Drought survival, summer dormancy and dehydrin accumulation in contrasting cultivars of Dactylis glomerata

Florence Volaire

Laboratoire d’Ecophysiologie des Plantes sous Stress Environnementaux, INRA (Institut National de Recherche Agronomique), 2 Place Viala, 34060 Montpellier, Cedex 1 France
e-mail: volaire@ensam.inra.fr

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To study survival under prolonged and severe drought in the perennial grass Dactylis glomerata we compared dormant, resistant and sensitive cultivars (cvs.) in both field and glasshouse experiments. Water status, membrane stability and expression of dehydrins were assessed in the immature leaf bases, which are the last surviving organs. Analysis of leaf elongation and senescence of aerial tissues showed that dormancy was exhibited by the potentially dormant cultivar (cv) only in the field. This cultivar exhibited a high survival rate, similar levels of dehydration and expression of a low-molecular weight (22–24 kDa) dehydrin in both drought and irri-gated plants, whether fully dormant or not. At the same level of soil water deficit, there were no differences between the non-dormant drought resistant and drought sensitive cultivars in plant water status and membrane stability. However, the accumulation of dehydrins as drought progressed was markedly different between these cultivars and was associated with their contrasting survival. The possible role of the major low-molecular dehydrins in maintenance of cell integrity under dehydration is discussed with reference to both summer dormancy and survival under severe drought.

Introduction

Drought resistance is generally defined as the maintenance of plant production during moderate water deficit (Turner 1997). In contrast, tolerance of intense and pro-longed water deficits determines plant survival (Blum 1996). In Mediterranean areas subjected to such severe summer droughts, survival varies greatly both between and within perennial grass species, e.g. Dactylis glomerata (Volaire 1995, Volaire and Lelievre 1997, Volaire et al. 1998a). To avoid death of apices, drought resistant genotypes of Dactylis exhibit a combination of adaptive traits to delay dehydration by increasing root development and water uptake (Garwood and Sinclair 1979, Volaire and Lelievre 2001) and limit water loss by hastening senescence of most aerial tissues (Volaire et al. 1998a). De-hydration tolerance was also shown to contribute to drought survival since meristematic tissues can tolerate low water status through solute accumulation and osmotic adjustment (Volaire et al. 1998b). Dormancy that is a ‘temporary suspension of visible growth of any structure containing a meristem’ (Lang et al. 1987) is present over summer in some perennial grasses (Laude 1953, Silsbury 1961, M cWilliam 1968) and has also been linked to survival in semiarid environments (Oram 1983, Ofir 1986). We showed that one of the most drought resistant, but non-dormant cultivars of Dactylis (cv. Medly) exhibited survival inferior to that of the summer dormant species Poa bulbosa which was also fully tolerant of desiccation (Ofir and Kigel 1998, Volaire et al. 2001). In this study, we analyse the contribution of summer dormancy to dehydration tolerance in contrasting genotypes of Dactylis, a species in which this trait has been reported but not studied (Knight 1966).

Although there are many strategies for desiccation toler-ance which involve both protection and repair mechanisms (Bewley 1995), maintenance of membrane stability may be a critical adaptive trait (Blum and Ebercon 1981), since cell membranes appear to be a major site of desiccation injury (Leopold et al. 1981, M cKersie and Leshem 1994). The responses of dehydration tolerance in plants subjected to extreme cold, drought or salt stresses, involve the activation of a range of genes (K u-ang et al. 1995) among which, some encode for polypeptides with substantial homologies to proteins expressed during late embryogenesis (Bray 1993, Bartels et al.
The dehydrins are a subfamily of these ‘late embryogenesis abundant’ (LEA) proteins which accumulate in some dehydrated species (Close 1996, Ismail et al. 1999). These proteins may play a role in protection of other proteins or membranes, thereby preserving structural integrity (Dure 1993, Close 1997). They may also act as regulators of cell osmotic potential (Nylander et al. 2001) and supplement the protection afforded by sucrose accumulation (Scott 2000).

