et al., 1987; Quatrano, 1987).

Abscisic acid (ABA) contents generally increase only after the completion of histodifferentiation. This PGR is thought to:

1. prevent precocious germination upon the parent
2. promote reserve accumulation and in particular the formation of storage proteins and
3. induce the production of late embryogenic abundant (LEA) proteins (reviewed by Kermode, 1990).

LEA proteins have been implicated in the mechanism of desiccation tolerance (Bartels et al., 1988; Blackman et al., 1991; Bradford and Chandler, 1992) and thus ABA may indirectly be involved in such a mechanism (Kermode, 1990).

Mature, non-dormant seeds have low contents of active PGRs, although there may be storage or inactive forms of cytokinins (Hocart et al., 1988). GAs (Pharis and King, 1985) and IAA (Cohen and Bandurski, 1982) present. There is evidence that ABA is degraded during maturation-drying (King, 1976; Kermode, 1990). Low ABA contents in non-dormant seeds allow the progression of germination upon imbibition. Cytokinin, GA and IAA generally increase in the germinating seed and have been implicated in the processes involved in the resumption of metabolism and growth (Jones and Stoddart, 1977; Cohen and Bandurski, 1982; van Staden et al., 1982). The GAs, and in some instances cytokinins, have also been implicated in the mobilization of storage reserves for utilization during the germination process (Fincher, 1989; Hocart et al., 1990).

During their development, the seeds of *A. marina*, like desiccation-tolerant seeds, undergo a period of histodifferentiation followed by a period of growth and reserve accumulation. Unlike orthodox seeds, there is no maturation-drying, the seeds remain metabolically active throughout development and germination is initiated shortly after shedding (Farrant et al., 1992b). Unlike most other seeds, whether desiccation-tolerant or -sensitive, the seeds of *A. marina* accumulate the majority of storage reserves in soluble form. This has been related to a strategy of immediate initiation of germination upon shedding (Farrant et al., 1992b). If the mature seed is shed onto a moist substrate, the pericarp is rapidly sloughed and root protrusion can occur within 24–48 h (Farrant et al., 1992b).

The seeds of *A. marina* are never tolerant of desiccation (Farrant et al., 1993). An analysis of the nature of protein synthesis during development showed that there were no qualitative changes in the patterns of proteins synthesized from the completion of histodifferentiation through to the onset of root protrusion (Farrant et al., 1992a). It was concluded that *A. marina* seeds do not appear to produce late embryogenic abundant (LEA) proteins, which may contribute towards the desiccation-sensitivity of this seed.

In the present study, a combined HPLC-radioimmunoassay (RIA) technique was used to determine the changes in selected PGRs during the development and germination of seeds of *A. marina*. The free forms of the following PGRs were analysed: the cytokinins, zeatin (Z), zeatin riboside (ZR) and isopentenyladenine (IPA); the combined contents of the GAs, GA<sub>1</sub> and IAA; and ABA.
Materials and methods

Seed material

Developing seeds of known age were collected as described previously (Farrant et al., 1992a, b). Seed development took 80–85 days after fruit set (DAFS). PGR analyses were conducted every 10 days up to 50 DAFS on whole seeds which were small and could not be readily dissected into component parts. After this stage, assessments were carried out separately on axes, cotyledons and pericarps at 5-day intervals. Newly-shed mature seeds were placed on a moist substrate, in simulation of the natural environment into which the seeds are shed, and were sampled daily until visible root growth had occurred (4 days after shedding [DAS]). The pericarp is sloughed when the seed comes into contact with moisture, and thus analyses of germinating material were performed on axes and cotyledons only. Due to the HPLC pre-purification procedure and the specificity of RIA, all the PGRs which were analysed could be detected in a single extraction of a given sample. At each developmental stage, duplicate, unpoled samples were extracted.

Extraction and purification

Prior to extraction, material from each developmental stage was lyophilized, finely ground and stored at −70°C until required. Samples (0.5 g) were extracted (24 h at 4°C, with stirring) in 10 ml of 70% methanol, containing 20 mg/litre butyldihydrate toluene and 50 mg/litre sodium ascorbate. The samples were centrifuged at 20 000 g for 10 min and a mixture of [14C]IAA, [3H]GA_4 and [3H]dihydroZ (10 000 dpm each) was added to the supernatant to determine recoveries. The supernatant was filtered using a 0.45 μm polytetrafluoroethylene filter and then passed through a C_8 Sep-Pak column. The filtrate was reduced to dryness in a Savant vacuum concentrator and stored at −20°C prior to HPLC separation.

