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How can resistant genotypes of *Dactylis glomerata* L. survive severe Mediterranean summer drought?

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RESUME – *"Survie de génotypes de dactyle (*Dactylis glomerata *L.) à la sécheresse estivale en Méditerranée". Dans les conditions d'intense sécheresse estivale méditerranéenne, la plupart des graminées fourragères pérennes ne maintiennent ni croissance ni développement mais doivent rester vivantes pour repousser après les pluies d'automne. Les réponses adaptatives du dactyle qui contribuent à la survie à la sécheresse en retardant la déshydratation ou en favorisant la tolérance à la dessication, ont été analysées dans de nombreuses expérimentations au champ et en conditions contrôlées. Les caractères les plus associés à une meilleure survie sont la précocité d'épiaison, la profondeur du système racinaire, l'extraction de l'eau à de faibles potentiels hydriques du sol, un pool important de réserves en sucres solubles et l'accumulation de déhydrines qui sont susceptibles de conférer une tolérance à la déshydratation des organes survivants.*

Mots-clès : Dactylis glomerata *L., survie à la sécheresse, tolérance à la déshydratation, système racinaire.*

Introduction

In rainfed Mediterranean areas, perennial grasses are important both as long-term pastures for extensive animal farming and cover-crops for soil protection and rehabilitation. In all cases, the interest in these perennial plants depends on their persistence over years, which is associated with their ability to survive successive severe summer droughts. Therefore, it is necessary to identify the physiological features most involved in survival under prolonged drought in order to contribute to breeding of suitable cultivars for semi-arid environments. Survival of severe drought varies greatly between and within forage grass species, a good example being *Dactylis glomerata* which we have chosen as a model plant. The main contrasting cultivars (cv.) we have tested have been cv. Medly (Mediterranean origin, INRA, Montpellier) and Lutetia (drought sensitive, INRA, Lusignan). In one field-trial, we also compared a range of 21 genotypes originating from arid Algeria to temperate Denmark. The experiments were carried out both in the field (full expression of root growth in dense swards) and in tubes (similar conditions of rooting and water reserve for all genotypes). The droughts were generally imposed on adult plants, during the summer period by stopping irrigation for 6 to 12 weeks. A number of traits were assessed during the drought and after rehydration when the survival rate (% of live tillers) was measured. The major focus of the studies has been to follow the kinetics (water status, carbohydrate accumulation,...) of the last surviving organs, i.e., the bases of the youngest enclosed leaves including the meristematic tissues. We summarise here the main adaptative responses of *Dactylis* for drought survival including delay of dehydration through limitation of water loss or increase of water uptake and dehydration tolerance of the surviving tissues.

Adaptative responses contributing to delay of dehydration

Responses associated with limitation of water loss

Flowering time

The comparison of 21 contrasting genotypes showed that the heading date was highly correlated to drought survival (Volaire and Lelièvre, 1997). This heading date, spread over 30 days, separated the *D. glomerata* populations (late flowering, poor survival), the *hispanica* (intermediate) and the Mediterranean cultivars (very early flowering, high survival). Early flowering is a drought escape mechanism (Levitt, 1972), which could facilitate a longer regrowth period, and consequently a greater allocation of assimilates to root growth between flowering time and onset of drought.

Overall growth pattern in summer (Volaire, 1995)

A field-experiment comparing five genotypes of *Dactylis* under drought and irrigated conditions showed that the poor persistence of the populations of northern origin was associated with 'summer activity' and continuous use of their carbohydrate reserves. Conversely, the populations of Mediterranean origin exhibited growth patterns relatively insensitive to irrigation and accumulated high levels of carbohydrates in summer, which were mobilized for active regrowth in autumn. The most extreme case of growth regulation in summer is exhibited by dormant populations for which senescence of aerial mature tissues is induced at the beginning of the summer even under irrigation (ex. cv. Kasbah). Dormancy confers the highest drought survival rate and is a trait currently under study (Volaire *et al.*, 2001; Volaire, 2002)

Leaf growth regulation and water use under water drought (Volaire et al., 1998a ; Volaire and Lelièvre, 2001)

The first response of plants to water deficit is to save water by decreasing leaf growth and therefore leaf area and transpiration. Reduction of leaf elongation and progression of senescence as drought progressed have not been significantly different between resistant and sensitive genotypes in various experiments (Fig. 1a). Moreover, when grown under similar rooting conditions, water use at the beginning of the drought period (before any mortality occurs) has not been significantly different between any genotypes of *Dactylis* (Fig. 1b).

