The effects of different maturation conditions on seed dormancy and germination of *Cenchrus ciliaris*

Farzad Sharif-Zadeh[†] and Alistair J. Murdoch[*]

Department of Agriculture, The University of Reading, Earley Gate, PO Box 236, Reading RG6 6AT, UK

Abstract

Seeds of *Cenchrus ciliaris* L. were produced under different hydro–photo–thermal environments with and without fertilizer. Dormancy loss of spikelets and extracted caryopses was tested during dry after-ripening at 40°C and 43% equilibrium relative humidity. Caryopses had higher initial germination and lost their dormancy faster than spikelets. Dormancy of both caryopses and spikelets generally decreased with an increase of maturation temperature and fertility, whereas dormancy increased if water stress was imposed during maturation. The latter effect was smaller when the mother plants were exposed to water stress after caryopses were fully formed than when water stress cycles were applied throughout maturation. Daylength extension (to 14 or 18 h d^{-1}) by artificial light increased dormancy of both caryopses and spikelets. The effect of long days declined when plants were exposed to natural daylight for more than 10 h d^{-1}. The after-ripening curves were consistent with the hypothesis that dormancy periods of individual seeds are normally distributed within each seed lot. Rates of loss of dormancy were quantified by the slopes of these curves. In a given experiment, these rates were identical for caryopses but not always for spikelets that matured in diverse environments. Even for caryopses, however, the slopes varied between experiments. Therefore, the results do not support the hypothesis that a dormancy model can be applied universally to all seed lots of *Cenchrus ciliaris*. Methods of predicting the period of after-ripening required to achieve desired levels of dormancy for reseeding degraded rangelands are discussed.

*Correspondence
Fax: +44 (0)118 931 8297
Email: a.j.murdoch@reading.ac.uk
[†] Present address: Department of Agronomy and Plant Breeding, College of Agriculture, The University of Tehran, Karaj, Iran.

Abbreviation: d.f., degrees of freedom. Note: degrees of freedom for F ratios are shown as a subscript in square brackets.

Keywords: after-ripening, *Cenchrus ciliaris*, rangeland regeneration, seed dormancy, seed germination, seed maturation, water stress

Introduction

Temperature, photoperiod, and water and nutrient availability during seed development affect subsequent seed dormancy and germination. A low maturation temperature generally increases the dormancy of grass seeds including *Aegilops kotschyii* (Wurzburger and Koller, 1976), *Festuca arundinacea* (Boyce, 1973), *Hordeum vulgare* (Rauber, 1984; Buraas and Skinnes, 1985), *Lolium* spp. (Wiesner and Grabe, 1972) and *Setaria* spp. (Mohamed *et al.*, 1985). High maturation temperatures are often associated with water stress, which has shown contrasting effects on seed dormancy. Seed dormancy of *Avena fatua* and *Sorghum halepense* decreased if water stress occurred during seed development (Peters, 1982; Sawhney and Naylor, 1982; Benech Arnold *et al.*, 1991). By contrast, Aspinall (1969) found that drought during barley seed development could increase seed dormancy. Conversely, high levels of nitrate are correlated with lower dormancy in various species (Roberts and Smith, 1977; Ellis *et al.*, 1985a, b). Increasing nitrogen application to the mother plant enhanced seed germination of *Festuca arundinacea* (Watson and Watson, 1982) and, by implication, reduced seed dormancy. The effect of photoperiod during maturation may be important in day-neutral plants like *Cenchrus ciliaris* because seed dormancy could vary with flowering time. In general, long days increase seed dormancy (Karssen, 1970; Gutterman, 1973; Wurzburger and Koller, 1976; Fenner, 1991) but, unusually, the opposite effect occurred in *Avena* (Somody *et al.*, 1984).

This paper describes the effects of different temperature, watering-nutrient and photoperiodic regimes during seed development on seed dormancy of *Cenchrus ciliaris*. Dormancy was evaluated both by the germination of the seeds after harvest and by probit analysis of the subsequent loss of dormancy during after-ripening. Rates of after-ripening within

https://doi.org/10.1017/S0960258500000490 Published online by Cambridge University Press

the seed population (not in individual seeds) were then estimated by the slopes of the after-ripening curves. The hypothesis tested is that the rates of after-ripening in specified storage conditions are the same for seeds produced in different maturation environments. If so, the dormancy of each seed lot could be quantified by a seed lot 'non-dormancy' constant (K_d; Favier and Woods, 1993), which is analogous to the seed lot constant (K_i) of the viability equation (Ellis and Roberts, 1980). This constant estimates the fraction of non-dormant seeds in the seed lot prior to after-ripening. The germination of any seed lot after storage in known conditions could then be predicted as a function of its germination on receipt and the after-ripening period (Favier and Woods, 1993).

Seed dormancy was studied in *Cenchrus ciliaris* to help in developing a strategy for reseeding degraded rangelands of arid and semi-arid environments. Hay quality and drought resistance have made it one of the best perennial forage grasses in such environments (Hacker and Ratcliff, 1989). Winkworth (1971) found that non-dormant *Cenchrus ciliaris* seeds disappeared rapidly from the soil seed bank. It is speculated that, by sowing seeds (i.e. spikelets) with appropriate levels of dormancy, it may be possible to achieve both satisfactory regeneration and some persistence of seeds in the soil seed bank. This work was carried out to identify ways of producing seeds with specified levels of dormancy.

Materials and methods

Seeds of *Cenchrus ciliaris* were collected from southwest Iran in 1990 and were kept at 10°C in the seed store of the Research Centre of Natural Resources, Khuzistan, Iran. On receipt in Reading in 1995, the seeds were sealed in laminated aluminium foil packets and stored at –20°C and approx. 12% moisture content (fresh weight basis) until required. Germination percentages of spikelets and extracted caryopses were 0% and 82%, respectively. Seedlings were established by sowing at least four caryopses on the surface of 15-cm-diameter plastic pots. The pots contained a mixture by volume of four parts Vermiculite (Grade size DM), four parts gravel (6 mm, crushed), two parts sharp sand (coarse and washed) and one part Levington compost M2.