HPLC separation of PGRs

The partially purified dried extracts were redissolved in 1 ml HPLC starting buffer, filtered through a 0.45 μm HV filter and 400 μl were injected into the HPLC. Separations were achieved on a Waters (Milford, MA) gradient HPLC fitted with a 10 × 250 mm Zorbax 5 μm semiprep ODS column (Dupont, Wilmington, DE) and a U6k variable volume injector. The column was eluted with a gradient starting at 10% methanol in 0.1 M acetic acid buffered to pH 3.5 with triethylamine, and changing to 50% methanol over 100 minutes, at a flow rate of 1 ml/min.

With the exception of GA, retention times of the PGRs were determined by injecting authentic standards using a UV detector (Fig. 2a). GA retention time was determined by injecting [3H] GA_4. One minute fractions were collected and the radioactive fractions were identified by scintillation counting. Retention times of the PGRs were verified (with the exception of IAA) by the production of an immunohistogram obtained from one minute fractions of the injected sample collected from 11 to 100 min (Fig. 2b–e). IAA retention time was verified by injection of 14C IAA and the retention times were calculated as described for GA.

Fractions (3–4 min) corresponding to the elution times determined for each PGR were collected, dried in a Savant concentrator, and used for the determination of PGR concentration using specific RIAs.

Quantitation of PGRs by RIA

HPLC fractions were dissolved in 4 ml of 100% methanol and subjected to RIA. Verified protocols exist for the RIA of each of the PGRs tested (Cutting and Bower, 1989; Cutting et al., 1983, 1986; Hofman et al., 1985). Serial dilution tests were carried out on all fractions showing immunological activity. All RIA quantitations were done in triplicate. Raw data were analysed using an on-line computer and the Securia data reduction radioimmunoassay package (Packard Instrument Company, 1986, publication No. 169–3016). Data were then corrected for cross-reactivity and recoveries.

![Figure 2](https://example.com/figure2.png)

**Figure 2.** (a) UV trace showing the retention times of authentic plant growth regulator standards after separation by HPLC. (b–d) immunohistograms of IPA, ABA, GA, respectively, and (e) immunohistograms of Z and ZR.
Results and discussion

Histodifferentiation takes place between 0 and about 50 DAFS after which seed growth and reserve accumulation occur until seed abscission at 83–85 DAFS (Farrant et al., 1992b). In the current study, root protrusion had occurred by 2 DAS and root growth by 4 DAS.

Cytokinins

The changes in cytokinin contents during development and germination are shown in Fig. 3. IPA content in the whole seed was high during the first 20 DAFS and declined at the completion of histodifferentiation (Fig. 3a). The pericarp had low amounts of this PGR during the remainder of seed development, but IPA increased in the axis and cotyledons during the initial stages of growth and reserve accumulation, peaking at 70 DAFS. After that stage, IPA amounts declined in those organs and were relatively low in the mature seed and remained low during germination.

Like IPA, Z content was high during the first 20 DAFS and declined during the completion of histodifferentiation (Fig. 3b). The whole seed Z content was higher than that recorded for IPA, particularly during the initial stage of this developmental phase. Z contents increased in all the seed components during the period of growth and reserve accumulation, and, as for IPA, peak contents occurred at 70 DAFS, the increase being greatest in the cotyledons. After 70 DAFS, Z declined in all the seed parts and the mature seed had low contents of Z relative to earlier developmental stages. During germination, cotyledon Z continued to decline. In the axis, Z contents showed an initial decline during the first 2 DAS but increased slightly thereafter.

