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Morpho-physiological traits associated with drought survival in bi-specific perennial herbaceous swards

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SUMMARY – Perennial grasslands provide numerous environmental benefits but their response to severe drought and therefore their sustainability in arid and Mediterranean areas have been little studied. Our work aimed to investigate the morpho-physiological traits associated with drought survival for bi-specific mixtures of perennial forage plants, and to test whether growth potential in spring was correlated with the capacity to survive subsequent summer droughts. Five cultivars (two of tall fescue, two of cocksfoot and one of Lucerne) were grown in monoculture and mixtures. Standard leaf functional traits and aerial biomass were assessed under non-limiting water supply in spring. In summer, under continuous severe drought, leaf water status, foliage senescence and plant survival were measured. Senescence of aerial tissues at the end of spring, associated with endogenous summer dormancy were the variables best correlated with drought survival. Specific leaf area under spring irrigation was also correlated with drought survival. These traits associated with dehydration tolerance strategies in pots should be completed with root traits contributing to dehydration delay in the field.

Keywords: Grassland, functional trait, drought survival, summer dormancy.

RESUME – *"Caractères morphophysiologiques associés à la survie à la sécheresse dans des prairies herbacées pérennes bispécifiques". Les enherbements pérennes ont des fonctions environnementales reconnues mais leur réponse à des sécheresses sévères et donc leur durabilité pluri-annuelle dans les zones à climat semi-aride et méditerranéen ont été peu étudiées. Notre objectif était d'étudier les caractères morpho-physiologiques associés à la survie à une sécheresse sévère dans des mélanges bi-spécifiques de plantes fourragères pérennes et de tester si le potentiel de croissance printanier était corrélé à la capacité ultérieure de survie à la sécheresse. Cinq cultivars (deux de fétuque élevée, deux de dactyle et un de luzerne) ont été étudiés en monocultures et en mélanges. Les caractères fonctionnels foliaires standards et la biomasse aérienne ont été mesurés en conditions hydriques non limitantes au printemps. En été, sous sécheresse sévère, la teneur en eau des tissus, la sénescence foliaire et les taux de survie ont été évalués. Le taux de sénescence des tissus aériens en fin de printemps, associé au niveau de dormance estivale endogène ainsi que la surface foliaire spécifique ont été les variables les plus corrélées à la survie au stress hydrique. Ces caractères associés à des stratégies de tolérance à la déshydratation en pots doivent être complétés par l'analyse des caractères racinaires contribuant aux prélèvements hydriques différentiels au champ.*

Mots-clés : *Enherbement, caractère fonctionnel foliaire, survie à la sécheresse, dormance estivale.*

Introduction

Grasslands dominated by perennial herbaceous species are acknowledged to enhance sustainability of agricultural systems since perennial species improve soil structure (McCallum *et al*., 2004), reduce soil nitrate leaching and enhance biodiversity. To maximise environmental benefits, these swards should be a mixture of species to optimise persistence over a number of years. In Mediterranean areas, the persistence of perennial grasses is mainly determined by the ability to survive summer droughts. For example, in monospecific swards, the ability of *Dactylis glomerata* (cocksfoot) or *Festuca arundinacea* (tall fescue) to cope with drought was associated with strategies to delay or tolerate dehydration (Volaire *et al.*, 2001; Volaire *et al.*, 1998a; Volaire *et al.*, 1998b) and with the expression of summer dormancy (Volaire and Norton, 2006). However, ecophysiological studies have limitations when an analysis of the structure and evolution of multi-species communities is attempted. Conversely, functional ecology that aims to define functional types which describe the response of multi-specific groups to environmental variations and changes at the community level (Cornelissen *et al*., 2003) might be a suitable approach. Functional traits have been proposed to understand the dynamics of grasslands but information is sparse on the response of herbaceous swards to severe drought in arid and Mediterranean areas (Michalet, 2006). Our objective was to

analyse bi-specific mixtures of perennial forage plants to define the traits best associated with drought survival. These traits may be used for further research on more complex mixtures in order to define functional groups of herbaceous plants useful to understand and model herbage persistence and production of herbaceous pluri-specific swards.

Material and methods

The five cultivars were: *Dactylis glomerata*, cultivar (cv) Medly ('D. Medly' - sub-humid Mediterranean origin, drought resistant, summer active), and cv. Kasbah ('D. Kasbah' - semi-arid Moroccco, completely summer dormant, very highly drought resistant); *Festuca arundinacea*, cv. Demeter ('F. Demeter' mixed Mediterranean/Temperate origin, summer active, moderatly drought sensitive) and cv. Flecha ('F. Flecha' - Mediterranean, incomplete summer dormancy, drought resistant); *Medicago sativa*, cv. Coussouls ('M. Coussouls' derived from a southern French population).

