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Drought Rhizogenesis in *Arabidopsis thaliana*[1]

Differential Responses of Hormonal Mutants

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Drought rhizogenesis is an adaptive strategy that occurs during progressive drought stress and is characterized in the Brassicaceae and related families by the formation of short, tuberized, hairless roots. These roots are capable of withstanding a prolonged drought period and give rise to a new functional root system upon rehydration. The kinetics of drought rhizogenesis during progressive water shortage was analyzed in the *Arabidopsis thaliana* wild-type ecotypes Landsberg *erecta* and Columbia. In both genotypes, this response started from a similar threshold of soil humidity (about 2%). The intensity of drought rhizogenesis was compared in various *A. thaliana* hormonal mutants. The wild-type lines and most of the mutants achieved a similar drought rhizogenetic index (DRI), defined as the maximum number of short roots produced per mg of root biomass, after progressive drought stress. However, this DRI was dramatically reduced in the abscisic acid (ABA)-deficient *aba*, ABA-insensitive *abi1-1*, and auxin-resistant *axr1-3* mutants. These data indicate that endogenous ABA and auxin play a promotive role in drought rhizogenesis. The DRI was highly increased in the gibberellin (GA) biosynthetic mutant *ga5*, suggesting that some GAs might also participate in this process. The possible role and identity of the GA species involved is discussed in view of the unaltered DRI values of the *ga2*, *ga3*, and *ga4* mutants. The present analysis also allowed further discrimination among the various ABA-insensitive (*abi1* versus *abi2* and *abi3*) and auxin-resistant (*axr1* versus *aux1*) mutants tested. In particular, drought rhizogenesis is the first physiological response shown to be differentially affected by the *abi1-1* and *abi2-1* mutations.

Drought rhizogenesis is an original root morphogenetic differentiation process that has been shown to occur in the Brassicaceae and in other phylogenetically related dicotyledonous families (Vartanian, 1984). Under progressive drought stress, the new lateral roots that emerge at a threshold plant water potential remain short, do not form hairs, and often take a tuberized shape related to cortical cell enlargement and starch accumulation (Vartanian, 1981). Among various structural and biochemical changes observed in the drought-induced short roots, particularly noticeable was an increase in polyamine levels (Geay et al., 1984), high Pro accumulation (Vartanian et al., 1992), and an altered two-dimensional protein pattern compared with normal lateral roots (Damerval et al., 1988). These highly differentiated short roots remain alive under prolonged drought stress. Upon rehydration, they rapidly recover elongation and hair formation (Vartanian et al., 1983), giving rise to a new absorbing root system, and their protein pattern returns to that of normal, well-watered lateral roots (Damerval et al., 1988). Therefore, development of the "short root system" during a drought period appears to be a forecast strategy that is a significant component of the overall plant adaptation for poststress recovery.

Although phytohormones might be expected to play a regulatory role in various aspects (root primordia initiation, cell proliferation, growth, and differentiation) of this neomorphogenesis, the precise mechanisms underlying this complex adaptive process remain to be elucidated. *Arabidopsis thaliana* offers several advantages for studying such a physiological response by genetic and molecular approaches (Meyerowitz, 1989), including numerous hormonal mutants. The adaptive behavior of this model species to progressive drought has not been described so far.

In the present paper, we report that the characteristic drought rhizogenesis is expressed at a similar threshold of soil moisture in the two commonly used *Arabidopsis* ecotypes Landsberg *erecta* and Columbia. Also, differential intensities of drought rhizogenesis were observed in various hormonal mutants, indicating multiple hormonal controls of this response.

MATERIALS AND METHODS

Plant Material

The *Arabidopsis thaliana* L. Heynh. lines used in this study were the Landsberg *erecta* and Columbia wild types as well as derived hormonal mutants. Mutants in the Landsberg *erecta* background were kindly provided by Dr. M. Koornneef. These are the ABA-deficient (Koornneef et al., 1982) *aba-1* (isolation number A26); the nonallelic ABA-insensitive (Koornneef et al., 1984) *abi1-1* (AII), *abi2-1* (EII), and *abi3-1* (CIV); and the nonallelic GA-deficient (Koornneef and van der Veen, 1980) *ga2-1* (L44), *ga3-1* (U344), *ga4-1* (C320), and *ga5-1* (B019) mutants. The auxin-resistant *axr1-3* (ME-3) (Estelle and Somerville, 1987) and *aux1-7* (Pickett et al., 1990)

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Abbreviation: DRI, drought rhizogenetic index.

mutants in the Columbia background were kindly provided by Dr. M. Estelle.