The ZR content of the whole seed increased during histodifferentiation, the rate of increase slowing after 30 DAFS (Fig. 3c). At the onset of seed growth considerable increases in ZR contents occurred in the axis and cotyledons, with peaks of 14 000 and 17 500 ng/g respectively, occurring 60–65 DAFS. Pericarp ZR content also increased during this stage, but to a lesser extent. As was the case for the other cytokinins, ZR contents declined during the latter stages of development. However, the ZR content during all stages of development was greater than that of the other cytokinins (Figs. 3a–c), and the mature seed still contained relatively high amounts of ZR, particularly in the cotyledons. The cotyledon ZR contents continued to decline during germination. After an initial slight decline during the first day after shedding, those in the axis increased and became equivalent to that of the cotyledons by 4 DAS.

High contents of cytokinin during histodifferentiation occur in desiccation-tolerant seeds also, and it is generally accepted that the cytokinins are involved in embryo and endosperm formation, and endosperm utilization where this occurs (Blumenfeld and Gazit, 1970; Davey

Figure 3. Changes in concentrations of cytokinins during development and germination of seeds of Avicennia marina. (a) isopentenyladenine, (b) zeatin, (c) zeatin riboside. For the sake of clarity error bars in this and subsequent figures have been omitted. Standard deviations were generally less than 15% of the means.
and van Staden, 1979; van Staden et al., 1982; Lorenzi et al., 1988). It is likely that similar control processes exist in *A. marina*. Large increases in cytokinin contents during growth and reserve accumulation are unusual, and similar trends have not been widely reported for desiccation-tolerant seeds (van Staden et al., 1982). The total cytokinin content of *A. marina* cotyledon tissue at 70 DAFS of 21,300 ng/g is considerably higher than the maximum concentrations reported in the literature for desiccation-tolerant seeds. In lupin (*Lupinus luteus*) seeds for example, maximum levels (as determined by RIA) of 2,109 ng/g fresh mass occurred during histodifferentiation (Badenoch-Jones et al., 1984). Similarly, in the desiccation-sensitive seeds of *Podocarpus henkelii*, maximum cytokinin concentrations of 2,600 ng/g Z equivalents dry mass (determined from bioassay studies) occurred during the initial stages of development (Dodd, 1982). The high cytokinin contents in *A. marina* seeds during growth and reserve accumulation are probably not a feature specific to desiccation-sensitive seeds, and their occurrence in this species is more likely to be related to the patterns of accumulation of soluble reserves and the reproductive strategy of immediate germination on shedding (Farrant et al., 1992b). The high cytokinin content of both axes and cotyledons may create sinks for the import of soluble sugars (which accumulate to high concentrations), as is known to occur in vegetative tissue (Mothes and Engelbrecht, 1961). The decline in cytokinins after 70 DAFS is coincident with the attainment of full germinability by the developing seeds (Farrant et al., 1993) and slightly precedes a small decline in starch levels in the axis (Farrant et al., 1992b).

The changes in concentrations of cytokinins during germination are consistent with the concept of cytokinin control of cell division in the axis, and the change in the role of the cotyledons from a reserve sink to a source.

**Indoleacetic acid**

The patterns of changes in IAA observed during development (Fig. 4) are similar to those reported for orthodox seeds (Eeuwens and Schwabe, 1975; Cohen and Bandurski, 1982; Sandberg et al., 1987; Bialek and Cohen, 1989; Valpuesta et al., 1989). Concentrations were high during histodifferentiation and IAA probably plays the same roles in *A. marina* during this developmental stage as it does in desiccation-tolerant seeds. During reserve accumulation there was a gradual decline in the IAA concentration in both axes and cotyledons, and it was high but declining in the pericarp. IAA does not appear to be involved in reserve accumulation by the embryo. The significance of the high contents in the pericarp is not clear, but IAA has been implicated in fruit or pod growth in some desiccation-tolerant species (Eeuwens and Schwabe, 1975; Varga and Bruinsma, 1984; Bialek and Cohen, 1989; Valpuesta et al., 1989), and it might play a similar role in the growth of the pericarp in *A. marina*.