Seeds were produced in various controlled environments. In each case, the progress of flowering was monitored in the central portion of each inflorescence in the upper parts of stems. Flowers produced over a period of 2–3 days were labelled and used in subsequent investigations. When the glumes of >75% of the spikelets in each head had changed from green to brown, they were harvested. In addition, because the developmental stage of the top and bottom of each inflorescence was different and could influence dormancy, these parts were discarded and only seeds from the central 50% were used in germination tests.

Harvested seeds were dried in a cabinet at approx. 15% relative humidity and 15–20°C to reduce seed moisture to about 43% equilibrium relative humidity (e.r.h., measured at 20°C). After separating empty seeds visually, the seeds were sealed in laminated aluminium foil packets and stored until required at –20°C to prevent significant after-ripening (cf. Sharif-Zadeh, 1999).

Loss of dormancy during after-ripening was assessed in all seed lots. Before after-ripening, the spikelets of all seed lots from a given experiment were adjusted to a uniform equilibrium relative humidity by sealing in a laminated aluminium foil packet and storing for 3 days at 3°C. After equilibration at 43 ± 2% e.r.h., spikelets were subdivided into batches and repackaged in laminated aluminium foil packets and stored at 40°C. Sample packets were removed after various storage periods. Germination tests were carried out on spikelets and extracted caryopses.

At least two replicates of 25 caryopses/spikelets were used in germination tests, the number varying according to the amount of seed available from each maturation condition. Tests were carried out in sterile 9 cm polystyrene Petri dishes which were lined with two circles of Whatman 181 paper and moistened with 4.5 ml deionised water. The tests lasted at least 30 days at 25°C in darkness imposed by wrapping dishes with one layer of aluminium foil. The germination criterion was ≥3 mm radicle emergence.

Loss of dormancy was quantified using probit analysis. Fitted lines (Figs 3–5) show the after-ripening periods included in these analyses. Rates of after-ripening in the seed population were estimated by the slopes of the probit lines. These lines reflect seed-to-seed variation in dormancy in the seed population, and the standard deviation of the dormancy periods of individual seeds (σ) was calculated by the reciprocals of the slopes (Murdoch and Ellis, 2000). Parallel line models were fitted to test the hypothesis that rates of after-ripening were the same for seeds from different maturation environments. The mean dormancy period was taken as the time to achieve 50% germination, calculated from the regression coefficients of the after-ripening curves in each maturation environment.

Experiments concerned the effects of maturation conditions on seed dormancy. The first examined temperature, water stress and nutrient treatments; the second, water stress in more detail and the third, the effects of photoperiod. Expts 1 and 3 were carried out at the Plant Environment Laboratory and Expt 2 at the Seed Science Laboratory, University of Reading.

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Experiment 1 – effects of temperature, water stress and nutrients

From sowing (21 December 1995) to flowering (31 May 1996), all plants were grown in a glasshouse at 25°C. Where necessary, the natural photoperiod was extended to 16 h d^{-1} with 150 W tungsten bulbs. Plants were automatically irrigated with a balanced nutrient solution (Summerfield *et al.*, 1974) containing 100 ppm nitrogen (Volumatic Drip System; Volumatic Systems, Dunstable, UK). Sufficient nutrient solution was used so that drainage was observed from the bottom of the pots.

To ensure pollination occurred in the same environment, the plants were transferred to maturation glasshouses 5 d after anthesis. Maturation temperatures (Fig. 1) comprised 32°/27°C and 27°/20°C (13h/11h day/night) and were generally controlled within ± 1.5°C. Watering regimes were (1) water stress, (2) well-watered without nutrients and (3) well-watered with the nutrient solution used during vegetative growth.

In well-watered regimes, plants were irrigated three times daily. The water stress treatment consisted of successive cycles in which water was withheld until the first signs of wilting were observed, after which the pot was returned to field capacity by watering without nutrients. Soil moisture content (volume basis) was measured at the end of each cycle before rewatering using a ThetaProbe Soil Moisture Sensor type ML1 (Delta-T Devices Ltd., Cambridge, UK). The soil moisture contents at the end of each water stress cycle during seed maturation are shown in Table 1. These cycles continued until harvest. Maturation periods for each environment are presented in Table 2. The natural daylength during seed development was 16–18 h d^{-1} (Fig. 2). The experimental plants in each glasshouse were surrounded by a protective row of 'guard' plants.

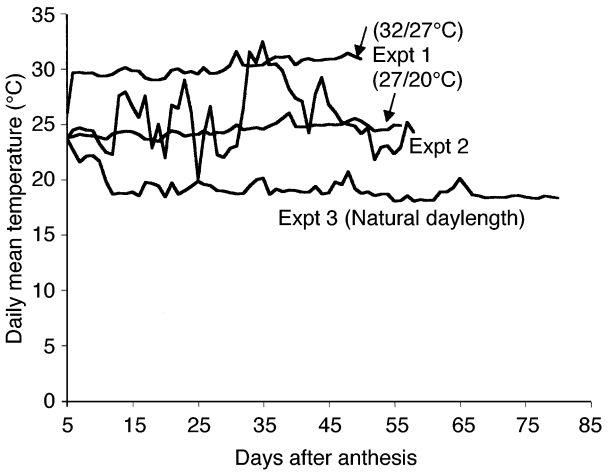

Figure 1. Mean daily temperatures (°C) during seed development in the three maturation environment experiments.

Experiment 2 – effects of moisture stress at different times

Seeds were sown in May 1997 into compost mixed with a controlled release fertilizer (Osmocote Plus, Scotts UK Ltd.). During vegetative growth, the natural photoperiod was 17–18 h d^{-1}, and the minimum daily temperature in the glasshouse was 20°C. The plants were watered daily by hand up to anthesis on 6 July 1997 before subjecting them to the following water stress treatments:

1. moisture stress cycles beginning 5 days after anthesis and continuing to harvest;
2. moisture stress cycles commencing after full formation of caryopses (of middle part of the inflorescence) but before they changed colour from white to brown and continuing until harvest;

Table 1. Soil moisture content (θ_v, m^3/m^3) at the end of each water stress cycle at two different maturation temperatures in Expt 1 (effects of temperature, moisture and nutrients)

Maturation temperature (13 h/11 h)	Date of irrigation (1996)	Days after anthesis	Length of cycle (d)	Soil moisture at the end of each cycle (θ_v, m^3/m^3)
32°/27°C	8 May	8	3	0.05
	12 May	12	4	0.04
	15 May	15	3	0.04
27°/20°C	11 May	11	6	0.05
	15 May	15	4	0.03
	21 May	21	6	0.04

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3. terminal drought: plants were not watered after full formation of caryopses (before changing colour);
4. control: plants were well watered until harvest.