Experiments both in a controlled environment and in the field, aiming to impose realistic and progressive drought conditions, were carried out to compare dormant, drought resistant and drought sensitive genotypes of Dactylis. The main objectives of this study were to analyse water status, membrane stability and accumulation of dehydrins in meristematic tissues, and relate these to the ability of contrasting genotypes to survive severe drought.

Materials and methods

Plant material

The highly drought resistant and summer active cultivar of D. glomerata L. Medly (syn. K M 2), which is of Mediterranean origin (INRA, Montpellier, France), was compared to the drought sensitive and summer active cv. Lutetia, which is of oceanic origin (INRA, Lusignan, France) and to a summer dormant and highly drought resistant cv. Kasbah, which is of Moroccan origin and was bred in Australia (Oram 1990). A local ecotype of P. bulbosa was used as a control of full dehydration and summer dormancy (Volaire et al. 2001).

Experimental design and conditions

The first experiment was carried out in a glasshouse at INRA (Montpellier, France) over the summer of 1999. PVC tubes, 60 cm deep \( \times \) 5.5 cm diameter, were filled with the same quantity of substrate (80% sand, 10% loam, 10% clay). Seeds of cvs. Medly and Lutetia and P. bulbosa were sown on 6 October, Kasbah was sown later on 30 March 1999 to prevent dormancy induction that has been associated with the reproductive phase in other grasses (Ofir and Koller 1972, 1974). On 10 June, three plants of each cultivar of Dactylis were transplanted into each tube (66 per cultivar) which were fully randomised within two treatments (168 and 30 tubes, respectively, for the drought and irrigated treatments). Plants of P. bulbosa were transplanted in 12 additional tubes (6 irrigated and 6 drought). Irrigation was terminated on the 2 July with no water being supplied for 60 days to plants of the drought treatment. After this period, full irrigation was restored for two weeks to measure survival.

The second experiment was carried out in the field at INRA (Mauguio, near Montpellier). The soil was a deep loamy clay. The full irrigation and drought treatment areas consisted of one and three blocks, respectively, each containing 1.1 m \( \times \) 0.9 m plots with 6 drills into which seeds of the three cultivars of Dactylis was sown at a rate of 2 g m\(^{-2}\) on 16 November 1999. A adjacent small plots were sown with P. bulbosa, both in drought and irrigated areas. All plots were fertilized at rates commonly used for semi-intensive Mediterranean grasslands (80 kg N ha\(^{-1}\) from November to March). Plots were defoliated on 15 May and 16 June. On 28 June, all plots including the irrigated block were covered with clear polythene shelters high enough to ensure good ventilation. The soil was saturated with a full irrigation on 30 June and then no water was supplied to the drought plots until 6 October, a period of 98 days. After that date, plots were fully irrigated to measure survival. The control treatment was irrigated twice a week throughout the whole period. Environmental conditions were relatively similar between both experiments (Table 1).

Table 1. Environmental conditions during two experiments (glasshouse and field). Mean daily temperatures (\( ^{\circ}\mathrm{C} \)) for air and soil (at -1 cm depth, i.e. at apices depth, in drought and irrigated treatments) and mean daily vapour pressure deficit (kPa). Standard deviations (into brackets).