We carried out two experiments (Exp). Exp1 comprised two pots (20 cm height, 25 cm diameter) of each of the five populations, i.e. 14 pots, each with 20 plants. These plants, acting as monospecific swards, were only used to measure standard leaf traits in Spring under the optimal conditions of appropriate exposure to light and water supply (Cornelissen *et al*., 2003). Pots were kept fully irrigated and out-of-doors until June when measurements were stopped.

Exp2 comprised five replicates of six bi-specific mixtures in pots (38 cm height, 27 cm diameter) with 12 plants of each cv. The six treatments were:

Fescue Flecha + cocksfoot Medly (FM); Fescue Flecha + cocksfoot Kasbah (FK);

Lucerne Coussouls + cocksfoot Medly (LM); Lucerne Coussouls + cocksfoot Kasbah (LK);

Fescue Demeter + cocksfoot Medly (DM); Fescue Demeter + Lucerne Coussouls (DL)

Pots were kept fully irrigated and out-of-doors until the 13 June when they were placed in a glasshouse to begin imposition of drought (irrigation withdrawn) and rehydrated when soil moisture reached between 3.5 and 3%, mean threshold of mortality for sensitive cvs. (Volaire *et al.*, 2001).

The same soil (80% sand, 10% loam, 10% clay) was used and plant density was around 25 cm^2 $plant^{-1}$ for both experiments. Plants (3 months-old) were transplanted in February. Nitrogen fertilisation (corresponding to 60 kg N ha^{-1}) was supplied on 4 April. Four defoliations were performed above 5 cm on 4 April (starting point), 27 April, 30 May and 15 June.

In Exp1, on 24 April, leaves of ten replicates were sampled to measure specific leaf area (SLA, mm^2 mg^{-1}) and leaf dry matter content (LDMC, mg g^{-1}). In Exp2, the same leaf functional traits were measured and also the Leaf Area Index (above 5 cm) at the cuts on 27 April (LAIA), 30 May (LAIM) and 15 June (LAIJ). Along summer drought, leaf dry matter content (LDMC1) could be measured only on 15 June while lamina senescence was minimum but the protocole was modified and tissues were not rehydrated. Water content was measured on basal tissues (the first 2 cm fraction of the enclosed leaf bases for grasses, the first 2 cm of the shoot bases for the lucerne) which are the tissues that survive longest under severe drought. This leaf trait was called BWC (basal tissue water content) and measured at the last irrigation (13 June, BWC1), on 29 June (BWC2) and just before final rehydration after drought (BWC3). Survival rates were measured ten days after final rehydration by counting dead and regrowing tillers or shoots for lucerne (SURV).

Results and discussion

In pots restricting the development of rooting systems, the drought survival rate for each cultivar was rather similar whatever the associated cultivar in the mixture (Table 1). Cocksfoot Kasbah survived at 100%; cocksfoot Medly and tall fescue Flecha at 90 and 80% respectively. On the other hand, lucerne Coussouls survived very poorly (between 0 and 6%) whereas fescue Demeter survived at 33% when associated with lucerne Coussouls and at 3% only when associated with cocksfoot

Medly. A similar ranking was found for some of these cultivars grown as mono-specific swards (Volaire and Lelievre, 2001). Cocksfoot Kasbah had the lowest biomass production in spring with a mean LAI four to five fold lower than that exhibited by the lucerne, cocksfoot Medly and fescue Flecha. The biomass production of fescue Demeter was intermediate. On 13 June, just before imposition of the drought, cocksfoot Kasbah hardly produced any green aerial biomass, had a high leaf dry matter content associated with a low content of water in the basal tissues. Conversely, lucerne and fescue Demeter were the most hydrated with over 82% of water in basal tissues on average and 200 mg DM g^{-1} FM in lamina. Fescue Flecha and cocksfoot Medly were intermediate.

Table 1. LAIA (Leaf area index on 27 April, cm^2 cm^{-2} of soil); LAIM (3 May); LAIJ (15 June); LDMC1 (Leaf dry matter content before drought on 13 June, mg g^{-1} DM FM); BWC1 (Basal tissue water content on 13 June, %); BWC2 (29 June); BWC3 (at soil moisture content of 3 to 3.5%); SURV (Survival rate, %) for lucerne Coussouls (L), cocksfoot Kasbah (K) and Medly (M), fescue Flecha (F) and Demeter (D)

