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The effect of seed maturity, drying temperature, and storage temperature on germination and viability in Icelandic *Poa pratensis* L.

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SUMMARY

In an Icelandic *Poa pratensis* L. population, stage of seed maturity at harvest, drying temperature and storage temperature had profound interacting effects on germination (%), and germination rate (days to 50% germination). Germination and germination rate ranged between 9–88% and 7–18 days, respectively, depending on the treatment factor combination. Storage for five months improved germination and germination rate for most lots. Storage at 20–25°C was more beneficial than storage at 6°C, increasing germination by 21% and increasing the germination rate by 5 days on average for all harvest dates and drying treatment combinations. This effect, however, ranged depending on harvest date and drying treatment from –33% to 66% and –1 to 9 days, for germination and germination rate respectively. The germination rate was increased on average for harvest dates by 0.9–3.4 days when seed lots were stored at 20–25°C compared to 6°C. Drying at 35°C and 45°C reduced seed viability in immature lots, compared to drying at 20–25°C, but had no effect when seed had obtained physiological maturity. Seed dormancy was markedly enhanced with delayed harvest. In a germination test one month after the last harvest date, germination declined, on average, from 49% at physiological maturity (12th of August), to 13% when harvested two weeks later (26th of August).

Key words: dormancy, germination, *Poa pratensis*, seed drying, seed maturity, seed storage, seed viability.

YFIRLIT

Áhrif fræþroska, þurrkhita og geymsluhita á spírun og lífhlutfall í íslensku vallarsveifgrasi

Fræ af íslenska vallarsveifgrasstofninum 08 var safnað af frærækturspildu á Geitasandi sumarið 1986 með viku millibili frá 22. júlí til 26. ágúst. Fræið var þurrkað við stofuhita, við 35ºC í 48 klst. eða við 45ºC í 18 klst. Sýni voru sett í spírunarpróf mánuði eftir síðasta söfnunardag og aftur eftir geymslu við 6ºC eða stofuhita (20–25ºC) í fimm mánuði. Allir meðferðarþættirnir, þ.e. söfnunartími (fræþroski), þurrkhiti og geymsla, höfðu mikil og víxlverkandi áhrif á spírun (%) og spírunarhraða (dagar fram að ½ spírun). Spírun og spírunarhraði var á bilinu 9–88% og 7–18 dagar allt eftir samsetningu meðferðarþátta. Geymsla í fimm mánuði jók spírun og spírunarhraða í langflestum tilvikum. Undantekningin var fræ frá fyrsta og öðrum söfnunardegi sem hafði verið þurrkað við 45ºC. Geymsla við stofuhita jók spírunarhraðann um 0,9–3,4 daga í samanburði við fræ sem geymt hafði verið við 6ºC í fimm mánuði og hún reyndist einnig árangursríkari við að auka spírun, en víxlverkun við söfnunardag og þurrkhita var mikil. Þannig breyttist spírunin eftir fimm mánaða geymslu frá –33% til +66% og spírunarhraðinn

frá –1 til +9 daga. Spírunin lækkaði allt að –33% við geymslu í óþroskuðu fræi sem hafði verið þurrkað við 45ºC. Þurrkun við 35ºC og 45ºC lækkaði lífhlutfallið (viability) marktækt í fræi sem var safnað áður en það náði fullum þroska. Fræið náði hámarksþunga, þ.e. fullum lífeðlisfræðilegum þroska, 12. ágúst. Frædvali (100% – spírun) jókst marktækt eftir því sem lengra leið frá 12. ágúst. Þannig var spírunin í fyrsta spírunarprófinu 49% í fræi sem var safnað 12. ágúst, en einungis 13% í því sem safnað var 26. ágúst. Niðurstöðurnar benda til þess að söfnunartími og þurrkhiti hafi veruleg áhrif á endanlegt dvalastig í vallarsveifgrasfræi. Hægt er að flýta dvalarofi með því að stjórna geymsluhita.

INTRODUCTION

Systematic studies on grass seed production in Iceland began in 1924. Kristjánsson (1969), former head of the Sámsstaðir Experimental Station, was a pioneer in this field, experimenting with 15 perennial grass species over a period of 41 years. One of these species was *Poa pratensis* which is one of the most important and the most common forage grass species in Iceland (Thorvaldsson, 1994). Mean annual germination in "first grade" seed lots, in 20 harvest years, ranged from 31 to 78% with an average of 56%. Highest germination obtained from a seed lot was 97% and lowest 2%. It has been suggested that seed dormancy not only varies between growing seasons, but also within the season depending on location and genotype (Sveinsson, 1987). Kristjánsson (1969) reported that seed lots exhibiting poor germination in standard germination tests could germinate satisfactorily when sown in the field. It is more common, however, that *P. pratensis* seed produced in Iceland manifests poor seedling establishment in the year of sowing compared to imported seed (Björnsson and Thorvaldsson, 1983; Helgadóttir, 1982).