<table>
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<tr>
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<th>Glasshouse</th>
<th>Field</th>
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<tbody>
<tr>
<td></td>
<td>Summer 1999</td>
<td>Summer 2000</td>
</tr>
<tr>
<td></td>
<td>(2 July – 31 August)</td>
<td>(1 July – 31 August)</td>
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<tr>
<td>Mean temperature:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Air</td>
<td>25.4 (1.4)</td>
<td>23.4 (1.8)</td>
</tr>
<tr>
<td>- 1 cm (drought)</td>
<td>28.9 (2.4)</td>
<td>27.7 (4.2)</td>
</tr>
<tr>
<td>- 1 cm (irrigated)</td>
<td>26.4 (1.6)</td>
<td>24.2 (1.6)</td>
</tr>
<tr>
<td>Mean Vapour pressure deficit</td>
<td>1.0 (0.4)</td>
<td>1.2 (0.4)</td>
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coefficient of membrane stability (CMS) was calculated for 90 min and the conductivity measured again (C2). The samples were then boiled in 4 ml deionized water for 1 h, cooled, and once on day 58 of both experiments in the fully irrigated control. As the only aerial tissues that remained alive during most of the drought periods were the bases of immature leaves, the aerial parts of the plants were divided into two fractions (1) the first 20 mm above root insertion (mainly sheaths and leaf bases) and (2) the remaining upper tissues (mainly mature lamina). This second fraction was divided into green and senescent tissues. FW and DW (after 48 h at 80°C) were measured on these tissues to assess green and senescent biomass.

In the fraction containing the lowest 20-mm part of the tillers, bases of immature leaves (the surviving organs) were dissected out and split into two subsamples. One subsample was immediately weighed and then dried (48 h at 80°C) to determine tissue water content. The other subsample was used to measure membrane stability since the rate of injury to cell membranes by drought may be estimated through measurement of electrolyte leakage from the cells (Blum and Ebercon 1981). Membrane stability was assessed as follows (Howarth et al. 1997): after incubation in 4 ml of deionized water at 20°C in the dark for 22 h, conductivity (C1) was measured with a seed analyser (G 2000, Wavefront, Inc, Ann Arbor, USA). Samples were then boiled in 4 ml deionized water for 1 h, cooled for 90 min and the conductivity measured again (C2). The coefficient of membrane stability (CMS) was calculated as: CMS = 1 - (C1/(C1 + C2))100).

<table>
<thead>
<tr>
<th>Cultivars</th>
<th>1999</th>
<th>2000</th>
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<tbody>
<tr>
<td>Lutetia</td>
<td>62 (n = 24)</td>
<td>45 – ssd = 13 (n = 120)</td>
</tr>
<tr>
<td>Medly</td>
<td>92 (n = 24)</td>
<td>87 – ssd = 2 (n = 100)</td>
</tr>
<tr>
<td>Kasbah</td>
<td>83 (n = 24)</td>
<td>91 – ssd = 9 (n = 70)</td>
</tr>
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Protein extraction, electrophoresis and Western blotting

Samples were taken at the same dates as for the above plant measurements (glasshouse) and on days 4, 24 and 76 for drought plants and on day 58 for irrigated plants (field). Samples were also taken on 7 September (glasshouse) and 8 November (field) from rehydrated plots. In addition, samples of P. bulbosa were taken on the last date of samples from drought plants and from irrigated plants in both experiments. Plants were dissected and after discarding dead tissues, bases of immature leaves (as defined earlier) or bulbs (P. bulbosa) were frozen in liquid nitrogen and stored at −40°C. Total protein was extracted from seeds of cv. Medly and used as a control in all blots. Plant tissues were homogenized in a mortar in the presence of liquid nitrogen and extracted using a buffer containing 5 mM Tris-HCl, pH 8, 500 mM NaCl, 2 mM ascorbic acid, 0.5 mM phenylmethylsulphonyl fluoride and 1 mM dithiothreitol. The homogenate was heated at 80°C for 10 min and centrifuged at 17000 g. Supernatants were thawed and heat stable proteins were quantified by the dye-binding assay (Bradford 1976). Proteins were separated by 10% SDS-PAGE using a Mini protein 3 electrophoresis cell (Bio-RAD, Hercules, CA, USA) overnight at 4°C. The membrane was then incubated for 2 h with the antidehydrin polyclonal antibody (StressGen Biotechnologies Corp., Victoria, BC, Canada) at a dilution of 1:1000 in phosphate-buffered saline (PBS) (Close et al. 1993). After three consecutive washes of 15 min each in PBS, the membrane was incubated for 1 h with the secondary antibody, goat antirabbit IgG alkaline phosphatase conjugate at a dilution of 1:1000 in PBS, and the Aurora Western Blotting kit (ICN) was used for detection. Running of gels and preparation of Western blots were repeated at least three times. Densitometric analyses were performed on the best represen-