![Figure 4. Changes in concentrations of indoleacetic acid during development and germination of seeds of *Avicennia marina*.](image)

Low quantities of free IAA in mature seeds are common (Cohen and Bandurski, 1982; Bialek and Cohen, 1989). There was a slight increase in concentrations of IAA in axes of *A. marina* during germination. This is consistent with its suggested role in controlling growth of this structure during germination of desiccation-tolerant seeds (Tillberg, 1977; Cohen and Bandurski, 1982; Reinecke and Bandurski, 1987; Sandberg et al., 1987). The significance of the slightly greater increase in the cotyledons is not clear. Two possibilities exist. IAA may facilitate reserve mobilization in the cotyledons as has been suggested to occur in pea (Hirisawa, 1989). Alternatively or additionally, increased contents of IAA might stimulate cotyledonary photosynthesis. This PGR has been shown to stimulate photosynthesis in vegetative tissues (reviewed by Higgins and Jacobsen, 1978; Brenner, 1987). Cotyledons of *A. marina* have fully formed chloroplasts on shedding, and within a day of shedding active photosynthesis can occur (Steinke and Naidoo, 1991).

**Gibberellins**

The total of only two of the range of gibberellins was assayed and so the data cannot be interpreted in terms of the putative roles of the different gibberellins in the control of development and germination. However, GA1 is considered to be the primary gibberellin regulating cell elongation, and occurs as an important gibberellin in most perennial hardwoods.
Changes in the amounts of gibberellins during histodifferentiation (Fig. 5) are similar to those that occurred in the cytokinins IPA, Z and ZR. The patterns of the changes in GAs during this growth phase in A. marina are also similar to those reported for desiccation-tolerant seeds (reviewed by Khan, 1982; Pharis and King, 1985) and their roles in the control of this developmental stage are probably similar.

Following the decline in GAs at the end of histodifferentiation, there was an increase in the embryo during reserve accumulation up to 70 DAFS, after which concentrations remained constant until the seeds were shed. GA contents were higher in the axis than in the cotyledon. There is considerable variation in reported patterns of GAs during reserve accumulation in desiccation-tolerant seeds (Khan, 1982). It is generally accepted that GAs are involved in the control of growth, but there is less certainty as to whether they are involved in the process of reserve accumulation itself. Dual peaks in GA contents do occur during development of some desiccation-tolerant seeds (for example wheat, Radley, 1976), but unlike in A. marina, amounts of active GAs are generally low in desiccation-tolerant seeds (Khan, 1982; Pharis and King, 1985). There are few data in the literature that relate GA concentrations in developing desiccation-tolerant seeds to their ability to germinate precociously. In A. marina, GAs reach maximum concentrations in the axis at 70 DAFS. At this stage the seed will germinate and establish a seedling if the pericarp is removed (Farrant et al., 1993). At 65 DAFS isolated axes will show root protrusion in culture, only if GA is included in the medium (Farrant, 1992). It is tempting to speculate that the high contents of GA confer on the axis the ability to germinate.

During germination there was an increase in GA concentrations in the axes and a decrease in the cotyledons. The increase in the axis suggests that, as is the case for desiccation-tolerant seeds, GAs may be involved in the processes of root protrusion and growth (Jones and Stoddart, 1977; Pharis and King, 1985; Karssen et al., 1989).

Abscisic acid

The ABA content of whole seeds was highest during the initial stages of histodifferentiation and declined progressively thereafter (Fig. 6). This differs from the patterns reported for most desiccation-tolerant seeds where ABA increases only after completion of differentiation (King, 1982) and the significance of this difference is not known. The high ABA content during early histodifferentiation might act as an abortifacient as 57–68% of initiated seeds abort during the first 20 DAFS (Farrant, 1992). After histodifferentiation there was a further slight decrease in ABA concentrations in both axes and cotyledons and these remained low throughout reserve accumulation. Pericarp contents of ABA, however, increased during the later phases of growth and reserve accumulation. Neither pre-mature nor mature seeds can complete germination unless the pericarp is removed (Farrant et al., 1993), and it is possible that pericarp ABA is involved in preventing precocious germination. Concentrations of ABA in mature A. marina embryos are low, and remain so during germination, which is similar to the situation in non-dormant desiccation-tolerant seeds.

**PGR control of development in A. marina seeds**

During the stage of histodifferentiation trends in the PGR contents in A. marina are similar to those in most desiccation-tolerant seeds and it is likely that this stage is under the same hormonal control. Anatomical and biochemical studies support this view (Farrant et al., 1992b). During the period of growth and reserve accumulation cytokinins are particularly high and probably create a sink for the import of soluble reserves. The increases in GAs might facilitate the cell growth associated with this process. The lack of protein reserves in A. marina could be related to the low quantities of ABA in the embryo during this developmental phase.