Iceland is located just south of the arctic circle and has a maritime climate. The growing season is short and is characterized by relatively low temperatures, long photoperiods and frequent precipitation. Low temperature and high relative humidity may prolong the seed maturation period and sometimes cause inadequate pollination and/or fertilization. Low temperature during seed maturation has been reported to increase seed dormancy in *Avena fatua* (Bewley and Black, 1985; Sawhney and Naylor, 1979), *Festuca arundinacea* (Boyce *et al.*, 1976), *Dactylis glomerata* (Shimizu *et al.*, 1979), *Poa annua* (Sgambatti-Araujo, 1978), *Lolium* spp. (Roberts, 1972; Shimizu *et al.*, 1979), *Triticum* spp. (Bewley and Black, 1985) and *Hordeum vulgare* (Bewley and Black, 1985; Curran and McCarthy, 1986). Similarly, long photoperiods induce seed dormancy in several species (Roberts, 1972; Khan, 1982). Geographic adaptation in European *Dactylis glomerata* in relation to germination performance has been well documented in a series of papers (Probert *et al.*, 1985ab). It is therefore not unexpected that seed dormancy can be severe in some Icelandic grasses such as *P. pratensis*.

In this study, an Icelandic population of *P. pratensis* was harvested on successive dates in order to evaluate the effect of seed maturity, drying temperature and storage temperature on viability, germination and dormancy.

MATERIALS AND METHODS

Material and study sites

Seed from the *Poa pratensis* population '08', originating from Breiðafjörður (65°20'N and 22°30'W) in western Iceland was used in the study. Seeds were collected at one week intervals from 22 July to 26 August 1986 (labelled H_1...H_6, respectively) from a seed field on a sandy outwashed gravel plain at Geitasandur (63°45'N and 20°10'W) in southern Iceland. Climatic data from the meteorological station, Hella, approximately 10 km from the experimental field site are presented in Table 1.

The seeds were postharvest conditioned (dried, brushed and cleaned) at Korpa Experimental Station, Iceland. All seed tests were done at North Dakota State Seed Department

Table 1. Climatic data from the meteorological station (Hella) closest to the experimental site (10 km), in June (month of anthesis) to August (month of harvest) 1986, and deviations from the 1931 to 1960 mean. *1. tafla. Niðurstöður veðurmælinga á Hellu, sem er um 10 km frá tilraunastaðnum, sumarið 1986 ásamt frávikum frá 30 ára meðaltölum (1931–1960).*

Month *Mánuður*	Temperature[a], °C—*Hiti* Mean 1986 *Meðaltal*	Deviation *Frávik*	Low/High *Lágm./Hám.*	Precipitation, mm 1986 *Úrkoma*	Deviation *Frávik*	Relative humidity, % *Loftraki*	Photoperiod, h *Daglengd*
June	8.7	–1.0	6.6–12.0	81.2	+22.4	84	21.0
July	10.8	–0.6	7.1–15.0	80.7	+8.7	78	18.2
August	9.9	–0.6	6.3–14.2	162.1	+54.0	84	15.4

a) The mean is the mean 24 hour temperature. The low-high is the mean minimum and maximum temperature.

and Department of Agronomy at North Dakota State University, Fargo ND, USA. Data were analyzed at the Agricultural Research Institute, Keldnaholt, Iceland, using the GLIM (Generalised Linear Interactive Modelling) system (Baker and Nelder, 1978).

Sampling and treatments

At each collection date, plots were harvested by hand along an imaginary line until a desirable lot size, approximately 500 g of clean seed, was achieved.

Lots from each harvest date were divided into three equal parts (sublots) for different drying treatments, excluding the first harvest date (H_1) which only was used to determine 1000 seed weight and seed dry matter content at harvest. Sublots were dried and labelled as follows:

- D_1 At room temperature (20 to 25°C). The lots were spread out on a table and allowed to dry for five to six days.
- D_2 At 35°C (±3°C) in a drying cabinet for approximately 48 h.
- D_3 At 45°C (±4°C) in a drying cabinet for approximately 18 h.

Twelve samples, 10 g each, were drawn for each harvest date and drying treatment. These were tested for germination one month after the last harvest date (G_1), stored at 6°C with a 45% relative humidity (G_2), or at room temperature (20 to 25°C) with uncontrolled humidity levels (G_3).