![Graph](image-url)

**Fig. 1.** Relationships between leaf elongation rate and number of days without irrigation in a glasshouse (A) and field experiment (B) for D. glomerata cv. Medly (○, ■), cv. Lutetia (□, ■) and cv. Kasbah (△, ■). Means ± SD (n = 15). Drought treatment: open symbols, control irrigated treatment: closed symbols.
Fig. 2. Relationship between leaf elongation rate and soil water content (%) in D. glomerata cv. M edly (○), r = 0.93, cv. Lutetia (□) r = 0.95; and cv. K asbah (△) r = 0.99, subjected to a severe summer drought in a glasshouse experiment. Means ± SD (n = 15).

Growth and development
As a negative control, samples of all cultivars were tested against pre-immune rabbit serum (StressGen) at the same dilution as the antidehydrin antibody with no trace being detected.

Results
Whole-plant responses
Plant survival rate
In both experiments, the survival rate of the drought sensitive cv. Lutetia was one third (tube) to a half (field) lower than those of cvs. M edly and K asbah which exhibited similar rates both higher than 80% (Table 2).

Leaf extension
In tubes, leaf extension of control plants of all cultivars oscillated between 50 and 80% of the initial rate (Fig. 1A). Leaf elongation of drought plants decreased linearly with declining soil moisture (Fig. 2) and stopped at a SWC of 3.3 and 4% for M edly and Lutetia, respectively. Leaf extension of cv. K asbah ceased at a significantly higher SWC (5.6%). In the field, leaf extension was similar in plants of cvs. M edly and Lutetia which were subjected to drought and ceased 15 days later than in cv. K asbah (Fig. 1B). Leaf growth of K asbah declined rapidly and stopped at the same time irrespective of whether the plants were irrigated (control) or exposed to drought. In contrast, leaf extension in irrigated plants of M edly and Lutetia oscillated around 50% of the initial rate over the same period.

Biomass
The proportion of senescent tissues in total aerial biomass increased from 10 to 90% on average in all cultivars as drought progressed in the glasshouse experiment (Fig. 3A). The rate of biomass senescence was similar between cultivars although delayed in Lutetia between days 20 and 45 of drought. In the field, the proportion of senescent tissues increased similarly from 20 to 70% in Lutetia and M edly (Fig. 3B). The response of K asbah was very different since the senescent biomass reached 50% of the total aerial biomass at the beginning of the experiment and increased up to over 90% after 40 days of drought. At this observation date, control plants of K asbah also exhibited 70% of senescent tissues whereas only 15% of tissues were senescent in irrigated plants of Lutetia and M edly.

Immature leaf bases
Water content and membrane stability
In the glasshouse, the water content of immature leaf bases of M edly and Lutetia declined similarly from over 80% to 25-30% at the lowest SWC (approximately 3%). This decline was less significant in K asbah, since the hydration of its surviving tissues was approximately 60% at the onset of the drought declining to approximately 40% just before rehydration (Fig. 4). In the field, the leaf base water content of M edly and Lutetia declined from 85 to 50% in the first half of the drought (although more slowly for Lutetia), and then was stable for the subsequent 45 days without irrigation (Fig. 5). In contrast, the hydration of leaf bases of K asbah fell to 50% within 10 days of water deficit. It was then stable during most of the drought period with an increase to 55-60% at the last sampling date of the drought period (beginning of October).
In both experiments, the coefficient of membrane stability of leaf bases was very variable but tended to decline along with water content of the same tissues (Fig. 6). In tubes, this decline was parallel for all cultivars, but at similar water contents, the membrane stability was on average 10% higher in leaf bases of K asbah than in those of M edly and L utetia (Fig. 6A). In the field, the relationship between water content and membrane stability of leaf bases was similar for all cultivars and final values of membrane stability were all above 65% (Fig. 6B).