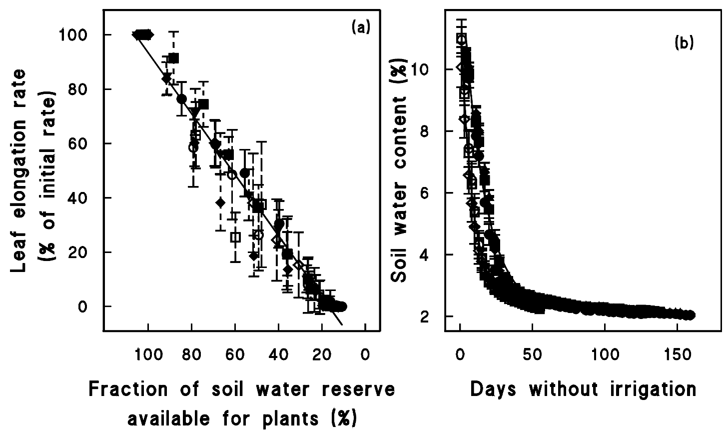

Fig. 1. (a) Reduction of leaf elongation rate with increasing water deficit for two genotypes of *Dactylis* (Medly, Lutetia) and (b) water use by three genotypes of *Dactylis* (Medly, Lutetia, Currie) under water stress imposed in two tube experiments with similar rooting conditions.

Responses associated to increase of water uptake

Root system

In the field, the maximum root depth and the root density of the drought sensitive cv. Lutetia were significantly less that those of the drought resistant Medly (Volaire *et al.*, 1998a). The importance of rooting in maintaining a continuous, if small, supply of water during severe drought, has been described in many forage grasses (Garwood and Sinclair, 1979) and is a major trait contributing to survival under these conditions.

Water uptake at low soil water potential

In a tube experiment, with similar rooting conditions for all genotypes, the ability to extract water at low soil water potential was shown to be significantly different between cv. Lutetia and the drought resistant cultivars (Table 1). In addition to a deep root system, this trait may also have a significant influence on survival of prolonged droughts since it increases the available water for transpiration when the soil is very dry and evapotranspiration rate very low.

Table 1. Soil water potential at plant death for 3 cultivars of *Dactylis*. Significant different cultivars (P<5%) have different superscripts

Cultivars	Number of days to reach death of 75% of the plants	Soil water potential at death of plants
Lutetia (drought sensitive)	141	-3.0*a*
Currie (drought resistant)	155	-3.6*b*
Medly (drought resistant)	155	-3.8*b*

Adaptative responses contributing to dehydration tolerance

Thresholds of dehydration tolerance

The water content of immature leaf bases including the meristematic tissues declines constantly as drought progress (Fig. 2a). Although significantly lower in resistant genotypes for most of the summer period, this water content reaches final lethal levels (30-40%) not significantly different for all populations in all experiments. We also showed that plant survival depends more on how long the surviving tissues can maintain cell integrity at a given moisture content, rather than on the actual minimum threshold of dehydration reached by the tissues (Volaire *et al.*, 1998*b*).

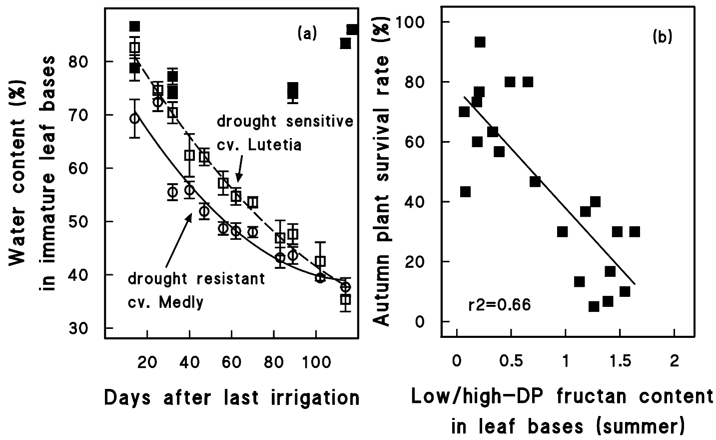

Fig. 2. (a) Water content in surviving organs of two cultivars of *Dactylis* subjected to severe drought in the field ; (b) Survival rate and relative accumulation of low and high degree of polymerisation (DP)-fructans in leaf bases of 21 genotypes of *Dactylis* subjected to summer drought in the field.

Dehydration tolerance factors

The comparison of 21 genotypes of *Dactylis* showed that they accumulated total *water soluble carbohydrate* (WSC) in leaf bases during the drought period and that sucrose and fructans were the most abundant WSC (Volaire and Lelièvre, 1997). Drought survival was correlated with a relatively large pool of highly polymerised fructans (Fig. 2b). These compounds could contribute to the stabilisation of membranes of surviving tissues thus enhancing long-term dehydration tolerance.

In addition to carbohydrates, the expression of proteins such as *dehydrins*, which accumulate in many plants in response to dehydration (Close, 1997) have been shown to vary between genotypes. Their expression in droughted tissues of the resistant cv. Medly was much higher than that of the sensitive cv. Lutetia (Volaire, 2002). These proteins play a role in preserving structural integrity and may be an important factor in dehydration tolerance.

Conclusion

In the field, a high efficiency for water uptake, a deep root system and a high level of dehydration tolerance are combined adaptative responses that confer superior survival to resistant genotypes of *Dactylis*. However, the management of the sward (defoliation frequency, ...) also affects plant responses such as root depth, tillering rate or carbohydrate accumulation and therefore interacts with overall plant drought survival (Volaire, 1994).

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