The periods from anthesis to harvest were 18, 31, 27 and 45 d for treatments 1–4, respectively. Moisture stress cycles were applied as in Expt 1 (Table 3). Temperature and daylengths during maturation are shown in Figs 1 and 2. Six pots were harvested for each treatment from each of four blocks.

Experiment 3 – effect of photoperiod

From sowing to flowering, the plants were grown in a glasshouse at 27°/20°C (13 h/11 h day/night) with the natural photoperiod declining from 17.5 to 16 h d^{-1}. Plants were automatically irrigated as in Expt 1, twice daily before and four times daily during seed maturation.

Photoperiod treatments during seed development were 10, 14 and 18 h d^{-1} and a control. The control was kept in the main glasshouse compartment, where the natural photoperiod declined from 15.8 to 10.6 h d^{-1} (Fig. 2). The glasshouse contained three night compartments, which provided daylength extension for 0, 4 or 8 h with 60 W tungsten bulbs. Trolleys containing the plants were moved out of the night compartments at 08:00 h and returned at 18:00 h each day so that all plants were exposed to natural light for 10 h d^{-1}. The minimum daytime temperature during maturation was 18°C, while the night temperature was 18°C for all compartments. Mean daily temperatures in the control are illustrated (Fig. 1), the temperatures for the other photoperiods being similar.

Results

The results were consistent with the hypothesis that loss of dormancy during after-ripening is normally distributed with binomial errors as a function of storage period. χ^2 values ($P > 0.05$) were 29.9 (33 d.f.), 20.7 (12 d.f.) and 20.0 (16 d.f.) for caryopses in Expts 1, 2 and 3, respectively. Corresponding values for the spikelets were 38.3 (34 d.f.), 39.0 (32 d.f.) and 32.2 (28 d.f.). This deduction must be treated with caution as the small amounts of seeds produced in some maturation environments meant that only two points

Table 2. Periods between anthesis and harvest for maturation environments in Expt 1

	Period from anthesis to harvest (d) at temperatures of:	
Watering regime	32°/27°C	27°/20°C
Water stress cycles	17	21
Water	34	43
Nutrient	49	63

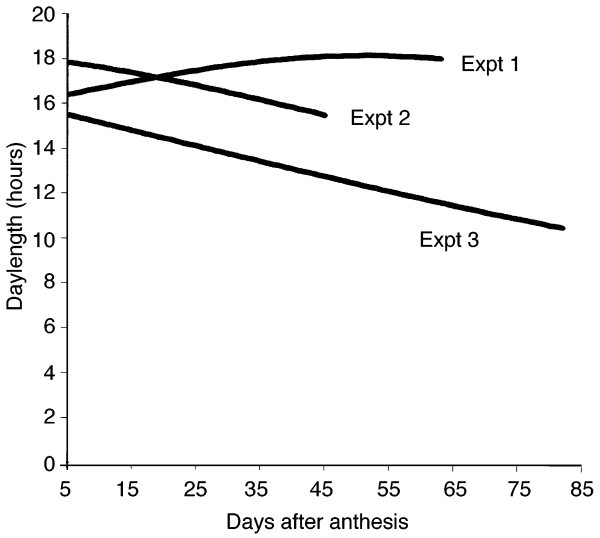

Figure 2. Daylengths during seed development in Experiments 1–3. In the case of Expt 3, the natural photoperiod regime is shown.

Table 3. Soil moisture content (θ_v, m^3/m^3) at the end of each cycle for the two cycling water stress treatments in Expt 2 (effects of moisture stress at different times)

Stage of application of water stress cycles	Date of irrigation (1997)	Days after anthesis	Length of cycle (d)	Soil moisture at the end of each cycle (θ_v, m^3/m^3)
Throughout seed maturation	14 July	8	3	0.08
	21 July	15	7	0.05
After full formation of caryopses	27 July	21	5	0.07
	31 July	25	4	0.06

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were available for analysis in some treatments (e.g. in Expt 2). In principle, however, these normal distributions imply that straight lines may be fitted by probit analysis to the germination data as a function of after-ripening period.

Germination after harvest was higher, mean dormancy periods were shorter and rates of after-ripening were greater for caryopses than for spikelets (Figs 3–5).

In Expt 1, caryopses and spikelets that matured under water stress at 27°/20°C were the most dormant at harvest (Fig. 3). The least dormant were those produced with nutrient solution at 32°/27°C. The initial germination rates of seeds from these two environments were 11% and 82% for caryopses and 0% and 13% for spikelets, respectively (0 d treatments in Fig. 3). Watering with nutrients rather than water only during maturation generally decreased dormancy (Figs 3a and b).