![Figure 4](image)

Fig. 4. Relationships between the soil moisture (%) and the water content of immature leaf bases (%) of living tillers of D. glomerata cv. M edly (○, ●), cv. L utetia (□, △) and cv. K asbah (△, ▲) subjected to a severe summer drought in a glasshouse experiment. Drought treatment: open symbols, control irrigated treatment: closed symbols.

![Figure 5](image)

Fig. 5. Relationships between the number of days without irrigation and the water content of immature leaf bases (%) of living tillers of D. glomerata cv. M edly (○, ●), cv. L utetia (□, △) and cv. K asbah (△, ▲) subjected to a severe summer drought in a field experiment. Drought treatment: open symbols, control irrigated treatment: closed symbols.

**Accumulation of dehydrins**

In the glasshouse experiment, the pattern of dehydrin accumulation differed greatly between cultivars. As drought progressed, four proteins of approximately 44, 32, 22 and 15 kDa were found in immature leaf bases of cv. M edly (Fig. 7A). From day 27 (lane 3), the rate of accumulation of the 15 kDa-protein was relatively low and stable whereas that of the other proteins increased and reached a maximum after 58 days of drought (lane 5). Traces of the 15 kDa-protein appeared in leaf bases of cv. L utetia on day 27 (Fig. 7B, lane 3) but accumulation of other dehydrins (approximately 44, 22 and 19 kDa) was evident on day 46 (lane 4) but tended to decline by day 58 (lane 5). In either cultivar, no dehydrin was found in any irrigated tissues (beginning of the experiment, control and rehydrated plants: lanes 2, 6 and 7). Conversely, in cv. K asbah (Fig. 8A), two proteins (approximately 24 and 51 kDa) were found in irrigated plants (beginning of the experiment and control: lanes 2 and 6). As drought increased, three additional dehydrins were detected (approximately 14, 21 and 40 kDa). However, only the 24 kDa-compound continued to accumulate to reach a maximum level on day 46 (lane 4). Relative overall accumulation of total dehydrins measured after 58 days of drought, was 2.4- and 3.2-fold higher in leaf bases of K asbah and M edly, respectively, than in those of cv. L utetia. Relative accumulation of low molecular weight proteins (÷30 kDa) in bases of cv. L utetia was 2 and 2.8 times lower than in those of M edly and K asbah, respectively (Fig. 9A).

In the field experiment, no dehydrin was detected in leaf bases of irrigated plants of M edly and L utetia or in drought leaf bases of L utetia (Fig. 9B). However, when the methodology was slightly altered to increase the quantity of proteins tested (15 μg), three dehydrins (approximately 44, 32 and 22 kDa) were found in leaf bases of M edly at the end of the drought period (Fig. 10, lane 2). The immunoblots revealed that a major protein of approximately 24 kDa was present in leaf bases of K asbah as traces at the beginning of the experimentation (lane 2) and after 27 days of drought (Fig. 9B, lane 3). Its accumulation was similar after 76 days of drought (lane 3). Other proteins were found (of approximately 14, 21, 40 and 51 kDa) but at a relatively low intensity. The approximately 24 kDa-dehydrin was also expressed in irrigated control tissues (lane 5).

Both in pot and field experiments, a large quantity of abundant dehydrins were found in bulbs of P. bulbosa subjected to drought. When irrigated, some proteins such as the approximate 20 and 22 kDa-dehydrins were also abundant (Fig. 9B).