A working sample for each treatment factor combination, weighing approximately 2 g, was obtained by passing samples through a mechanical divider by repeated halving and then through a uniform airflow (New Brunswick General Seed Blower) for 3 min to remove chaff and empty florets as prescribed by the Association of Official Seed Analysts rules for testing seed (AOSA, 1978). The working samples were divided into the number of replicates required for the various tests. One hundred seeds were then drawn from each division, representing one experimental unit.

Tests

Dry matter content at harvest, before cleaning, was determined by drawing 16 samples for each harvest date. The samples were placed in paper bags, allowing removal of surface water, and sealed in plastic bags, to avoid dehydration of the seed during transportation. The seeds were dried at 35°C (±3°C) for 5 to 6 days.

Seed moisture content determination followed the high constant temperature oven method as described in International Seed Testing Association rules for testing seed (ISTA, 1985), except the samples were dried in four replicates instead of two, as recommended.

One thousand seed weight (mg) determination followed the ISTA international rules for testing seed (1985).

Seed viability for all sublots was deter-

mined by 1% 2,3,5-triphenyl tetrazolium chloride (TZ) gravity test following AOSA (1970) TZ testing rules using the puncturing method and lactophenol as a clearing agent. The TZ-tests were made in October–December 1986. Samples were stored at 6°C at 45% relative humidity.

Germination tests were conducted in a "dry" incubator with white fluorescent light (averaging 2.7 W m^{-2}) at 25°C for 8 h in the light and 15°C for 16 h in the dark. Replicates of 100 seeds were planted on one layer of regular weight seed germination paper with a steel blue seed germination paper below as blotters. Disposable sterilized petri dishes, 90 mm in diameter and 10 mm in height, were used. Deionized distilled water (7 ml) was applied to the seed and the dishes were sealed with parafilm to avoid excessive evaporation. The seeds were stratified for 5 days at approximately 6°C prior to incubation. Seeds were considered germinated when more than 3 to 4 mm of the coleoptile and the first leaf had emerged from the caryopsis. Seedlings missing either the radicle or the coleoptile and seedlings showing atypical bends were classified as abnormal following ISTA (1985). Polyembryonic seed were considered normal if an equal number of coleoptiles and radicles were present since these reportedly support normal growth (Åkerberg, 1942; Duich and Musser, 1959; Tinney, 1936). The incubation period lasted 30–40 days and germinated seeds were counted at 5 or 10 days intervals. The first germination test (G_1), was initiated approximately one month after the last harvest date and the latter (G_2 and G_3) 5 months later. A pre-study indicated that light intensity affected germination. The dishes were arranged in a four replicate randomized complete block design, since the light distribution in the incubator was not even.

Calculations and statistical analyses

Standard error (SE) of the arithmetic mean for harvest dates (H_i) was calculated for dry matter at harvest, seed moisture in storage and 1000 seed weight determination. Coefficient of variation (CV) for chaffy seed weight determination did not exceed the ISTA (1985) rules.

Seed viability (%) means for each harvest date (H_i) and drying treatment (D_j) were calculated from 4×100 seeds. Maximum tolerated ranges between replicates as related to ISTA rules for testing seed (1985) were not exceeded and the precision of means could be estimated from the binomial error.

From the germination tests the following calculations were made:

1) **Germination (*GR*)** is the ratio, expressed in percentages, between normal germinated seed and viable seed. Then, the degree to which *GR* is less than 100% is a measure of seed dormancy. Abnormal seedlings are not included.

   Analysis of deviance, an extension of the analysis of variance (ANOVA) to include generalized linear models, was used to analyse count data with binomial distribution. The deviances replace the sums of squares of the ANOVA and under the null hypothesis of zero response they are approximately χ^2 distributed (Aitkin *et al.*, 1989). In this study with 100 seeds per unit and 400 seeds per replicate the approximation is expected to be good. The variation between replicates was of the magnitude expected by binomial variation alone and no significant differences were found between blocks in the incubator. From this follows that an independent estimate of error for testing three factor interactions is not required so that the replicates could be pooled for the final analysis.

   In the analysis of germination data the binomial error applies to counts as a proportion of all tested seeds, while *GR* is calculated on viable seed only. Therefore, the observed germination may exceed the average proportion of viable seed and then *GR* becomes greater than 100%. *GR* is a ratio between two quanti-

ties that both are estimated with binomial error and its variance is:

$$\mathrm{Var}(GR)= [p_g(1-p_g)N_g/p_v^2+p_g^2(1-p_v)N_v/p_v^3]100^2$$

where p_g and p_v are the probabilities that a seed will germinate or is viable, respectively, and N_g and N_v are the numbers of seed that are used for determination of germination and viability, respectively, in this case 400 for both tests. An estimate of this variance is obtained by replacing p_g and p_v by the estimated probabilities. When different lots are being compared the covariances are zero and the error of differences can be estimated directly. A procedure analogous to ANOVA was not available for this case. For analyses within lots the viability is a constant and the analyses of *GR* becomes the same as for germinated seed, here the analysis of deviance. For the analysis of interaction of storage (G) with lots from different harvest dates and drying treatments (H×D) a user-defined model in GLIM was developed, based on ideas from Roger (1985) and designed by Hólmgeir Björnsson (unpublished). The errors are binomial, but the linearized part of the model is restricted to the viable proportion of the seeds. A model for the probability distribution of germination on time is required. For the purpose of this analysis the normal distribution was found to be adequate.