Plant Culture

Plants were grown in a microphytotron at 22°C under a photon flux density of about 200 $\mu E\ m^{-2}\ s^{-1}$ PAR during an 8-h light photoperiod (9 AM–5 PM). Seeds were germinated on a moistened sandy soil in Petri dishes, except for seeds of the *ga2* and *ga3* mutants, which were germinated on filter paper that had imbibed 10^{-5} M GA_3 or GA_{4+7} and were initially incubated at 4°C for 4 to 6 d to break dormancy. When the cotyledons emerged and the radicle was a few millimeters long, the seedlings were then planted (two per pot) in plastic pots filled with 1.5 kg of sandy soil watered to field capacity (5.6% dry weight humidity at a matrix potential of −0.1 MPa). The soil surface was protected from evaporation by a sheet of Parafilm.

Plants were first allowed to grow in well-watered conditions: each pot was enclosed in a polyethylene bag, which maintained the seedlings in a humid atmosphere (about 75% RH), and a few drops of water were added daily to keep the soil moisture at field capacity. After approximately 1 month, when the rosettes were about 1.5 to 2 cm wide, the polyethylene bags were removed to expose the plants to the drier atmosphere (50% RH) of the microphytotron. At the same time (designated d 0 in all subsequent experiments), the progressive drought-stress procedure was initiated by withholding water.

Physiological Measurements

From the onset of the progressive drought stress, water loss was monitored by weighing each pot every other day at the same hour (1 PM). These values were then used to calculate the plant transpiration rates and the remaining soil moisture. Water loss occurred primarily through plant transpiration, since evaporation was prevented by the Parafilm covering the soil surface. Also, the increase in plant biomass (mg) was negligible compared with the water loss.

To analyze drought rhizogenesis, whole root systems were individually collected on a 2-mm-diameter mesh, cleaned from the sandy soil, and examined under a binocular microscope. Expression of drought rhizogenesis in the Landsberg *erecta* and Columbia wild types was followed by counting the number of short roots present on four to six root systems every 2 d. For each mutant genotype, the number of short roots was counted on root systems sampled after the complete decline in transpiration rate. The total root biomass (dry matter weight) was measured after drying the entire root system at 70°C for 3 d. For each genotype, a DRI was then defined as the number of short roots produced per mg of total root biomass.

Leaf water deficit was measured on detached rosette leaves. The percentage of water deficit is $(W_S - W_F/W_S - W_D) \times 100$, where W_F is the fresh-matter weight measured upon harvest, W_S is the saturated weight measured after rehydration of the leaf at 4°C for 30 h in the dark, and W_D is the dry weight measured after drying the leaf at 70°C for 3 d.

RESULTS

Drought Rhizogenesis in the Landsberg *erecta* and Columbia Ecotypes of *Arabidopsis*

Arabidopsis plants grown under humid conditions for about 1 month were subjected to a progressive water stress by withholding water in a dry (50% RH) atmosphere. Since the soil surface was protected from evaporation, water loss occurred gradually through plant transpiration. As shown in Figure 1, this resulted in a progressive depletion of the water in the sandy soil. From the onset of the drought conditions (d 0), the soil moisture content decreased from the initial value of 5.6% (field capacity) to less than 1% dry weight humidity within about 3 weeks. The variations in the rate of soil moisture decrease were related to changes in the plant transpiration rate (Fig. 1).

The general trend was similar for both ecotypes (Fig. 1, A and B). A phase of increasing transpiration rate, corresponding to an increment in shoot biomass (data not shown), was observed during the first 12 to 14 d while soil water was readily available (i.e. soil moisture in the range from 5.6–2%). It was followed, starting from this critical soil moisture,