Increasing the maturation temperature from

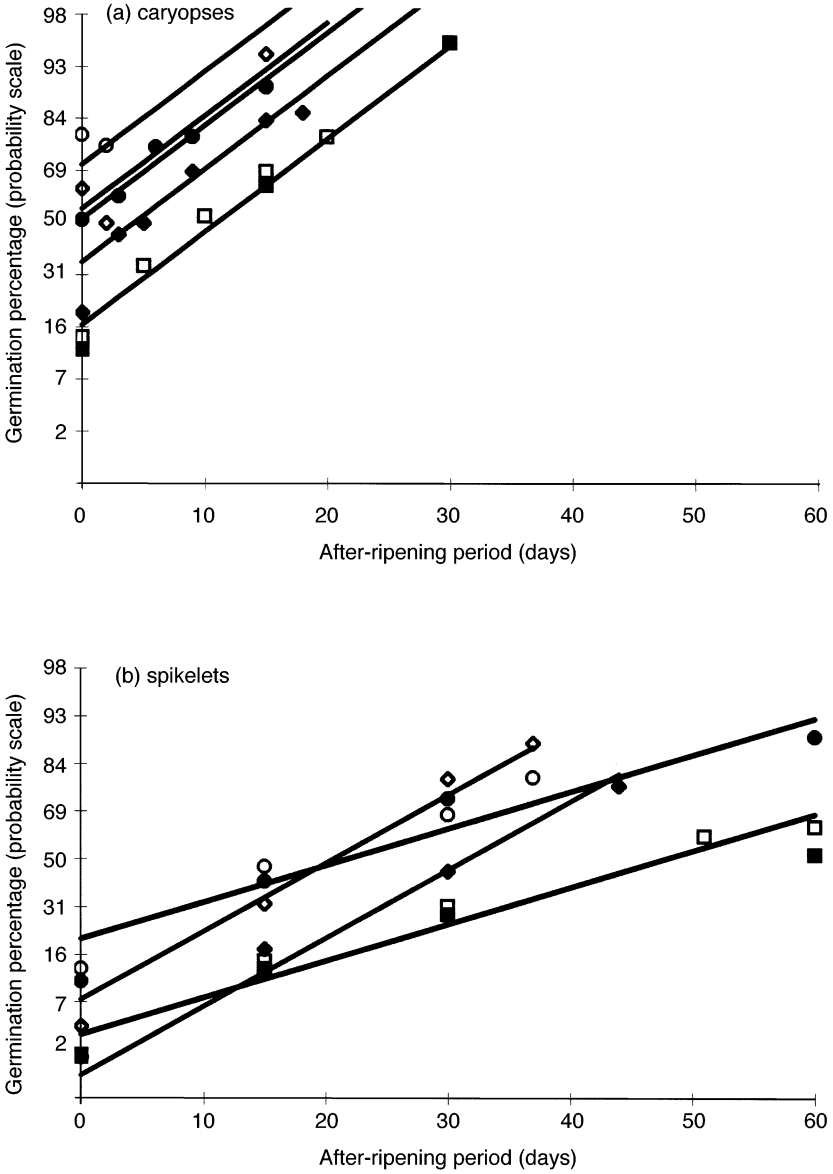

Figure 3. After-ripening of (a) caryopses and (b) spikelets of *Cenchrus ciliaris* matured at temperatures of 32°/27°C (open symbols) and 27°/20°C (closed symbols) and with water stress cycles (□,■), well-watered without nutrients (◇,◆) and well-watered with nutrients (○,●) in Expt 1 (effects of temperature, moisture and nutrients). The seeds were after-ripened as spikelets at 43% r.h., at 40°C. Parameter estimates of lines fitted by probit analysis are given in Table 4.

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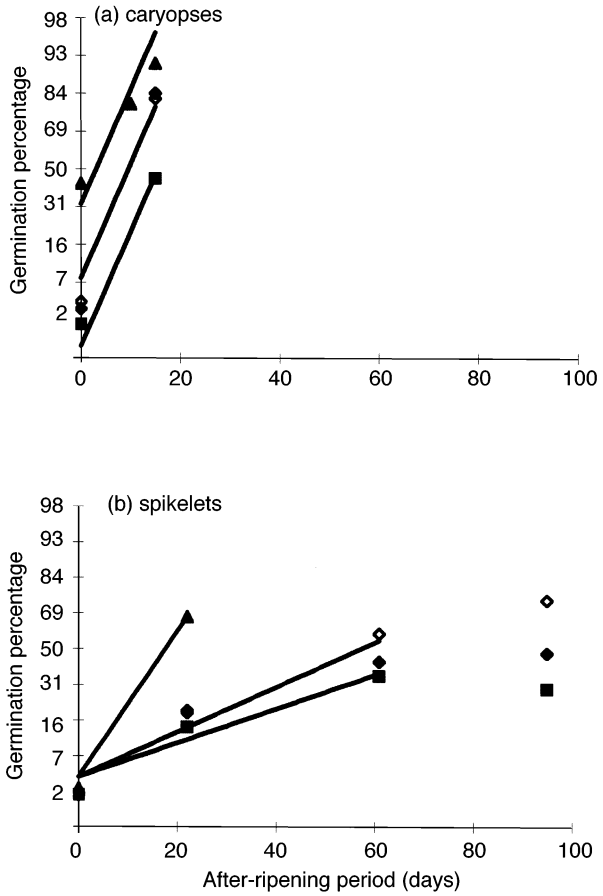

Figure 4. After-ripening of (a) caryopses and (b) spikelets of *Cenchrus ciliaris* matured in different watering regimes (Expt 2) including water stress cycles during the whole (■) and final (♦) period of seed development, terminal drought (◇) and control (watered daily) (▲). Seeds were after-ripened as spikelets at 41% r.h. at 40°C. Parameter estimates of lines fitted by probit analysis are given in Table 4.

27°/20°C to 32°/27°C decreased caryopsis dormancy except in water stress treatments (Fig. 3a). The effect of maturation temperature was also insignificant for spikelets in both water stressed and fertilized plants (Figs 3a and b). Where the effect of maturation temperature was not significant, the seeds had the same initial dormancy level and the same after-ripening rate. (Fitting a common line to the two maturation temperatures did not increase the residual significantly ($F = 1.71_{[6, 33]}$ and $F = 1.208_{[6, 34]}$, $P < 0.05$, for caryopses and spikelets, respectively).

For caryopses, the rate of loss of dormancy was the same for seeds produced in all maturation conditions (a parallel line model was accepted: $F=1.868_{[5, 33]}$, $P > 0.05$). By contrast, after-ripening was much faster in spikelets that matured without added nutrients (Table 4 and Fig. 3b), whereas the rate of loss of dormancy was the same for other maturation environments. This interaction was the same at the two maturation temperatures (Fig. 3b).