2) **Germination rate (DA_{50})** is the time (days) to 50% germination (*GR*). As germination is observed at discrete time points with unequal rate of germination between them a model for the distribution of the time to germination was selected. On the assumption that the probability of germination increases with time by the logistic function, the DA_{50} was estimated by the logit model (Finney, 1964):

$$\ln(p_x/(1-p_x))=a+bx$$

where p_x is the probability of germination x days from incubation, b and a are the slope and intercept of the logistic regression respectively. At the 50% germination point $p_x/(1-p_x)=1$ and the logarithm becomes zero. Under these con-ditions, a+bx=0 and the ratio –a/b is an estimate of the day of 50% germination, DA_{50}. The logistic slope, b, was found to vary between treatment factor combinations. Each DA_{50} and its standard er-ror was, therefore, estimated using the slope found for that treatment. These estimates were then analysed in a three way ANOVA. The pooled standard error of estimates can be used to test the significance of three factor interactions although the degrees of freedom are not known. However, the slopes are scale parameters of the logistic function and the variable slopes are the main reason for unequal errors of the DA_{50} estimates. Therefore, a weighted ANOVA was also done, with the weights inversely proportional to the variances.

RESULTS AND DISCUSSION

Dry matter, seed weight and seed moisture after curing

Seed dry matter increased from 24% at first harvest date to 76% six week later and one thousand seed weight increased from 296 mg to maximum 477 mg three weeks later, 12th of August (Table 2 and Figure 1). The results suggest that seed physiological maturity was reached around 12th of August (H_4). Seed moisture content in storage was 9–10% (Table 2) and was not affected by the treatment factors.

Seed viability

Seed viability was not affected by maturity at harvest when dried at room temperature (Table 3 and Figure 1), which is in agreement with Delouche's (1958) and Hite's (1919) work on *P. pratensis*. However, Garman and Vaughn (1916) found that germination of immature

Table 2. Seed weight, dry matter at harvest and seed moisture content in storage for *Poa pratensis* population '08' harvested in 1986 at Geitasandur, South-Iceland.
2. tafla. Þúsundkorna þyngd, þurrefni í fræi á söfnunardegi og raki í fræi í geymslu í vallarsveifgrasstofninum 08 sem var safnað á Geitasandi sumarið 1986.

Harvest dates *Söfnunardagur*	1000 seed weight mg±SE[a)] *1000 korna þyngd*	Dry matter %±SE *Þurrefni*	Seed moisture %±SE *Fræraki*
H_1 22.7.	296±3.6	23.5±0.40	
H_2 29.7.	390±3.6	26.2±0.43	9.80±0.03
H_3 5.8.	438±5.6	45.0±0.46	9.69±0.06
H_4 12.8.	477±9.1	59.3±0.84	9.05±0.05
H_5 19.8.	465±6.9	73.0±0.82	9.41±0.03
H_6 26.8.	460±4.7	75.6±1.61	9.34±0.01

a) SE = Standard error.

seed was never as good as that of mature seed even when carefully cured. According to Bass (1965), immature *P. pratensis* seed has reduced storability. The same seed lots as in the present study were tried in an accelerated ageing test which revealed lower vigour of the immature seed compared to mature seed (Sveinsson, 1987). Drying temperatures at 35 and 45°C reduced viability in immature seed lots, but had no effect at later harvest dates compared to drying at 20 to 25°C (Table 3 and Figure 2). This is in agreement with Griffeth and Harrison (1954), who, working with *Phalaris arundinacea*, concluded that drying temperatures above room temperatures reduced viability in immature seed lots.