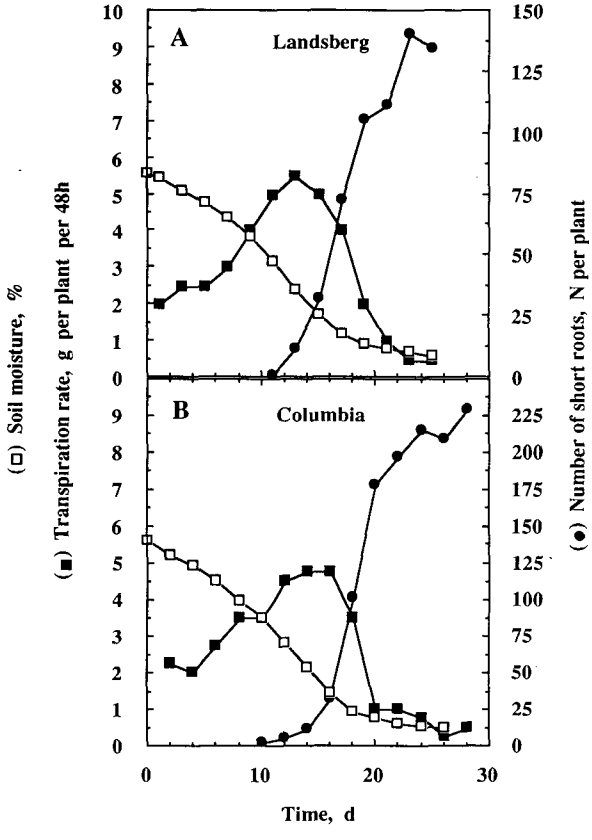

Figure 1. Kinetics of the drought rhizogenesis in *Arabidopsis* wild-type ecotypes Landsberg *erecta* (A) and Columbia (B). Progressive drought stress was initiated on d 0. Time course of the transpiration rate (■, g per plant per 48 h) and soil moisture content (□, % dry weight humidity) for individual representative plants. Mean number of short roots produced during the drought period (●), as counted on four to six root systems harvested every 2 d.

by a phase of decline in the transpiration rate that reached a basal level (0.5 g water loss per plant per 48 h) within another 12 d. During this second period, the leaf water deficit increased from 10% (leaves still turgid) to 80% (leaves permanently wilted). The leaf water deficit rose more slowly in the Columbia than in Landsberg *erecta* plants (data not shown), which resulted in a differential behavior of the aerial parts of these two ecotypes in terms of survival duration and adaptive strategy (Columbia being more drought tolerant than Landsberg *erecta*), as will be detailed elsewhere.

However, both ecotypes displayed the same root response to increasing soil and plant water deficit. A new root morphogenesis, characterized by the emergence of lateral roots that remained short (0.1–0.8 mm long) and did not form root hairs as long as drought was persistent (Fig. 2a), occurred concomitantly with the decline in the transpiration rate. These new roots often displayed a tuberized shape at their base (0.1–0.2 mm wide), related to rhizodermal and cortical radial cell enlargement (Fig. 2, b–d), and were typically twice as wide as the normal lateral roots bearing them (Fig. 2, a–c). Thus, although these drought-induced short roots exhibited some variability in their morphology, the various specific traits described above dramatically distinguished them from lateral roots emerging in well-watered conditions (Fig. 2e). In *Arabidopsis*, these drought-induced short roots were observed on the lateral roots only and not on the tap root.

Under prolonged drought stress, the normal lateral roots progressively exhibited hair decay and lignification (Fig. 2, a, b, and f). In contrast, the drought-induced short roots remained alive, withstanding soil desiccation below the permanent wilting point (<1% soil moisture). They were able to recover elongation and hair formation within 24 to 48 h after rehydration (Fig. 2f), thereby giving rise to a new branched absorbing root system.

In the course of the progressive drought stress, the short roots emerged mainly during the phase of transpiration decline. Their number increased with sigmoidal kinetics beginning between d 10 and 12 and reaching a plateau on d 23 to 24 (Fig. 1, A and B). Plotting the number of short roots as a function of soil moisture content revealed that in both genotypes, drought rhizogenesis started when the average soil moisture had reached a critical value of about 2% (Fig. 3). It should be kept in mind that these measurements of soil moisture content provide an estimation of the global soil humidity in the entire pot but do not reflect the heterogeneity of local conditions experienced by the root system. The few short roots that were formed at higher values of bulk soil humidity (Figs. 1 and 3) might thus correspond to local events of early dehydration beyond the threshold level. Indeed, on plants harvested at the beginning of drought rhizogenesis, the short roots were found close to the soil surface, where soil humidity decreases first.