At 70 DAFS noticeable changes occur in the developmental patterns. Although soluble sugars accumulate, the developing seed is metabolically active with high rates of respiration (Farrant et al., 1992b), and there will be concomitant utilization of some of these reserves. After 70
DAFS there are marked decreases in the concentrations of cytokinins which would weaken the sink, shifting the ratio between import and utilization. At this stage there is a decrease in the rate of accumulation of reserves, particularly in the axis, and there is ultrastructural evidence of starch utilization in the axis (Farrant et al., 1992b). Concentrations of gibberellins reach a maximum at this point and do not decline subsequently. It is at this stage also that full germinability is reached if the inhibiting influence of the pericarp is removed. There are no changes of patterns of proteins present or synthesized from the end of histodifferentiation to two days after root protrusion (Farrant et al., 1992a). In non-dormant desiccation-tolerant seeds, PGR contents are generally low and metabolic rates are insignificant. This is not the case for A. marina seeds which are metabolically active and have high concentrations of GA and ZR. The continued metabolism and the pre-shedding onset of starch utilization as well as the lack of identifiable changes in protein metabolism make it difficult to identify a point that can be considered to be the start of germination. This poses the question of what germination actually is in these seeds that do not go through a quiescent period.

Like desiccation-tolerant seeds, there must be a mechanism in A. marina that prevents precocious germination. Such a mechanism must: (1) prevent germination during development; (2) delay germination in the shed mature seed until suitable conditions prevail, at which point (3) the control must be removed. In desiccation-tolerant seeds, ABA contents are high prior to the onset of maturation drying, preventing precocious germination. On drying, it is the desiccated state that prevents germination after shedding. During desiccation of non-dormant seeds, concentrations of free ABA decline, and germination can occur under suitable conditions if water is supplied. In the desiccation-sensitive seeds of both Quercus robur (Grange and Finch-Savage, 1992) and Theobroma cacao L. (Pence, 1991), a similar mechanism appears to operate, in that high concentrations of embryonic ABA decline before the seed is shed. The pericarp-imposed prevention of precocious germination in seeds of A. marina fits the above criteria equally well, and is well suited to the habitat of these seeds. If the mature seed is shed onto a moist substrate, the pericarp is sloughed, ABA inhibition of germination is removed, and root protrusion occurs. If the seed is shed onto a dry substrate (e.g. during an intertidal period) the initial stages of germination might proceed, but root protrusion is delayed until the moisture required to slough the pericarp is supplied at the next high tide. A pericarp-induced inhibition of germination has also been found in mature seeds of Corylus avellana L. (Bradbeer, 1968), a temperate deciduous species which has been classed as recalcitrant (Chin and Roberts, 1980). For this mechanism to operate a pH gradient may be required to drive the transport of ABA from the pericarp to the root meristems of the axis. (In this study, the amounts of PGRs in the whole axis, which can be up to 20 mm in length in mature seeds, were measured. No information is available on the distribution of PGRs within the axis.)

Comparison between A. marina and desiccation-tolerant seeds

Compared with desiccation-tolerant seeds, the major differences in the patterns of PGRs occurring during the development of seeds of A. marina are high levels of cytokinins during the phase of growth and reserve accumulation, relatively high concentrations of ZR and GAs in seeds immediately prior to shedding, and low concentrations of ABA in embryonic structures after histodifferentiation. The high amounts of cytokinins during reserve accumulation are thought to be related more to the nature of reserves than to desiccation sensitivity. The high concentrations of ZR and GAs at shedding may simply be a consequence of the seed remaining metabolically active and not going through the period of quiescence associated with maturation drying.

High concentrations of ABA have been associated with the acquisition of desiccation tolerance in a wide range of orthodox seeds (reviewed by Kermode, 1990) as well as the desiccation-tolerant vegetative tissues of the so-called ‘resurrection’ plants (Piatkowski et al., 1990). The lack of LEA proteins in seeds of A. marina (Farrant et al., 1992a) could well be related to the low concentrations of ABA reported in this study. It is not known whether the mechanisms for the production of LEA
proteins are absent in A. marina, but are not induced because of low endogenous ABA levels, or whether the genes for the production of these proteins are absent.

References


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