Spikelets produced under water stress, therefore, showed greater initial dormancy and relatively slower loss of dormancy during after-ripening. The second experiment was carried out to elucidate whether this unexpected effect of water stress varied with the time when water stress was imposed and in particular whether a similar effect occurred when seeds matured under terminal drought.

In Expt 2, caryopses and spikelets which matured under drought stress cycles from 5 d after anthesis were the most dormant (Fig. 4; Table 4). None of the caryopses matured in this regime germinated at zero time compared with an initial germination of 42% for the well-watered control. Initial spikelet germination results were zero for all water stress treatments and 1% for the control. After 22 days of dry after-ripening, spikelet germination for the different water stress treatments ranged from 14 to 19%, compared with 67% for the control (Fig. 4b).

The rates of loss of dormancy in caryopses did not differ significantly between maturation regimes (Fig. 4a: a parallel line model did not significantly increase the residual ($F = 1.64_{[3, 12]}$, $P > 0.05$). Terminal and intermittent drought after full formation of caryopses had similar effects on caryopsis dormancy (a common after-ripening line could be fitted to these two treatments; Fig. 5a).

For spikelets, however, the effects of maturation environment only became evident during after-ripening (Fig. 4b). A parallel line model was rejected ($F = 11.6_{[3, 32]}$, $P < 0.001$), whereas a common intercept model did not differ significantly from the separate line model ($F = 0.16_{[3, 32]}$, $P > 0.05$). Spikelets that developed under moisture stress cycles throughout maturation after-ripened more slowly than those with such cycles only at the final stages of seed maturation. The faster rates of loss of dormancy in the latter and in the terminal drought treatments did not, however, differ significantly ($F = 2.68_{[4, 32]}$, $P > 0.05$; Table 4).

In the photoperiod experiment, germination of caryopses and spikelets that matured under the shortest photoperiod (10 h d^{-1}) was higher than of those that matured under photoperiods of 14 and 18 h d^{-1} (Fig. 5). This higher germination of seeds from the 10 h d^{-1} photoperiod continued throughout after-ripening. Caryopses, which matured under the natural photoperiod, were the least dormant (33% germinated; Fig. 5a, see also intercept estimates in Table 4). Spikelets produced under the natural photoperiod likewise had the highest initial germination (Fig. 5b, Table 4).

As in Expts 1 and 2, there were no significant differences in rates of loss of dormancy of caryopses that matured in different environments (Fig. 5a; a

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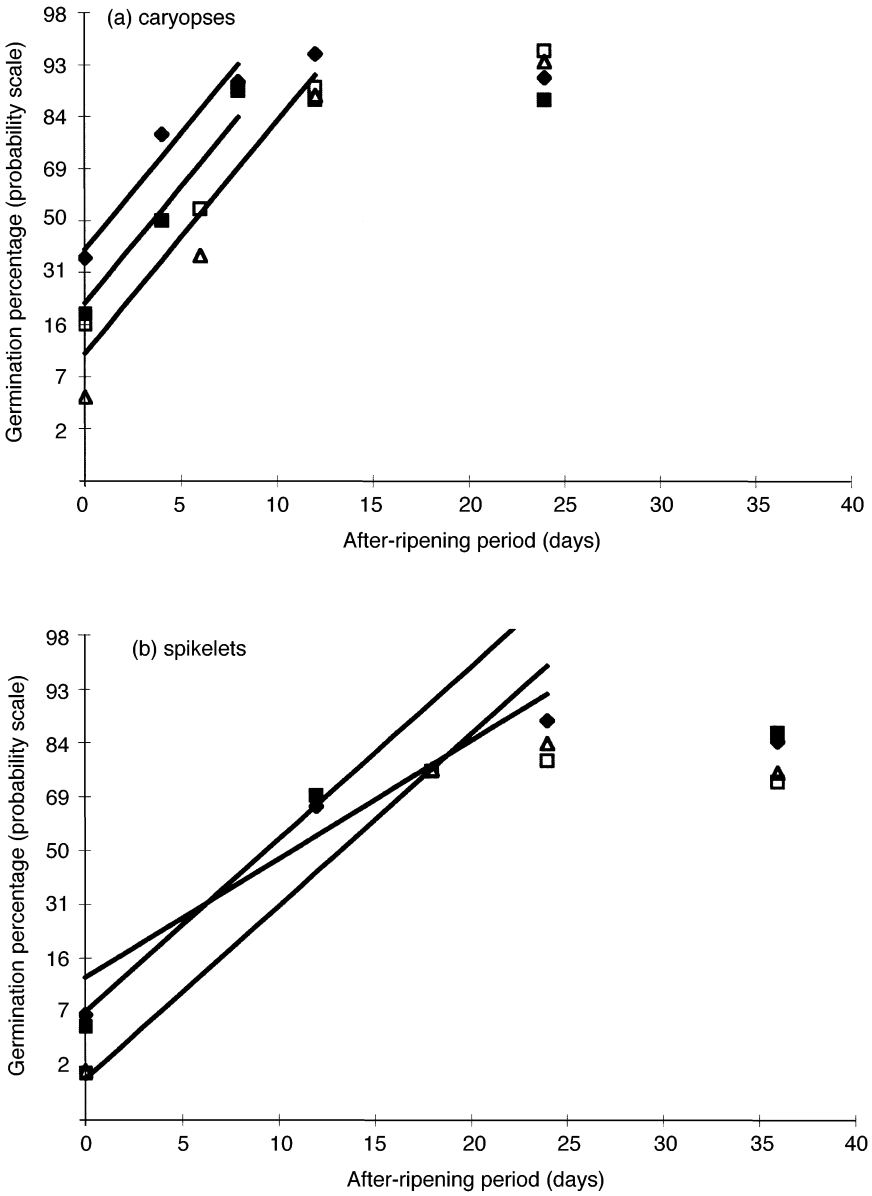

Figure 5. After-ripening of (a) caryopses and (b) spikelets of *Cenchrus ciliaris* matured in various daylengths of 10 (■), 14 (△) and 18 (□) h as well as natural photoperiod (♦) in Expt 3. Seeds were after-ripened as spikelets at 41% r.h. at 40°C. Parameter estimates of lines fitted by probit analysis are given in Table 4.

parallel line model was accepted, $F = 0.72_{[3,\ 7]}$, $P > 0.05$). The rates of after-ripening for spikelets that matured under photoperiods of 10, 14 and 18 h d^{-1} were also the same, and a common line could be fitted to the 14 and 18 h d^{-1} photoperiods (Fig. 5b, $F=0.08_{[3,\ 7]}$, $P > 0.05$, see also Table 4). Extending the photoperiod beyond 14 h d^{-1} did not, therefore, significantly increase spikelet dormancy. Spikelets produced under the natural photoperiod after-ripened more slowly, although the amount of data available was limited (Fig. 5b, Table 4).