Differential Expression of Drought Rhizogenesis in *Arabidopsis* Hormonal Mutants

As a first step toward analyzing the hormonal regulation of drought rhizogenesis in *Arabidopsis*, we sought to compare the maximum intensity of this process in a number of hormonal mutants that had been isolated in either the Landsberg *erecta* or Columbia genetic backgrounds (see "Materials and Methods"). As mentioned above, in these two wild-type ecotypes the number of short roots reached a plateau when the transpiration rate had dropped to a basal level (Fig. 1). Thus, we compared for each mutant and corresponding wild-type genotype the number of short roots produced on plants harvested after the complete decline of the transpiration rate. This stage was not reached at the same time for all mutant genotypes, due to differences in their drought behavior; however, in all cases the soil moisture had decreased below 1% at the time of harvest (data not shown). The intensity of drought rhizogenesis was expressed as the total number of short roots per root system (N). A DRI was also computed as the number of short roots per mg of dry matter weight of total root biomass (N mg^{-1}). The DRI was used to compensate for a possible effect of the mutation on total root development. The results obtained are presented in Table I.

An extremely low number of short roots was found on the *aba* mutant, which is impaired in ABA biosynthesis (Koornneef et al., 1982; Rock and Zeevaart, 1991). Although the *aba* mutation clearly led to a weak production of total root biomass under these growth conditions, its effect on the drought rhizogenesis per se was shown by the low value of the DRI.

In *Arabidopsis* three distinct classes of mutants (*abi1*, *abi2*, and *abi3* loci) displaying a reduced responsiveness to ABA have been isolated (Koornneef et al., 1984). The *abi1* mutant showed a dramatic reduction in both the number of short roots produced and the DRI. The number of short roots was unaltered in the *abi2* mutant and was slightly higher in *abi3*. Since *abi2* also had a lower total root biomass, this resulted in a statistically significantly higher DRI for both mutants.

The various *Arabidopsis ga* mutants are characterized by blocks at distinct steps of the biosynthetic pathways for GAs (Talon et al., 1990; Zeevaart and Talon, 1992). The DRI in the *ga2*, *ga3*, and *ga4* mutants did not significantly differ from that in the Landsberg *erecta* wild type. In the case of the *ga2* mutant, the slightly lower number of short roots per root system was compensated for by a small decrease in total root biomass. In contrast, the *ga5* mutant displayed a high increase in both the number of short roots and the DRI.

Finally, two distinct mutants that had both been isolated on the basis of a reduced sensitivity to auxin (Estelle and Somerville, 1987; Pickett et al., 1990) have been analyzed. The intensity of drought rhizogenesis was not affected by the *aux1–7* mutation. In contrast, the *axr1* mutant exhibited very few short roots and, thus, despite a slight reduction in root biomass, a dramatically decreased DRI.

DISCUSSION

When subjected to a progressive water stress, *Arabidopsis* plants developed an adaptive response at the root level. Once the water deficit in the soil-plant system had reached a threshold, the newly emerging roots remained short and hairless as long as drought persisted; but they were able to rapidly resume elongation and hair formation upon rehydration. Expression of this drought rhizogenesis occurred concomitantly with the decline in the transpiration rate. Despite differences in the whole-plant drought-adaptive strategies of