**Discussion**

This study of contrasting cultivars of D. glomerata characterizes plant survival under severe drought by analysing water status, membrane stability and levels of dehydr-
Fig. 6. Relationships between the coefficient of membrane stability (%) and the water content of immature leaf bases (%) of living tillers of D. glomerata cv. Medly (○, ●), cv. Lutetia (□, ■) and cv. Kasbah (▲, ▼) subjected to a severe summer drought in a glasshouse (A) and field experiment (B). Drought treatment: open symbols, control irrigated treatment: closed symbols.

Overall response to drought in the potentially dormant cv. Kasbah

The comparison of experiments shows that dormancy of cv. Kasbah in the field was expressed in both irrigated and drought treatments, by a rapid decline of leaf extension and high senescence of aerial tissues. Conversely, Kasbah was not fully dormant in the glasshouse, although its leaf elongation ceased at a higher water status than other cultivars, which suggests some degree of dormancy induction.

The comparison of Kasbah, in either a fully dormant or non-dormant state, may help to overcome the problem that dormancy and stress acclimation are expressed at the same time, which makes it difficult to associate physiological and molecular changes with one or the other states (Wisniewski and Arora 2000).

Dormant or not, cv. Kasbah exhibited the highest survival rate and a level of dehydration similar to that of other Dactylis during the major part of the drought period. Therefore the three traits, resistance to severe drought, dormancy and dehydration tolerance appear to be relatively independent, a result also shown previously in another dormant grass P. bulbosa (Volaire et al. 2001).

While the membrane stability of leaf bases of all cultivars was similar in the field, it remained higher and never fell under 70% in cv. Kasbah as drought progressed in the pots. The decline of membrane stability was slow as water deficit intensified and suggests that the surviving tissues were hardened as the water deficit developed progressively. We also showed that summer dormancy did not confer superior membrane stability. The measurement of electrolyte leakage has been extensively used to evaluate the response to temperature (Hownarth et al. 1997) but was variably correlated to drought resistance according to species (Blum and Ebercon 1981).

In both experiments, the accumulation of dehydrins in leaf bases of cv. Kasbah was comparable since a major (approximately 24 kDa) protein was expressed in all drought tissues, although its expression reached a maximum at a lower water deficit in dormant plants when their water content was stabilized. This specific protein was also detected in tissues of control plants. The parallel between Dactylis and P. bulbosa shows that only ‘potentially dormant’ genotypes express dehydrins under irrigated conditions. The reason for this expression in control plants, even in the apparently non-dormant Kasbah, remains unclear since it is not constitutive, but is expressed in summer whatever the conditions and confirm partial induction of dormancy. There is virtually no information relating the abundance of dehydrins to drought survival. If we refer to winter survival, the association between the abundance of dehydrins and degree of cold hardiness was proposed in various studies (Close 1996, Danyluk et al. 1998, Bravo et al. 1999). However, the accumulation of dehydrins was more correlated to freezing tolerance than to winter dormancy status (Wisniewski et al. 1996, A rora et al. 1997, Rinne et al. 1998) even though it is acknowledged that stress resistance can reach a maximum during dormancy (Bigras 1996, Cunningham et al. 2001).

Overall response to drought in-non-dormant cultivars

The survival rate of the sensitive cv. Lutetia was lower than that of the resistant cv. Medly in both field and pot conditions. We also confirmed that the response of leaf elongation to drought was similar in both cultivars (Volaire et al. 1998a, Volaire and Lelievre 2001). Although the percentage of green lamina in aerial biomass and higher water content of leaf bases was maintained for longer in the sensitive cultivar, neither the final level of dehydration nor the membrane stability of the surviving organs differed between these cultivars. This confirms that plant survival depends more on how long the surviving tissues can maintain cell integrity at a given moisture content, than on the actual minimum threshold of dehydration reached by the tissues (Volaire et al. 1998b).