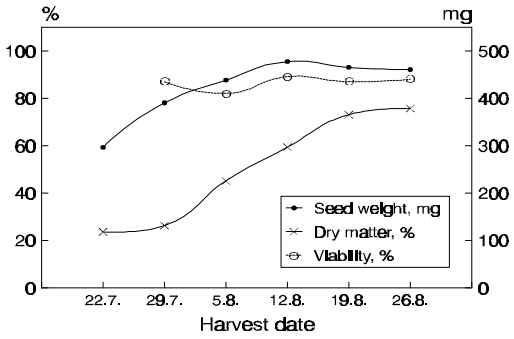

Figure 1. One thousand seed weight (mg), seed dry matter (%), and seed viability (%) in *P. pratensis* population '08' at 6 harvest dates.
1. mynd. Áhrif söfnunartíma fræs á þúsundkorna þyngd (mg), þurrefni á söfnunardegi (%) og lífhlutfall (%) í vallarsveifgrasstofninum 08 af Geitasandi sumarið 1986.

Table 3. Mean seed viability (%) determined in TZ-tests for *Poa pratensis* population '08' harvested in 1986 at Geitasandur, South-Iceland and using three drying treatments.
3. tafla. Áhrif þurrkhita (D_i) og fræþroska (H_i) á lífhlutfall (%) ákvarðað með TZ-prófi í vallarsveifgrasstofninum 08 frá sumrinu 1986 á Geitasandi.

Harvest date *Söfnunardagur*	Drying temperatures—*Þurrkhiti* 20–25°C (D_1)	35°C (D_2)	45°C (D_3)
H_2 29.7.	87	69	52
H_3 5.8.	82	76	66
H_4 12.8.	89	83	88
H_5 19.8.	87	89	87
H_6 26.8.	89	89	90

Germination and germination rate

Harvest dates, drying treatments and storage for five months had substantial effects on germination and germination rate. The effects depended on the combination of treatment factor levels, resulting in strong two- and three-way interactions (Table 4, 5 and 6 and Figure 3). Germination of seed lots from different harvest dates ($H_{2,3,4,5,6}$) ranged between 9–

Table 4. The effect of different harvest dates (H_i), drying temperature (D_j) and storage temperature (G_k) on germination (*GR*) and germination rate (DA_{50}) in *Poa pratensis* population '08' from Geitasandur, South-Iceland.
*4. tafla. Áhrif fræþroska (H_i), þurrkhita (D_j) og geymsluhita (G_k) á spírun (*GR*) og spírunarhraða (DA_{50}) í vallarsveifgrasstofninum 08 af Geitasandi.*

Harvest dates *Söfnunardagur*	Drying temperature—*Þurrkhiti* 20–25°C (D_1) *GR*	DA_{50}	35°C (D_2) *GR*	DA_{50}	45°C (D_3) *GR*	DA_{50}	Grand mean *Meðaltöl* *GR*	DA_{50}
G_1 (One month after the last harvest date)								
H_2 29.7	38.2	15.0	22.5	14.7	52.9	16.1		
H_3 5.8.	38.4	14.4	27.0	16.8	39.8	18.0		
H_4 12.8.	48.6	13.1	54.2	14.9	44.0	13.6		
H_5 19.8.	14.4	14.0	18.0	13.8	20.4	13.9		
H_6 26.8.	13.2	16.2	9.5	15.3	16.1	14.9		
							30.5	15.0
G_2 (Stored at 6°C for 5 months)								
H_2 29.7.	57.8	12.0	47.8	16.2	9.6	17.6		
H_3 5.8.	39.9	15.5	33.9	13.6	28.4	14.2		
H_4 12.8.	31.5	13.0	37.9	16.4	66.5	12.7		
H_5 19.8.	46.0	13.1	13.8	11.7	38.8	13.6		
H_6 26.8.	18.0	11.7	67.1	11.3	23.1	11.3		
							37.4	13.6
G_3 (Stored at 20–25°C for 5 months)								
H_2 29.7.	70.4	9.3	88.4	13.5	20.2	17.4		
H_3 5.8.	62.5	13.3	51.0	10.7	36.7	9.5		
H_4 12.8.	41.6	10.5	55.1	13.2	72.2	9.3		
H_5 19.8.	62.3	12.3	19.1	9.7	64.1	13.7		
H_6 26.8.	18.3	7.2	75.0	8.8	38.6	10.0		
							51.7	11.2

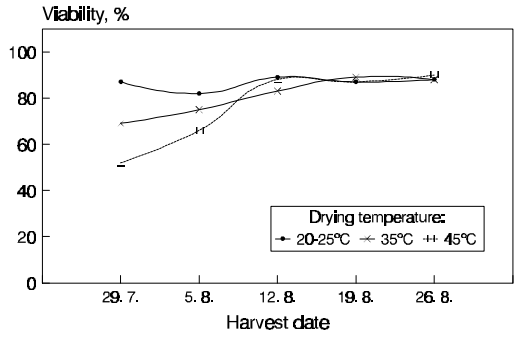

Figure 2. Seed viability in *P. pratensis* population '08' at 5 harvest dates and dried at 3 temperature levels.
2. mynd. Áhrif söfnunartíma fræs og þurrkhita á lífhlutfall í vallarsveifgrasstofninum 08 af Geitasandi sumarið 1986.