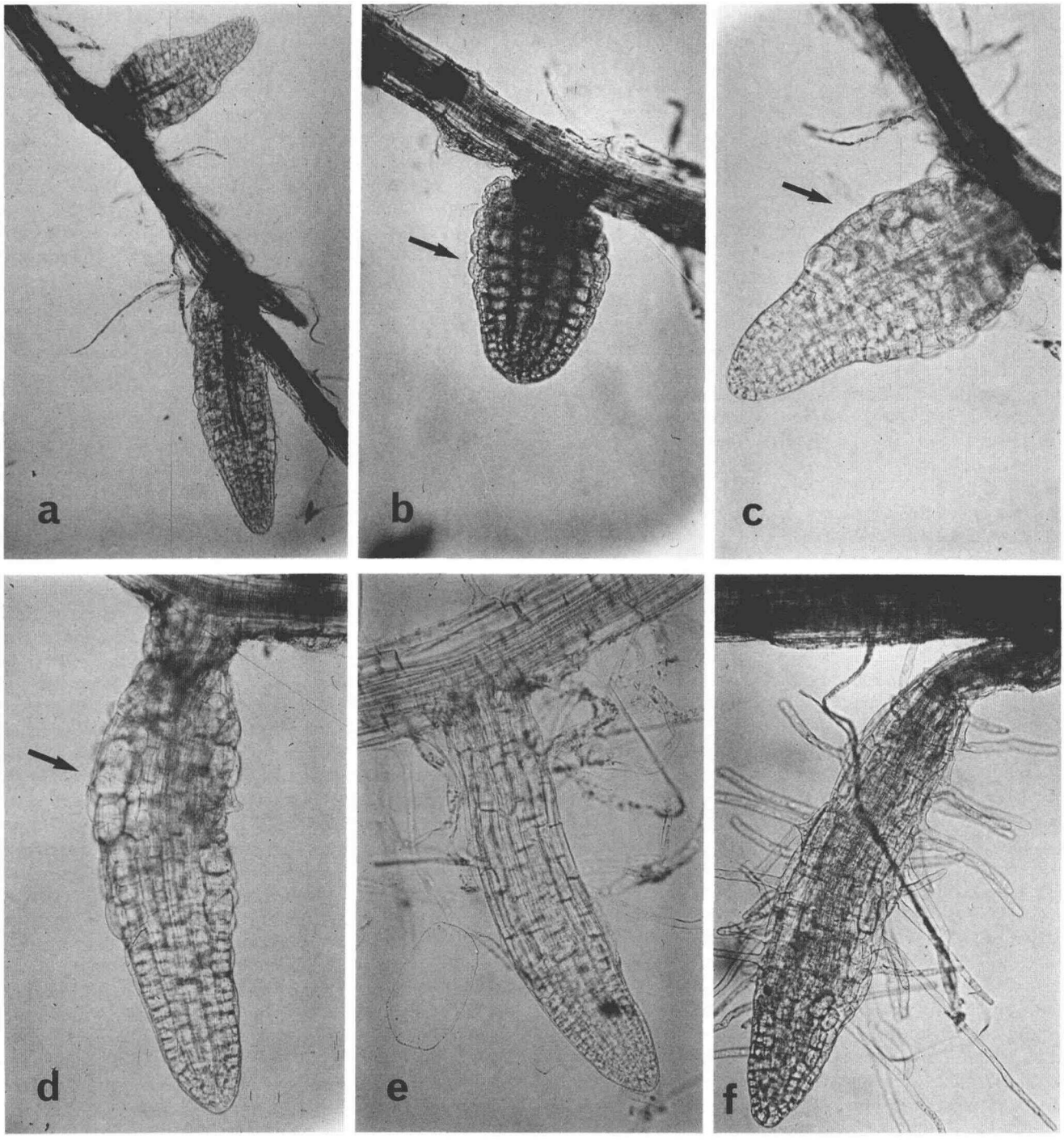

Figure 2. Light photomicrographs of *Arabidopsis* roots. a to d, Different morphological aspects of drought-induced short roots on normal lateral roots after 20 d of progressive drought stress: very short and stubby root (b), short root with enlarged base (c), more elongated and less tuberized root (d). The black arrows point to radial enlargement of rhizodermal cells. e, A young and elongating normal lateral root on a well-watered plant. f, Morphological changes of a drought-induced short root 48 h after rehydration. (a, ×50; b–f, ×100).

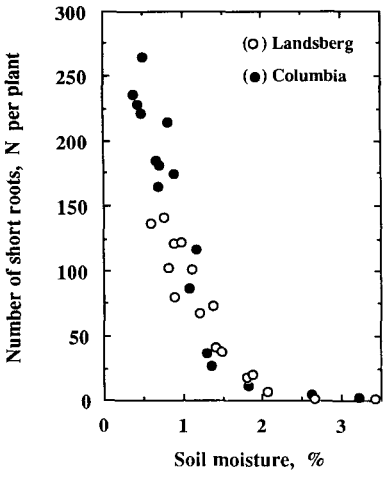

Figure 3. Intensity of the drought rhizogenesis expression as a function of soil moisture content in *Arabidopsis* wild-type ecotypes Landsberg *erecta* (O) and Columbia (●) subjected to progressive drought stress. Plants were harvested every 2 d after the onset of the progressive drought stress. Each point represents the mean number of short roots present per root system at a given soil moisture content (% dry weight humidity).

Landsberg *erecta* and Columbia (as will be described elsewhere), expression of the drought rhizogenesis began at very similar values of bulk soil moisture (about 2%) in these two ecotypes. Also, the Landsberg *erecta* and Columbia wild types had similar DRI values (between 9 and 10). This average DRI value thus seems to be a characteristic of the drought response in *Arabidopsis* under these experimental conditions.

