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Ecophysiology of annual legumes

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Summary - We review and briefly analyse some of the main ecophysiological attributes found in annual legumes in evolutionary and ecological response to the environmental factors affecting their development, reproduction and and survival in Mediterraean Type Ecosystems. We also give some examples of inter-and intra-specific differences that need to be taken into account when introducing or disseminating annual legumes for pasture improvement, rehabilitation efforts, erosion control and/or long term soil restoration programmes.

Key-words: *Medicago, Trifolium, Ornithopus, Biserrula*, reproductive phenology, hardseededness, relative growth rate

Resumé - *Les principaux attributs écophysiologiques des légumineuses annuelles sont analysés en tant que réponse évolutive et écologique aux facteurs environnementaux affectant leur développement, leur reproduction et leur survie dans les écosystèmes méditerranéens. Quelques exemples de différences inter- et intra-spécifiques sont proposés pour être pris en compte lors de l'introduction ou de la dissémination de légumineuses annuelles pour l'amélioration pastorale, la réhabilitation des parcours, le contrôle de l'érosion ou la restauration des sols.*

Mots-clés: Medicago, Trifolium, Ornithopus, Biserrula, *phénologie de la reproduction, dureté des graines, taux de croissance relatif*

Introduction

In mediterranean-type ecosystems (MTEs), vascular plants are exposed to various stresses as the result of interactions with abiotic factors like temperature (especially low and high extremes), excess or insufficient soil water availability (i.e., temporary water logging and prolonged drought), soil acidity or salinity, and nutrient deficiencies. Biotic factors also play a major role in plant ecology and evolution in these regions, including plant-plant interactions (e.g., intra and interspecific competition, neighbor relationships, shading), herbivore impact (e.g., insect defoliation, overgrazing) and mutualist or other kinds of interactions with fungi, bacteria and other micro-organisms. Like all other plants and animals in the MTEs, annual plants must also cope with highly seasonal environments, and a remarkable degree of climatic unpredictability. Under these conditions, being an annual clearly has many advantages, especially in the Mediterranean Basin itself, where annuals may be considered something of a regional 'speciality', often constituting half the regional vegetation whereas they rarely amount to more than one-tenth in other parts of the world (Raven, 1973; Blondel and Aronson, 1999). Clearly, the diversity and abundance of annuals in the Mediterranean region is related to the long history of anthropic disturbances, as pointed out by many authors. Accordingly, it is not surprising how many ruderal and segetal Mediterranean annuals – especially from the eastern part of the Basin and adjacent steppe regions of the Middle East – have successfully colonized California, Chile and, to a lesser extent, south Australia and the Cape Province of South Africa. Among these Mediterranean annual 'invaders' only one group is normally greeted with any enthusiasm: the annual, nitrogen-fixing legumes of high pastoral value such as *Medicago, Trifolium* and many others. In addition to various suites of

adaptations allowing survival during periods of prolonged drought, for example, these annual legumes also have remarkable capacity to 'capitalize' rapidly on short, intense periods of resource availability and thereby increase their number of offspring dramatically under such conditions.

Despite their numbers, annual Mediterranean legume species can conveniently be considered as a single "functional group" in fields or pastures, i.e., a group of species with similar responses to a given factor, and having a set of common biological (and physiological) attributes that correlate with their overall performance and fitness (Lavorel *et al.*, 1998). However, they do of course differ in many ways, including their responses to a given disturbance or stress, among genera, species and even accessions of a given species. In this short review we briefly analyse the main ecophysiological attributes of annual legumes and some of the environmental factors that affect their development, reproduction and resource allocation patterns, with special emphasis on conditions found in MTEs. We will also give some examples of inter-specific differences that need to be taken into account when introducing or disseminating annual legumes for pasture improvement, rehabilitation efforts, erosion control and/or long term soil restoration programmes.

Plant development and adaptation to seasonality and unpredictability

In the Mediterranean region, and in MTEs in general, annual legumes tend to grow and reproduce during the cool and wet seasons only. In addition to rainfall unpredictability the length of the growing is also very variable in MTEs, and annual legumes show ecotypic differentiation for flowering time in more or less close correlation to the aridity of the collection site (e.g. Piano *et al.*, 1996; Ehrman and Cocks, 1996; Del Pozo *et al.*, 1999a), since increasing aridity and unpredictability go together (Le Houérou, 1984). It has frequently been demonstrated that flowering time plasticity is a common feature of adaptive significance for annuals, including legumes, in arid or semiarid environments including MTEs (Fox, 1989, 1990; Ehrman and Cocks, 1996).