54%, 10–67% and 18–88% when germinated one month after the last harvest date, after five months of storage at 6ºC and after five months of storage at 20–25ºC (G_1,G_2 and G_3), respectively, and germination rate ranged between 13–17, 11–18 and 7–17 days, respectively. The most apparent source of interaction is when germination before storage (G_1) is compared with germination after storage ($G_{2,3}$) at different drying treatments and harvest dates. This possibly indicates endogenous germination rhythms, as reported by Maquire (1969). He studied two cultivars of *P. pratensis* and found that the rhythms were affected by the year of harvest, geographical location of production and genotype, but harvest dates

and storage temperatures did not have any effect on the rhythm. Phaneendranath and Funk (1981) reported germination fluctuations in *P. pratensis* between tests conducted at

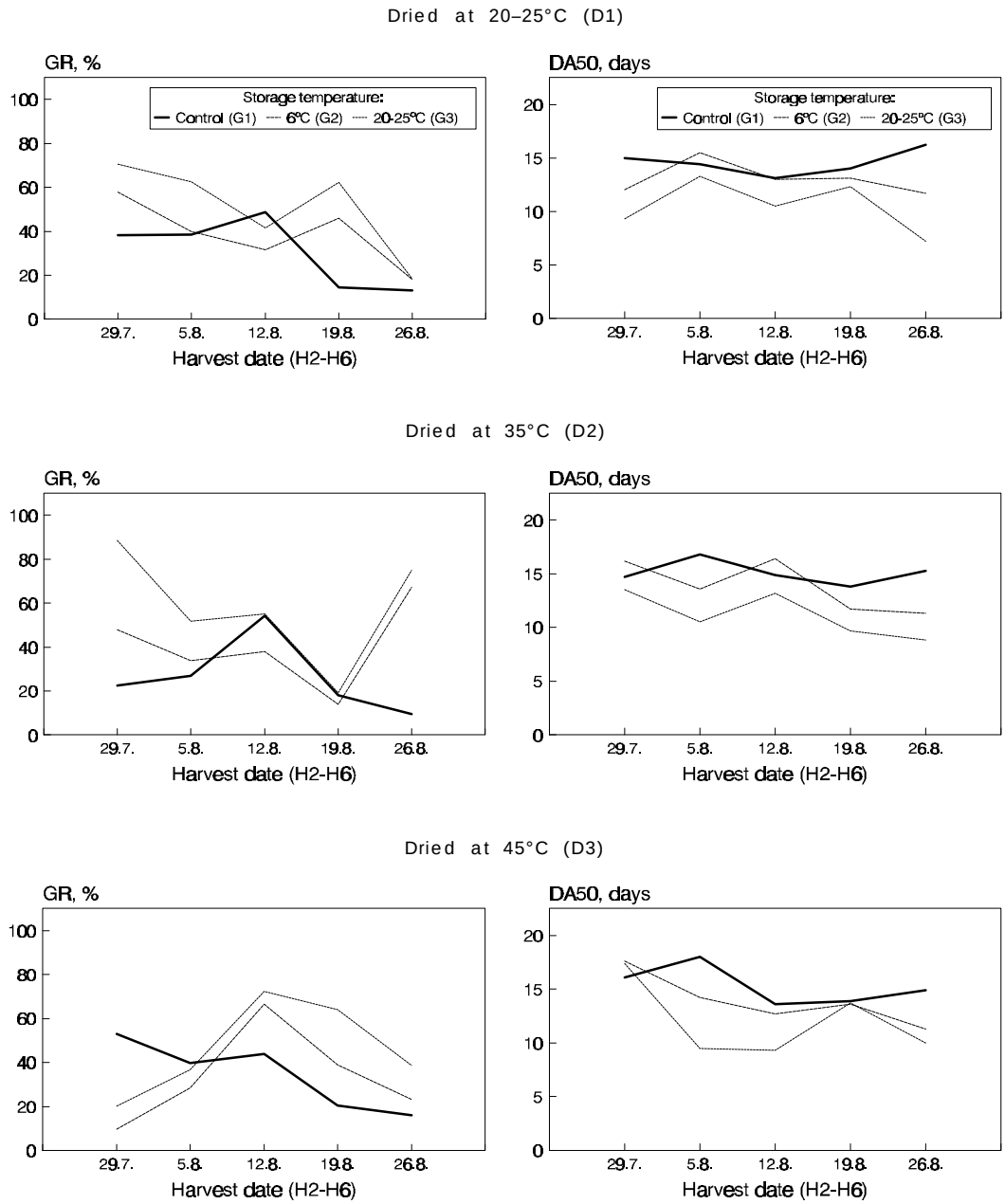

Figure 3. Germination (*GR*) and germination rate (DA_{50}) for *P. pratensis* population '08' as affected by harvest dates (H_i), storage temperatures (G_j) and drying at 20 to 25°C, 35°C and 45°C.
*3. mynd. Áhrif söfnunartíma (H_i) fræs, þurrkhita (D_j) og geymsluhita (G_k) á spírun (*GR*) og spírunarhraða (*DA_{50}*) í vallasveifgrasstofninum 08 af Geitasandi sumarið 1986.*