The general features of the drought rhizogenesis developed by *Arabidopsis* are similar to those described for other Brassicaceae species (Vartanian, 1984). In particular, the kinetics of short root production in *Arabidopsis* resembles that of *Sinapis alba* (Sabatier and Vartanian, 1983), which could be fitted by a mathematical probit model (Vartanian and Lesquoy, 1984). In *Arabidopsis* the drought-induced short roots formed on the lateral roots only. A similar localization has also been observed in some Brassicaceae species such as *S. alba, Raphanus raphanistrum,* or *Brassica campestris,* whereas in others such as *Brassica oleracea, Brassica napus,* or *Brassica nigra* the short roots emerge both on tap roots and laterals (Vartanian, 1981; Balestrini and Vartanian, 1983; Vartanian, 1984). These two patterns most likely reflect the different ability of the corresponding species to maintain meristematic and differentiation potentialities in the tap root until high water deficits are reached.

The analysis of a series of *Arabidopsis* hormonal mutants demonstrated that several phytohormones may participate in regulating the intensity of drought rhizogenesis. The low DRI of both the ABA-deficient *aba* and ABA-insensitive *abi1* mutants indicates that this hormone plays a promotive role in the expression of drought rhizogenesis. This result is in agreement with the numerous lines of evidence supporting the critical role that ABA plays in plant adaptation to various forms of environmental water stress. For instance, the *Arabidopsis aba* mutant is impaired in cold acclimation (Heino et al., 1990; Gilmour and Thomashow, 1991).

Mutations at the *abi1* versus *abi2* or *abi3* loci clearly have a distinct effect on the intensity of drought rhizogenesis. The observation that in contrast to *abi1*, the *abi2* mutation does not impair the production of drought-induced short roots is remarkable, since, in previous studies, these two mutations were shown to have similar effects on several physiological processes. For instance, both mutants exhibit disturbed water relations and reduced seed dormancy (Koornneef et al., 1984), and neither of them has altered cold acclimation (Gilmour and Thomashow, 1991). The present results thus suggest that

Table I. *Comparative analysis of the maximal intensity of drought rhizogenesis in various wild-type and mutant Arabidopsis genotypes*

For each parameter, statistical inferences about the difference between the means observed for a given mutant and the corresponding wild type were made using the Mann-Whitney *U* test, and when applicable (i.e. when the variances differed by a factor of less than 3) by a two-sample unpaired *t* test. When both tests could be applied, they yielded identical results. $^+$, Mean of the mutant higher than mean of the wild type, $P < 0.025$. $^-$, Mean of the mutant lower than mean of the wild type, $P < 0.025$. Data are mean ± SD.

	Number of Short Roots per Plant		Root Biomass	DRI
	N	*n*	*mg*	*N/mg*
Landsberg *erecta*	157 ± 21	(12)	16.6 ± 4.2	9.8 ± 1.6
aba-1	4.7 ± 1.7$^-$	(9)	2.4 ± 1.8$^-$	2.3 ± 0.7$^-$
abi1-1	20 ± 8$^-$	(25)	6.4 ± 1.9$^-$	3.7 ± 1.9$^-$
abi2-1	147 ± 32	(10)	11.9 ± 2.0$^-$	12.4 ± 1.1$^+$
abi3-1	206 ± 38$^+$	(15)	14.7 ± 2.8	14.0 ± 2.2$^+$
ga2-1	134 ± 29$^-$	(8)	11.5 ± 2.0$^-$	11.8 ± 2.2
ga3-1	152 ± 41	(14)	14.5 ± 2.5	10.6 ± 1.9
ga4-1	167 ± 19	(6)	13.5 ± 2.1	12.6 ± 2.9
ga5-1	347 ± 86$^+$	(11)	11.9 ± 3.3	32 ± 11$^+$
Columbia	268 ± 58	(12)	29.3 ± 4.5	9.3 ± 2.5
axr1-3	11 ± 6$^-$	(13)	21.4 ± 5.3$^-$	0.5 ± 0.3$^-$
aux1-7	249 ± 40	(12)	28.5 ± 3.0	8.8 ± 1.6

the *abi2* locus controls only a subset of the endogenous processes regulated by the *abi1* locus and provide an additional example of the pleiotropic effects of the *abi1* mutation (Koornneef et al., 1984; Finkelstein and Somerville, 1990).