Discussion

In all the maturation environments examined, the spikelets gave much lower initial germination than caryopses (Figs 3–5), implying an inhibitory effect of

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Table 4. Parameter estimates of regressions of germination (in probits) of caryopses and spikelets as a function of after-ripening period (d). Seeds developed in various maturation environments and fitted lines are shown in Figs 3, 4 and 5 for Expts 1, 2 and 3, respectively. Common parameter estimates are based on non-significant differences in the residual deviance from a separate line model ($P < 0.05$)

		Intercepts (SE)		Slopes (SE)	
Maturation environment		Caryopses	Spikelets	Caryopses	Spikelets
Expt 1 (temperature, moisture and nutrients)					
Water stress cycles	32/27°C	−0.975 (0.103)	−1.838 (0.133)	0.089 (0.007)	0.039 (0.003)
	27/20°C				
Nutrients (well-watered)	32/27°C	0.562 (0.132)	−0.837 (0.094)		
	27/20°C	0.043 (0.097)			
Well-watered	32/27°C	0.136 (0.160)	−1.470 (0.216)		0.071 (0.007)
(no nutrients)	27/20°C	−0.373 (0.095)	−2.257 (0.239)		
Expt 2 (water stress at different times)					
Water stress cycles throughout maturation		−2.344 (0.248)	−1.796 (0.096)	0.151 (0.012)	0.024 (0.003)
Water stress cycles *and* terminal drought after caryopses fully formed		−1.447 (0.164)			0.031 (0.002)
Well-watered control		−0.464 (0.155)			0.102 (0.009)
Expt 3 (photoperiods)					
Natural photoperiod		−0.278 (0.114)	−1.180 (0.160)	0.223 (0.017)	0.110 (0.011)
10 h d^{-1}		−0.791 (0.145)	−1.493 (0.142)		0.160 (0.010)
14 and 18 h d^{-1}		−1.274 (0.137)	−2.114 (0.179)		

the glumes and pales that surround the caryopsis. Akamine (1944) likewise found that dormancy of *Cenchrus ciliaris* was primarily caused by the spikelet, and enclosing the caryopses within the glumes greatly inhibited germination (Ernst *et al.*, 1991).

As in other species (see Introduction), dormancy of *Cenchrus ciliaris* decreased with increasing maturation temperature, although this effect of temperature was not significant for seeds produced under water stress (Fig. 3). The effects of nutrients in decreasing dormancy are also compatible with earlier work (e.g. Watson and Watson, 1982), although the more rapid after-ripening of spikelets that matured on well-watered plants without nutrients seems inconsistent (Fig. 3b). A possible explanation is that these well-watered plants were deficient in the nutrients required for synthesis of phenolic seed germination inhibitors known to be present in the spikelets of *Cenchrus ciliaris* (Parihar and Patil, 1984; Sharif-Zadeh, 1999).

The increase in dormancy associated with water stress was evident in both caryopses and spikelets of *Cenchrus ciliaris* (Table 4). This greater dormancy contrasts with the lower dormancy reported for *Avena fatua* (Peters, 1982) and *Sorghum halepense* (Benech Arnold *et al.*, 1992) seeds that matured under water stress. Since *Cenchrus ciliaris* is highly resistant to drought, the water stress cycles, which lasted up to the first sign of wilting, may have been more severe than those tested by Peters (1982) and Benech Arnold *et al.* (1992). The effect of water deficit on seed dormancy varied with stage of seed maturation. Imposing water stress cycles throughout seed development induced more dormancy than drought during the final stages of seed maturation (Fig. 4). Aspinall (1965) likewise found that water stress increased dormancy of *Hordeum vulgare* when it occurred close to anthesis. The greater dormancy of *Cenchrus ciliaris* seeds from water-stressed plants is in part due to the glumes and could be an adaptive characteristic of plants such as *Cenchrus ciliaris* from arid areas. The glumes may be less permeable to water and oxygen, and thus they may not only protect seeds in times of drought but also impose dormancy, which is itself an important survival mechanism (Murdoch and Ellis, 2000).

With the respect to photoperiod, caryopses and spikelets that matured under 14 or 18 h d^{-1} photoperiods were more dormant than those produced under short days (10 h d^{-1}) (Fig. 5). Dormancy may be induced by long days at least when tungsten bulbs are used for daylength extension. Less dormancy, however, was found when seeds were exposed to natural photoperiods of

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15.8–10.6 h d^{-1}. Taking the results of all three experiments together suggests that dormancy may also be greater when seeds mature under long natural photoperiods. Seeds produced without water or nutrient deficiency (Expt 1) during May and June 1996 were exposed to photoperiods that increased from 16 to 18 h d^{-1} during maturation (Fig. 2). These seeds were more dormant than those produced under natural daylength in Expt 3. This last lot also was less dormant than those produced by control plants in Expt 2 which matured under photoperiods that decreased from 18 to 15.5 h d^{-1} (Fig. 2). Therefore, higher dormancy is correlated with longer photoperiods as reported for most other species (Fenner, 1991). This inference was confirmed by correlating the coefficients of the after-ripening regression lines for the three experiments with temperature and photoperiod during seed development (Table 5). These correlations were limited to environments in which no environmental stresses were imposed and showed a high correlation (r^2=0.93) between the mean dormancy period of the spikelets and daylength (Table 5). Caryopsis dormancy was also correlated with mean daily temperature during seed development (Fig. 1, Table 5). The highest correlations obtained were between the rate of dormancy loss (either the slope or σ) and both daylength during final 1/3 of maturation period (0.99) and mean daily temperature (–0.95 and 0.92 for slope and σ, respectively) during seed maturation. Correlations of spikelet dormancy period with both photoperiod and mean temperature during maturation were positive, while the correlations with dormancy period were not significant in the case of caryopses (Table 5).