Table 5. Deviances for various interactions in germination (*GR*) between harvest dates (H_i), drying temperatures (D_j) and storage temperatures (G_k).
*5. tafla. Víxlverkunarhrif söfnunardags (H_i), þurrkhita (D_j) og geymsluhita (G_k) á spírun (*GR*), sýnd sem reiknihending leidd af sennileikahlutfalli.*

Source of variation *Orsök breytileika*	DF *Frítölur*	Deviance
$H_{2,3,4,5,6}\times D_{1,2,3}\times G_{1,2,3}$	16	568.01***
Germination after storage (excluding G_1)		
$H_{2,3,4,5,6}\times D_{1,2,3}$	8	1131.00***
$H_{2,3,4,5,6}\times G_{2,3}$	4	17.09***
$D_{1,2,3}\times G_{2,3}$	2	3.81
$H_{2,3,4,5,6}\times D_{1,2,3}\times G_{2,3}$	8	41.03***
Germination after storage (excluding $H_{4,5,6}$ and G_1)		
$H_{2,3}\times D_{1,2,3}$	2	96.31***
$H_{2,3}\times G_{2,3}$	1	2.79
$D_{1,2,3}\times G_{2,3}$	2	9.37***
$H_{2,3}\times D_{1,2,3}\times G_{2,3}$	2	16.07***
Germination after storage (excluding $H_{2,3,4}$ and G_1)		
$H_{5,6}\times D_{1,2,3}$	2	649.36***
$H_{5,6}\times G_{2,3}$	1	5.60*
$D_{1,2,3}\times G_{2,3}$	2	12.25***
$H_{5,6}\times D_{1,2,3}\times G_{2,3}$	2	3.92

* Probability <0.05 of a larger value of χ^2.
*** Probability <0.001 of a larger value of χ^2.

Table 6. Mean squares for various interactions in germination rate (DA_{50}) between harvest dates (H_i), drying temperatures (D_j) and storage temperatures (G_k).
6. tafla. Meðalfervik víxlhrifa söfnunardags (H_i), þurrkhita (D_j) og geymsluhita (G_k) á spírunarhraða (DA_{50}*).*

Source of variation *Orsök breytileika*	DF *Frítölur*	Mean squares—*Meðalfervik* Weighted *Vegið*	Unweighted *Óvegið*
$H_{2,3,4,5,6}\times D_{1,2,3}\times G_{1,2,3}$		161.8100	2.4770
Germination after storage (excluding G_1)			
$H_{2,3,4,5,6}\times D_{1,2,3}\times G_{2,3}$		80.4277	0.8490
$H_{2,3,4,5,6}\times D_{1,2,3}$		88.8200	9.5000
$H_{2,3,4,5,6}\times G_{2,3}$		41.7360	1.5150
$D_{1,2,3}\times G_{2,3}$		20.1450	0.4724
Mean error variance of germination rate *Meðaldreifni*		0.1949	0.3608

different times, and despite of being aware of Maquire's (1969) studies, they concluded that it was due to secondary dormancy developed in storage. Here, harvest dates do have a profound effect on germination as do drying treatments, leading to the conclusion that these factors are involved in adjusting or regulating the biological rhythm, or in inducing different levels of secondary dormancy. A study whith four Icelandic populations (including '08'), which were germinated at regular time intervals, did not indicate the presence of endogenous rhythms nor induction of secondary dormancy in storage (Sveinsson, 1990). The effect of storage temperature is best explained by having an influence on the time required for after-ripening, since the difference between the storage treatments (G_2 and G_3) was fairly independent of harvest dates and drying temperature.