This study shows that a greater number and abundance of dehydrins were expressed, at lower water deficits, and throughout the drought, in leaf bases of M edly than in those of L utetia. The main dehydrins were also expressed but at a lower intensity, in leaf bases of Medly exposed to drought in the field, whereas none was de-
Fig. 7. Immunoblots from glasshouse experiment-sample of D. glomerata cv. Medly (A) and cv. Lutetia (B). Dehydrins expressed in 5 mg of heat stable proteins from seeds of cv. Medly (lane 1), and last surviving leaf bases of plants subjected to a 60-day drought beginning from 2 July. Last irrigated on 2 July, day 2 (lane 2), drought of day 27 (lane 3), drought of day 46 (lane 4), drought of day 58 (lane 5). Control irrigated plants sampled on day 58 (lane 6). Rehydrated plants on 7 September (lane 7).

In a former field experiment, we found no difference in levels of dehydrin mRNAs in immature leaf bases of the same cultivars subjected to an equivalent drought (Volaire et al. 1998b). This tends to prove the important role for post-transcriptional regulation of gene expression during stress (Bray 1993, de Vienne et al. 1999). Our results suggest a likely association between drought survival and dehydrin expression. In various species, levels of expression of dehydrins during moderate water deficit related to the level of acclimation (Labhilili et al. 1995, Cellier et al. 1998, Tabaei-Aghdaei et al. 2000). In transgenic rice, the expression of an LEA gene conferred higher tolerance to water deficit and salt stress (Xu et al. 1996) although in sorghum, expression of dehydrins in contrasting cultivars could not explain the differences observed between genotypes (Wood and Goldsbrough 1997). We suggest that as dehydration becomes more intense, the more likely it is that dehydrins are involved in promoting dehydration tolerance. This role was sug-
Fig. 9. Immunoblots of *D. glomerata* cv. Medly, cv. Lutetia and cv. Kasbah and of *P. bulbosa* subjected to a severe drought in a glasshouse experiment (A) and in a field experiment (B). Dehydrins expressed in 5 μg of heat stable proteins from seeds of cv. Medly (lane 1), and last surviving leaf bases of plants (or bulbs of *P. bulbosa*). Plants subjected to severe drought, 58 days without irrigation (A) and 76 days without irrigation (B) for lanes 2–5, Control irrigated plants on day 58 (A and B) for lanes 6–9. *P. bulbosa* (lanes 2 and 6); Kasbah (lanes 3 and 7); Medly (lanes 4 and 8); Lutetia (lanes 5 and 9).

Suggested by their association with recovery after desiccation in resurrection plants (Kuang et al. 1995, Blomstedt et al. 1998, Scott 2000).

**Comparison of cultivars**

The comparison of dormant and non-dormant cultivars permits the proposition of the two following hypothesis: (1) the expression of dehydrins in the potentially dormant cultivar may be more endogenously controlled than environmentally imposed. In both experiments, dehydrin expression was comparable and stable throughout the summer period what would confer an efficient adaptation against dehydration irrespective of the environment; (2) of the dehydrins expressed, the low-molecular weight (approximately 22-24 kDa) proteins may have a major role in dehydration tolerance. They were the main ones present in the dormant cv. Kasbah (drought and irrigated) and the most abundant in the resistant cv. Medly. Moreover, in a former experiment, a decreasing expression of these specific proteins in leaf bases of cv. Medly at the end of drought was associated with a soaring mortality of this genotype (Volaire et al. 2001). The specific function of dehydrins remains unclear although they appear to be a key component of dehydration tolerance (Close 1996). Our results indicate that the increasing expression of dehydrins is associated with declining water content of tissues in correlation with maintenance of cell integrity at low water status and consequently reduced mortality in resistant genotypes.

In conclusion, this study shows an association between specific dehydrins and both summer dormancy and drought survival in *D. glomerata*. Further research will test the relevance of this association for other perennial grasses.

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