The effect of natural light on spikelet dormancy differed from that on caryopses, in that spikelets produced under natural light may have after-ripened slower than those in other photoperiods (compare the slopes in Fig. 5b). Karssen (1970) also found the dormancy period of *Chenopodium album* seeds was longer in seeds that matured under natural long days than in short days with a night break. In *Chenopodium album*, long days during seed development may increase dormancy through a greater impermeability of the seed to water or through a reduction in gas exchange between the embryo and the environment around the seeds (Karssen, 1970). Seeds of both *Ononis sicula* (Evenari et al., 1966; Gutterman and Heydecker, 1973) and *Trigonela arabica* (Gutterman, 1978) had seed coats that were relatively permeable to water in short days, and their seeds germinated immediately after imbibition. In contrast, their seed coats were impermeable to water when matured under long days such that seeds did not imbibe immediately and germinate.

In *Cenchrus ciliaris*, it is possible that an inhibitory morphological characteristic, e.g. the thickness of the seed covers, increases with the amount of light received and with photosynthetic activity. Alternatively, amounts or types of phenolic inhibitors may vary with total irradiance.

Table 5. Correlation matrix of parameters of regression lines for after-ripening of spikelets and caryopses with photoperiod and mean temperature during seed maturation. The analysis was limited to environments in the three experiments in which plants matured under natural daylength and no nutrient or water stress were imposed. D_{50} is the mean dormancy period and σ is the standard deviation of dormancy periods in the seed lot

Parameter	Mean photoperiod throughout maturation	Mean photoperiod for final 1/3 of maturation	Mean temperature during maturation
Spikelets			
Intercepts	0.26 n.s.	0.33 n.s.	0.14 n.s.
Slopes	−0.89 *	−0.90 *	−0.71 n.s.
σ	0.76 n.s.	0.84 n.s.	0.60 n.s.
D_{50}	0.93 *	0.97 **	0.78 n.s.
Caryopses			
Intercepts	0.93 *	0.85 n.s.	0.69 n.s.
Slopes	−0.98 **	−0.99 **	−0.95 *
σ	0.95 *	0.99 ***	0.92 *
D_{50}	−0.69 n.s.	−0.49 n.s.	−0.30 n.s.

n.s., not significant ($P > 0.05$), * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

https://doi.org/10.1017/S0960258500000490 Published online by Cambridge University Press

Practical implications

In arid areas where rainfall patterns are unpredictable, seeds with different levels of dormancy enhance the chance of regeneration. For example, Winkworth (1971) compared the longevities of *Cenchrus ciliaris* seed lots that varied in dormancy at the time of sowing. Non-dormant seeds (94% germination) disappeared rapidly from the soil seed bank. Dormant seeds (<1% germinable at sowing) lost dormancy for the first 9 months in the soil, after which mortality rates were greater. Dormant seeds thus persisted in the soil and hence probably increased the likelihood of successful regeneration. Therefore, where reseeding is to be practised, the dormancy of seed lots may need to be manipulated to increase the opportunities for successful regeneration. Farmers could exploit the effects of maturation conditions to produce seeds with higher or lower dormancy. In a day-neutral plant like *Cenchrus ciliaris*, variable dormancy levels might be achieved by allowing the plants to flower in appropriate growing conditions.

The normal distributions of dormancy periods in each seed lot (Figs 3–5) suggested that it may be possible to predict the period of after-ripening required to decrease dormancy of *Cenchrus ciliaris* seeds produced in different environments to any desired level. Nevertheless, the initial germination of the spikelets at harvest was an unacceptable parameter to characterize the seed lot for three reasons:

1. the initial germination of the freshly collected spikelets was too low (0–13% in the three experiments, Figs 3b, 4b and 5b) to facilitate comparisons even if very large numbers of seeds were to be tested;
2. the estimated values of the initial germination (i.e. the intercepts of the fitted lines) gave a relatively poor fit to the initial germination of some seed lots (compare Figs 3–5);
3. the rates of loss of dormancy of spikelets varied with maturation condition.

These problems do not apply to the same extent for caryopses. The initial germination of caryopses varied widely between seed lots and thus could perhaps be used as a seed lot constant (Figs 3a, 4a and 5a). The rates of loss of dormancy of caryopses were also the same for all maturation conditions in a given experiment. Unexpectedly, however, these rates varied greatly between experiments (Table 4), an observation that merits further study.

In any event, the use of caryopses would be inappropriate because spikelets would be used for reseeding. To characterize the seed lots using spikelets, it is necessary to estimate the slope and intercept of the after-ripening curve for each seed lot. Using a probit model and assuming seeds are stored at constant temperature and moisture content, a minimum of three germination tests is required to define the after-ripening curve of a seed lot. Examination of Figs 3 and 4 suggests that after-ripening for up to 28 days at 40°C, 43% e.r.h. could be sufficient to characterize a seed lot.

Acknowledgements

The authors extend their thanks to the Ministry of Culture and Higher Education in Iran for a scholarship awarded to FS.

References

Akamine, E.K. (1944) Germination of Hawaiian range grasses. *Hawaii Agricultural Experiment Station Technical Bulletin* No. 2.

Aspinall, D.J. (1965) Effects of the soil moisture stress on the growth of barley. III. Germination of grain from plants subjected to water stress. *Journal of the Institute of Brewing* **72**, 174–176.

Benech Arnold, R.L., Fenner, M. and Edwards, P.J. (1991) Changes in germinability, ABA content and ABA embryonic sensitivity in developing seeds of *Sorghum bicolor* (L.) Moench. induced by water stress during grain filling. *New Phytologist* **118**, 339–347.

Benech Arnold, R.L., Fenner, M. and Edwards, P.J. (1992) Changes in dormancy level in *Sorghum halepense* seeds induced by water stress during seed development. *Functional Ecology* **6**, 596–605.