Also the occurrence of summer and early autumn rains in MTEs, which result in false breaks of season, i.e. an early germination of seeds which then die in the absence of follow-up rains, is another environmental constrain for annual plants. To cope this annual legumes show high levels of seed dormancy and mechanism that regulate the pattern of seed germination over more than one growing season. Seed survival in the seed bank is also of great importance to populations; predation by ants and other animals, fungal attack and premature germination of seeds leading to 'infant mortality' all impinge on seed bank longevity, and need to be studied carefully for individual species in a given environment (Quinlivan, 1966).

Therefore, the adaptation and long-term persistence of annual legumes in fluctuating environments of MTEs depends largely on the capacity of plants to complete their reproductive cycle, in order to ensure seed production, and on the survival of seeds in the soil over several seasons in what is commonly called a seed-bank.

Seed dormancy

Despite the fact that various mechanisms and components of seed dormancy have been described in legumes, hardseededness (seed coat impermeability) and high-temperature dormancy (*i.e.* the failure of seed to germinate at high temperature when moisture is adequate) are probably the most important ones in Mediterranean legumes. Hardseedness, or impermeability of the seed coat to water, prevents imbibition. This develops during seed maturation and is under both genetic and environmental control. Impermeability is broken by

the influence of diurnal fluctuating temperatures and other natural or artificial processes that scarify the seed coat to produce 'soft' seed (Jansen and Ison, 1995).

Newly ripened seeds of annual legumes have high levels of hardseededness, but the rate of seed softening under field conditions differs greatly among accessions and between species (Table 1). For example, seed softening occurs very rapidly in *Trifolium subterraneum* and *T. isthmocarpum*, but the opposite is true in *Ornithopus compressus* and *Biserrula pelecinus*. In annual medics (*Medicago* spp.) and *T. subterraneum*, the rate of seed softening decreases as depth of burial increases (Taylor and Ewing, 1996); in *O. compresus* and *B. pelecinus* softening occurs more rapidly at 2 cm depth than at 6 cm (Revell *et al.*, 1998; Loi *et al.*, 1999). Buried seeds of annual medics and subterranean clover can survive as hard seeds for up to 12 years without significant loss of viability, increasing in this way seed longevity and legume population persistence (Taylor and Ewing, 1996).

Table 1. Summary of studies reporting weight per seed and seed softening of annual legumes under field conditions.

Species	N° of accessions	Weight per seed (mg)	Hardseededness (%)			Source
			Initial	After 1 summer	After 2 summers	
Medicago						
Littoralis	1	2.2	98	-	33	(1)
Polymorpha	4	2.3-3.0	98-99	-	17-45	(1)
	1		98	85	50	(5)
	34	2-6.6	81-99	30-93	-	(6)
Orbicularis	1	3.9	95	-	75	(1)
Rugosa	1	7.6	96	-	0.5	(1)
Scutellata	4	15.0-17.7	95-98	-	5-30	(1)
Truncatula	8	2.9-4.5	93-99	-	20-60	(1)
Trifolium						
Angustifolium	1	n.a.	91	9	-	(3)
Argutum	1	n.a.	84	44	-	(3)
Cherleri	2	n.a.	93-96	30-47	-	(3)
Clusii	1	n.a.	98	78	-	(3)
Clypeatum	1	n.a.	87	45	-	(3)
Gladuliferum	2	n.a.	98-99	66-73	-	(3)
Lappaceum	1	n.a.	95	70	-	(3)
Isthmocarpum	1	n.a.	90	0.6	-	(3)
Nigrescens	1	n.a.	93	56	-	(3)
Obscurum	1	n.a.	73	32	-	(3)
Purpureum	2	n.a.	85-86	13-23	-	(3)
Subterraneum	1	9.8	98	-	10	(2)
Others						
Biserrula pelecinus	4	0.8-1.6	99.0	-	82-97	(2)
Ornithopus compressus	1	3.5	98.0	-	84-92	(2)
	4	1.7-3.0	96-98	-	35-50	(4)

(1): Lloyd *et al.* (1997); (2): Loi *et al.* (1999); (3): Norman *et al.* (1998); (4): Revell *et al.* (1998); (5): Avendaño *et al.* (1993); (6) Taylor (1996); n.a.: not available

High-temperature dormancy has been detected in various species of *Trifolium* (Jansen and Ison, 1995; Norman *et al.*, 1998). This is an enforced dormancy that occurs when seeds are exposed to temperatures of 30-40 °C. In this range of high temperatures, seeds imbibe water but fail to germinate, even though the same seeds germinate when subsequently placed at 15 °C (Jansen and Ison, 1994). It has been suggested that this type of seed dormancy could play a role in preventing seed from germinating in the case of false break (Jansen and Ison, 1994).