Mixture	CV	LAIA	LAIM	LAIJ	LDMC1	BWC1	BWC2	BWC3	SURV
LK	L	4.8	15.8	6.1	186	86.0	53.3	45.7	6.4
	K	1.2	2.2	0.1	280	59.1	43.3	43.1	100.0
		***	***	***	***	***	***	ns	***
LM	L	3.6	10.2	4.5	209	82.9	43.3	44.9	0
	M	3.6	7.7	2.9	252	80.8	52.2	31.5	93.3
		ns	Ns	ns	**	ns	**	*	***
FK	F	3.2	19.2	1.4	255	77.0	62.5	50.3	91.1
	K	1.8	3.8	0.2	318	64.9	50.0	40.5	100.0
		**	***	***	**	**	***	**	***
FM	F	2.7	14.0	1.0	255	71.2	59.3	50.6	70.0
	M	3.8	10.4	3.1	226	79.7	65.9	52.2	91.6
		ns	Ns	*	ns	***	**	ns	***
DL	D	2.2	6.3	2.9	186	81.8	57.0	45.4	32.7
	L	4.4	11.7	4.9	279	86.0	48.0	36.8	0
		**	**	**	***	**	***	ns	***
DM	D	1.6	7.5	2.7	203	81.3	58.2	45.2	3.1
	M	3.5	13.5	3.5	265	79.3	58.9	46.4	89.8
		**	**	ns	*	ns	Ns	ns	***

Analysis of variance are non significant (ns) or significant (*, **, *** for $P < 0.05$; 0.01; 0.001)

The cultivars had similar SLA and LDMC in spring, whether grown as mono- or bi-specific swards (Table 2). Both cocksfoots had significantly higher SLA and LDMC than the other cultivars.

Table 2. Specific leaf area (SLA, mm^2 mg-1 DM) and leaf dry matter content (LDMC, mg g-1 DM FM) measured in spring under full irrigation for 5 cultivars of forage species either grown in mono- or bi-specific swards. Values with the same letter do not differ significantly

Trait	Experiment	L : lucerne Coussouls	D : fescue Demeter	F: fescue Flecha	M: cocksfoot Medly	K: cocksfoot Kasbah
SLA	Monospecific	30.8 *a*	30.1 *a*	30.4 *a*	38.6 *b*	38.4 *b*
	Bi-specific	31.9 *b*	28.7 *a*	28.7 *a*	39.3 *c*	40.0 *c*
LDMC	Monospecific	177.0 *ab*	168.5 *a*	160.3 *a*	206.7 *c*	192.7 *bc*
	Bi-specific	171.7 *bc*	158.8 *ab*	154.6 *a*	177.4 *c*	184.7 *c*

The least productive cultivars in June (LAIJ) with a high senescence and therefore a high leaf dry matter content (LDMC1) and a low water content in basal tissues (BWC1) exhibited the highest drought survival (Table 3). This dehydration of basal tissues was inversely correlated with a high biomass production in April (LAIA). Although SLA and LDMC in Spring were not correlated with the leaf area potential of the cultivars between April and June, SLA was correlated with final plant survival after summer drought (SURV).

Table 3. Pearson linear correlations between leaf traits (SLA, LDMC), biomass production (LAIA,M, J) in Spring, water status during summer drought (LDMC1, BWC1, 2, 3) and drought survival (SURV) of five cultivars of perennial forage plants. See tables 1 and 2. Significant correlations at p <0.05 are in bold characters

	SLA	LDMC	LAIA	LAIM	LAIJ	LDMC1	BWC1	BWC2	BWC3
LDMC	**0.73**	1							
LAIA	-0.10	0.03	1						
LAIM	-0.54	-0.40	**0.68**	1					
LAIJ	-0.26	0.01	**0.81**	0.42	1				
LDMC1	0.54	0.39	-0.24	-0.23	**-0.59**	1			
BWC1	-0.42	-0.34	**0.73**	0.51	**0.89**	**-0.64**	1		
BWC2	-0.34	-0.36	0.12	0.49	-0.06	-0.24	0.23	1	
BWC3	-0.52	-0.19	-0.06	0.44	-0.12	-0.32	-0.06	**0.61**	1
SURV	**0.61**	0.34	-0.31	-0.15	**-0.72**	**0.61**	**-0.67**	0.26	0.07

Conclusion

The cultivars of cocksfoot with the highest specific leaf area in Spring, also had the best drought survival in pot. In addition, cv. Kasbah exhibited summer dormancy through endogenous dehydration at the end of spring and could survive optimally at very low residual soil water content whether in mono or bi-specific swards. Indirectly, the biomass production of the cultivars was associated with their response to drought, since the most productive (lucerne) had the lowest dehydration tolerance, whereas the least productive (cv. Kasbah) was the most dehydration tolerant. However, this relationship should be tested on a larger range of cultivars. The usual positive relationships between large SLA, low LDMC and high productivity were not found within this group of forage cultivars bred for their biomass production potential. The correlation between SLA and drought survival is likely due to a "species" effect since SLA was not directly correlated with any other variables associated with productivity or plant response under drought. In these conditions of restricted root development, the lucerne was poorly drought resistant, and the fescues intermediate. Their low dehydration tolerance is to some extent, compensated by efficient water uptake at depth in the field. The overall drought resistance of these cultivars in mixtures should therefore, also be assessed in field conditions.

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