Boyce, K.G. (1973) Seed dormancy in tall fescue (*Festuca arundinacea* Schreb.). Acquisition, effect on metabolic process and relief by temperature and growth regulators. *Dissertation Abstracts International. Section B. Science and Engineering* **33**, 5615–5616.

Buraas, T. and Skinnes, H. (1985) Development of seed dormancy in barley, wheat and *Triticale* under controlled conditions. *Acta Agriculturae Scandinavica* **35**, 233–244.

Ellis, R.H. and Roberts, E.H. (1980) The influence of temperature and moisture on seed viability period in barley (*Hordeum distichum* L.). *Annals of Botany* **45**, 31–37.

Ellis, R.H., Hong, T.D. and Roberts, E.H. (1985a) *Handbooks for genebanks.* No. 2. *Handbook of seed technology for genebanks*. Vol. 1. *Principles and methodology*. Rome, International Board for Plant Genetic Resources.

Ellis, R.H., Hong, T.D. and Roberts, E.H. (1985b) *Handbooks for genebanks*. No. 3. *Handbook of seed technology for genebanks*. Vol. 2. *Compendium of specific germination information and test recommendations*. Rome, International Board for Plant Genetic Resources.

Ernst, W.H.O., Kuiters, A.T. and Tolsma, D.J. (1991) Dormancy of annual and perennial grasses from a savanna of southeastern Botswana. *Acta Oecologica* **12**, 727–739.

Evenari, M., Koller, D. and Gutterman, Y. (1966) Effects of the environment of the mother plant on germination by

control of seed coat impermeability to water in *Ononis sicula* Guss. *Australian Journal of Biological Science* **19,** 1007–1016.

Favier, J.F. and Woods, J.L. (1993) The quantification of dormancy loss in barley (*Hordeum vulgare* L.). *Seed Science and Technology* **21**, 653–674.

Fenner, M. (1991) The effects of the parent environment on seed germinability. *Seed Science Research* **1**, 75–84.

Gutterman, Y. (1973) Differences in progeny due to daylength and hormone treatment of the mother plant. pp. 59–80 *in* Heydecker, W. (Ed.) *Seed ecology.* London, Butterworths.

Gutterman, Y. (1978) Seed coat permeability as a function of photoperiodical treatments of mother plants during seed maturation in a desert annual plant: *Trigonella arabica* Del. *Journal of Arid Environments* **1**, 141–144.

Gutterman, Y. and Heydecker, W. (1973) Studies of the surfaces of desert plant seeds. I. Effect of day length upon maturation of the seed coat on *Ononis sicula* Guss. *Annals of Botany* **37**, 1049–1050.

Hacker, J.B. and Ratcliff, D. (1989) Seed dormancy and factors controlling dormancy breakdown in buffel grass accessions from contrasting provenances. *Journal of Applied Ecology* **26**, 201–212.

Karssen, C.M. (1970) The light promoted germination of the seeds of *Chenopodium album* L. III. Effect of the photoperiod during growth and development of the plants on the dormancy of the produced seeds. *Acta Botanica Neerlandica* **19**, 81–94.

Mohamed, H.A., Clark, J.A. and Ong, C.K. (1985) The influence of temperature during seed development on the germination characteristics of millet seeds. *Plant, Cell and Environment* **8**, 361–362.

Murdoch, A.J. and Ellis, R.H. (2000) Dormancy, viability and longevity. *in* Fenner, M. (Ed.) *Seeds: The ecology of regeneration in plant communities.* (2nd edition) Wallingford, UK, CAB International, pp. 183–214.

Parihar, S.S. and Patil, B.D. (1984) Seed germination studies with *Cenchrus ciliaris* L. II. Isolation and characterization of germination inhibitors from the spikelets. *Current Science* **53**, 387–388.

Peters, N.C.B. (1982) Production and dormancy of wild oat (*Avena fatua*) seed from plants grown under soil water stress. *Annals of Applied Biology* **100**, 189–196.

Rauber, R. (1984) Dormancy in winter barley (*Hordeum vulgare*) – Influence of temperature during seed development and germination test. *Landwirtschaftliche Forschung* **37**, 102–110.

Roberts, E.H. and Smith, R.D. (1977) Dormancy and the pentose phosphate pathway. pp. 385–411 *in* Khan, A.A. (Ed.) *The physiology and biochemistry of seed dormancy and germination.* Amsterdam, Elsevier Biomedical Press.

Sawhney, R. and Naylor, J.M. (1982) Dormancy studies in seed of *Avena fatua*. 13. Influence of drought stress during seed development on duration of seed dormancy. *Canadian Journal of Botany* **60**, 1016–1020.

Sharif-Zadeh, F. (1999) Mechanism and modelling of seed dormancy and germination in *Cenchrus ciliaris* as affected by different conditions of maturation and storage. PhD Thesis, The University of Reading, UK.

Somody, C.N., Nalewaja, J.D. and Miller, S.D. (1984) The response of wild oat (*Avena fatua*) and *Avena sterilis* accessions to photoperiod and temperature. *Weed Science* **32**, 206–213.

Summerfield, R.J., Cockshull, K.E., Dickinson, D. and Richardson, A.C. (1974) Versatile irrigation systems for controlled environment growth chambers. *Journal of Horticultural Science* **49**, 161–166.

Watson, C.E. and Watson, V.H. (1982) Nitrogen and date of defoliation effects on seed yield and seed quality of tall fescue. *Agronomy Journal* **74,** 891–893.

Wiesner, L.E. and Grabe, D.F. (1972) Effect of temperature preconditioning and cultivar on ryegrass (*Lolium* sp.) seed dormancy. *Crop Science* **12**, 760–764.

Winkworth, R.E. (1971) Longevity of buffel grass seed sown in an arid Australian range. *Journal of Range Management* **24**, 141–145.

Wurzburger, J. and Koller, D. (1976) Differential effects of the parental photothermal environment on development of dormancy in caryopses of *Aegilops kotschyi*. *Journal of Experimental Botany* **27**, 43–48.

Received 22 February 2000
accepted after revision 11 May 2000