Seed germination

Once seed dormancy has been broken down and soil has enough moisture, the percentage and rate of seed germination depends largely on temperature. The relationship between seed germination and temperature has been studied for various annual legume species, including edible legumes (e.g. Covell *et al.*, 1986; Durmur *et. al.*, 1990) and forage legumes (e.g. Jansen and Ison, 1994; Norman *et al.*, 1998). A simple mathematical model has been developed to analyse the germination-temperature relationship and to determine critical temperatures for various species. In this model the rate of seed germination ($1/t$, days^{-1})- defined as the inverse of the time required to reach a certain percentage of germination -, increases linearly with temperature, from a base temperature (T_b) at which the rate is zero, up to an optimum temperature (T_o), at which this rate is maximal (García-Huidobro *et al.*, 1982; Covell *et al.*, 1986; Del Pozo *et al.*, 1987). The relationship can be described as follows:

$$1/t = a + b\,T \qquad T_b < T < T_o \qquad (1)$$

In this model $-a/b$ corresponds to the base temperature and $1/b$ is the thermal time (θ_1, °C day). However, above the optimum temperature, further increase in temperature reduces $1/t$ until a maximum temperature (T_m) is reached where the rate is again zero (García-Huidobro *et al.*, 1982; Durmur *et. al.*, 1990).

Cardinal temperatures (T_b, T_o and T_m) and thermal times for germination of various leguminous species and ecotypes have been determined by fitting linear regressions of rate of germination and sub- and above-optimal temperatures. For Mediterranean legumes, base temperatures ranged from 0 to 5 °C, optimum temperature ranged from 16 to 22 °C, whereas maximum temperature ranged from 30 to 40 °C (Covell *et al.*, 1986 for edible legumes; Norman *et al.*, 1998 for forage legumes).

Flowering time

As mentioned above, annual legumes show both ecotypic differentiation and a high degree of plasticity in flowering time. Although severe water deficits may affect the development of annual legumes, time to flowering is mainly influenced by genotype, temperature and photoperiod (Roberts *et al.*, 1997). Plants from MTEs are usually long-day plants, i.e. flowering is delayed when daylengths are shorter than a critical photoperiod (P_c).

The influence of temperature and photoperiod on flowering time has been studied in various leguminous taxa including *Medicago* spp. (Clarkson and Russell, 1975; 1979; Del Pozo *et al.*, 1999a) and *Trifolium* spp. (Evans *et al.*, 1992).

The analysis has been made using a linear model which relate the rate of progress to flowering ($1/f$) - defined as the inverse of time from emergence to flowering (f) - with mean diurnal temperature (T, °C) and mean photoperiod (P, h day^{-1}) (Summerfield *et al.*, 1991; Evans *et al.*, 1992; Del Pozo *et al.*, 1999a), according to the equation:

$$1/f = a' + b'T + c'P \qquad\qquad (2)$$

where a', b' and c' are constants specific to each accession (Summerfield *et al.*, 1991).

Studies of flowering responses to temperature and photoperiod conducted on eight cultivars of *Trifolium subterraneum* grown in Australia (Evans *et al.*, 1992), and nine accessions of *M. polymorpha* collected from a desert-mediterranean climatic gradient in Chile (Del Pozo *et al.*, 1999a), demonstrated a great variability in flowering time. In addition, in both studies the parameters b' and c' of model 2 differed among accessions, clearly indicating the existence of genotypic variation for sensitivity to both temperature and photoperiod. Detailed genetic studies are now underway to elucidate these differences and render them amenable to utilisation by breeders.

Growth and allocation

Legumes usually have higher nitrogen concentration in both vegetative and reproductive organs than grasses or other dicotyledenous plants (e.g. Del Pozo, 1992; McKey, 1994; Navas *et al.* 1995). According to McKey (1994), nitrogen-rich leaves of legumes should allow higher rates of photosynthesis, especially at high light intensities, and therefore favor rapid growth of leaves and plant production, during favourable periods.

However, several studies have shown that the high N content in vegetative organs of legumes does not lead to a higher relative growth rate (RGR) as compared with annual grasses and other families. For example, Elias and Chadwick (1979) compared the early seedling growth of 28 grasses and 12 legumes (all cultivated pasture species), and found that the relative growth rate of the legumes was slightly lower than that of the grasses (0.156 d^{-1} *vs.* 0.171 d^{-1}). Similarly, in a study comparing the growth of 27 annual species of three botanical families occurring in Mediterranean grasslands, Marañon and Grubb (1993) reported that the eight legume taxa tested showed lower relative growth rate than the 12 grasses or the seven Asteraceae studied.