The slightly elevated DRI values of the *abi2* and *abi3* mutants are intriguing in view of the markedly decreased DRI values of both *aba* and *abi1*. The increased DRI values of *abi2* and *abi3* might result from indirect effects of these mutations on, for instance, the endogenous hormonal balance rather than from alterations of ABA signaling pathways. It is indeed unlikely that distinct ABA cascades would have antagonist effects on the expression of drought rhizogenesis.

The observation that the GA-deficient *ga5* mutant displays a highly enhanced drought rhizogenesis indicates that some GAs also participate in controlling this process. Two distinct hypotheses can be considered: either some of the C_{19}-GAs that are reduced in the *ga5* biosynthetic mutant (Talon et al., 1990) exert a negative control on the production of short roots in the wild type, or in reverse, some of the C_{20}-GAs that accumulate upstream of the biosynthetic step blocked by the *ga5* mutation (Talon et al., 1990) enhance the expression of the drought rhizogenesis. The former possibility seems incompatible with the observation that the intensity of drought rhizogenesis is unaltered in the *ga2* and *ga3* mutants, which are blocked at early steps of the GA biosynthesis pathways and contain very low levels of all endogenous GA species (Zeevaart and Talon, 1992). Since the *ga4* mutant also displays short root production similar to that of Landsberg *erecta*, the most likely hypothesis would be that some of the GA species that accumulate in *ga5* and not in *ga4*, such as GA_{53}, GA_{12}, or GA_{36} (Talon et al., 1990), play a promotive role in drought rhizogenesis. Analyzing the effects of exogenously applied GA species or biosynthetic inhibitors on the production of short roots might help to confirm this interpretation.

The intensity of drought rhizogenesis is markedly decreased in the auxin-resistant *axr1-3* mutant, indicating that auxin is required for the expression of this process. It is noteworthy that *axr1-3* is a rather weak allele of this locus with respect to other phenotypes analyzed (Lincoln et al., 1990). An involvement of auxin in the expression of drought rhizogenesis had previously been suggested by the observation that in another Cruciferae species, *S. alba*, excision of the apical bud in plants subjected to progressive drought stress inhibits the formation of drought-induced short roots without altering the total root biomass (Vartanian, 1984). Auxin could conceivably participate in the initiation of the short roots, since this hormone is known to favor the formation of lateral roots under normal conditions (Torrey, 1986). Although in vitro-grown *axr1-3* seedlings have been reported to display a reduced branching during the early stages of root development (Estelle and Somerville, 1987), there was no obvious qualitative difference between the branching pattern of Columbia and *axr1-3* adult plants under the present experimental conditions. However, it would be valuable to compare quantitatively the kinetics of root branch formation during the development of these two genotypes.

In contrast to *axr1-3*, the *aux1-7* mutation does not impair the formation of short roots. *axr1* mutants display alterations in many tissues including roots, rosette, inflorescences, and flowers (Estelle and Somerville, 1987; Lincoln et al., 1990). The AXR1 gene product thus seems to be required for auxin-regulated growth processes in most if not all tissues of the plant. Mutations at the *aux1* locus do not have such pleiotropic effects; in particular, the anatomy and ultrastructure of *aux1-7* mutant roots are indistinguishable from those of the wild type (Pickett et al., 1990). The AUX1 gene product is thought to function primarily in the hormonal regulation of gravitropism (Maher and Martindale, 1980; Mirza et al., 1984; Pickett et al., 1990), although the *axr1-3* and *aux1-7* mutants are both resistant to the inhibition of seedling root growth by ammonium ions in the absence of potassium (Cao et al., 1993). The present data provide another example of the differential roles of the AXR1 and AUX1 gene products.

The present survey of drought rhizogenesis intensity in various *Arabidopsis* hormonal mutants brings new insights into the genetic and hormonal regulation of this process. They indicate that drought rhizogenesis is subjected to multiple hormonal control by at least auxin, ABA, and some GAs. They provide the basis for further experiments aimed at characterizing the exact roles and interplays of these hormones in the various aspects of this complex drought-adaptive process: stress perception, tolerance of root meristematic potentialities to water deficit, and differentiation. Also, the differential response of the *Arabidopsis* hormonal mutants allows the investigation of the contribution of drought rhizogenesis in the whole-plant adaptive strategy.

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