In contrast, a literature review for over 20 crop species indicated that the ratio between standing dry mass and nitrogen content (*i.e.*, nitrogen use efficiency, NUE), is lower in legumes than in C$_3$ grasses, suggesting that important differences in physiological characteristics may exist between the two groups, including the nitrogen and carbon allocation patterns, growth and rates of photosynthesis under varying conditions, between legumes and grasses (Del Pozo *et al.*, 1999b).

During the early stages of growth, relative growth rate (RGR) has often been found to be proportional to mean plant organic-N concentration (PNC: Ågren, 1985; Greenwood *et al.* 1991) :

$$RGR = NP \ x \ PNC \qquad\qquad (3)$$

where NP is plant nitrogen productivity (gDW mol N $^{-1}$ d^{-1}). NP thus expresses the way internal nitrogen is used for growth. More recently Garnier and Vancaeyzeele (1994) have shown that NP can be factored into two terms:

$$NP = LNR \ x \ N_LP \qquad\qquad (4)$$

where LNR is leaf nitrogen ratio (ratio between leaf and total plant nitrogen contents) and N_LP is the leaf nitrogen productivity, i.e. ratio of growth rate to leaf nitrogen concentration (gDW mol N $^{-1}$ d^{-1}).

Although there are few direct comparisons between legumes and non-legumes for these traits, it does seems that legumes have a lower nitrogen productivity and a greater x-intercept (i.e., the minimum N concentration where RGR is equal to zero) than non-legumes such as C_3 cereal grasses (Table 2). Furthermore, differences in nitrogen productivity between the two groups of species were mainly explained by differences in leaf nitrogen productivity (Table 2). This latter trait has been shown to be related to photosynthetic nitrogen use efficiency (PNUE), i.e. the ratio between rate of photosynthesis and leaf nitrogen concentration (Garnier *et al.*, 1995). In fact, PNUE was found to be lower in legumes than in cereals (Del Pozo *et al.*, 1999b). It seems that the high nitrogen concentration in legumes may have more to do with a high nitrogen demand for seed production at a time when nitrogen fixation is shut off than with a high production potential (Del Pozo *et al.*, 1999b).

Table 2. Plant nitrogen concentration (PNC), relative growth rate (RGR), nitrogen productivity (NP) and its components in annual C_3 grasses and legume plants. LNR and N_LP are the leaf nitrogen ratio and leaf nitrogen productivity, respectively (see text for definition of parameters). Source: Del Pozo *et al.* (1999b).

Species	PNC (mmol N g^{-1})	RGR (g g^{-1} d^{-1})	NP (g mol^{-1} d^{-1})	LNR (mol mol^{-1})	N_LP (g mol^{-1} d^{-1})
Medicago minima	2.70	0.055	19.8	0.66	30
Vicia faba	3.00	0.031	10.3	0.38	27.2
Bromus madritensis	1.94	0.061	30.6	0.51	60
Triticum aestivum	2.61	0.070	26.8	0.31	85.3

Concluding remarks

In our introduction, we suggested that despite their numbers, annual Mediterranean legumes could be considered as a single "functional group". Indeed, when compared to annual C_3 grasses, or other large but coherent groups of annuals, e.g., Asteraceae, this assertion appears to hold up. More detailed studies of specific responses to specific stresses are required to test this idea further, both in monocultures and, especially, in mixed cultures. However, we have also given examples of inter-and intra-specific differences that can be useful when introducing or disseminating annual legumes for pasture improvement, rehabilitation efforts, erosion control and/or long term soil restoration programmes. For example, flowering responses to temperature and photoperiod in *Trifolium subterraneum* and *Medicago polymorpha* accessions showed great variability in flowering time, which is a variable of critical importance to pasture management in seasonal, highly unpredictable environments such as most MTEs. Similar variablity is found in winter vigour, seed dormancy components and other agronomically important traits. More research is needed on genetic components of intra- and inter-specific variability in response to environmental conditions and, of course, performance of selected ecotypes or genotypes under field conditions.

In practical terms, one promising strategy for range managers is to develop appropriate *mixtures* of species and accessions for combined use. In this way, as Piano *et al.* (1996), Del Pozo *et al.* (1999b) and others have emphasized, it should be possible to increase chances of high productivity and at least some production of seeds regardless of the rainfall and temperature patterns of the current year.

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