If germination before storage (G_1) is examined, drying temperatures (D_j) appear to have strong influence on germination in immature seed lots (H_2 and H_3) but much less for mature ones (H_4, H_5 and H_6). Interestingly, germination is markedly reduced (i.e. increased dormancy) when harvest is delayed after physiological maturity. In 1983 and 1985, final germination and germination rate was lower in Icelandic *P. pratensis* seed lots that had been harvested late compared to lots harvested early (Jónatan Hermannsson, unpublished data). These findings conflict with observations in *P. pratensis* made by Bass (1954), Delouche (1958) and Phaneendranath *et al.* (1978). They found that immature, or early harvested, seed had deeper dormancy (lower germination) than mature, or late harvested seed. Further, Delouche (1958) concluded that after-ripening is completed at about the same

time irrespective of seed maturity and dormancy at harvest. Bjarnason (1982) studied the effect of harvest date on germination in two Icelandic *Leymus arenarius* populations and found that final germination (~90%) was not affected by harvest date, but early harvested seed had much lower germination rate. The environmental conditions under which the seeds in this study were grown (Table 1), are most likely responsible for increased dormancy with delayed harvest.

Analysis of interaction effects

The interactions, discussed above, become apparent in the statistical analyses. The analyses concentrated on locating the main sources of interactions. When all treatments were included in the model, strong three-way interactions were apparent for germination (Table 5) as well as germination rate (Table 6). The interactions were decidedly reduced by excluding the germination test before storage (G_1) from the analysis, but were still significant. In an attempt to further locate the three-way interaction for germination (*GR*), treatment combination from the immature lots (H_2 and H_3), and the postmature lots (H_5 and H_6), were analysed separately. Within this limited time scale, there still remains a significant three-way interaction in the immature lots. In the presence of three-way interactions, two-way interactions are difficult to interprete. This is seen in the $D_j \times G_{2,3}$ interaction, which gives nonsignificant deviances when all harvest dates (H_i) are included but becomes significant when restricted to two harvest dates. The only two-way interactions which are great compared to the three-way interactions are $H_i \times D_j$ (see Figure 3).

The three-way interactions for germination rate (DA_{50}) were nonsignificant when the germination test before storage (G_1) was excluded and then two-way interactions could be tested directly (Table 6). The analyses for germination rate indicate strong interactions between harvest dates (H_i) and drying treatments (D_j), some interactions between harvest dates and storage temperatures ($G_{2,3}$) and no interaction for $D_j \times G_{2,3}$.

Table 7. Estimated increase in germination rate (DA_{50}) by storing *Poa pratensis* seed at 20 to 25°C (G_3) compared to 6°C (G_2) for 5 months as related to harvest dates (See Table 4).
7. tafla. Áhrif söfnunardags (H_i) á aukningu spírunarhraða (DA_{50}) við að geyma vallarsveifgrasfræ við stofuhita (G_3) í stað 6°C hita (G_2) í fimm mánuði.

Harvest date *Söfnunardagur*		G_3–G_2 DA_{50} Weighted *Vegið*	Unweighted *Óvegið*
H_2	29.7.	2.52±0.45	1.86±0.72
H_3	5.8.	2.81±0.48	3.36±0.72
H_4	12.8.	3.13±0.44	3.04±0.72
H_5	19.8.	0.48±0.45	0.86±0.72
H_6	26.8.	2.48±0.58	2.76±0.72
Mean—*Meðaltal*		2.28	2.38
SE		0.61	0.77

The storage temperature effect

The germination and germination rate increased with storage for most lots, although some lots changed little, and one of the immature lots (H_2D_3) lost most of its germinability upon storage (Table 4). The germination rate was increased depending on harvest date, by 0.48 to 3.13 and 0.86 to 3.36 days for weighted and unweighted estimates respectively, when seed lots were stored at 20 to 25°C compared to 6°C (Table 7).

The effect of storage temperature and relative humidity on germination in *P. pratensis* has been reported by several authors (Hite, 1923; Sprague, 1940; Bass, 1954, 1965; Phaneendranath and Funk, 1981). In general, elevated storage temperature and low relative humidity improve germination and germination rate, compared to storage at low temperature. High relative humidity at any temperature level has decreasing or no effect. Bjarnason (1982) with *L. arenarius* and Sveinsson (1990) with *P. pratensis* seed, markedly improved the germination rate with prolonged

storage. In *L. arenarius* and *P. pratensis* the germination rate is regulated by the covering structures (the *lemma* and *palea*) of the caryopsis, and by carefully removing them just prior to incubation the seed will germinate at a maximum rate (Sveinsson, 1987, and unpublished data). This study indicates that the inhibitory effects of the coverings structures are reduced with storage at room temperature.

CONCLUSION

The data presented here and other studies with Icelandic *P. pratensis* (Sveinsson, 1987, 1990), indicate high sensitivity of the seed to its environment, causing various degrees of dormancy. Harvest dates and drying treatments appear to be the predominant factors in determining the germinability at a given time.

The open inflorescence of *P. pratensis* with its numerous 3 to 5 flowered spiklets produces 150 to 300 seeds (Sveinsson, unpublished data) which develop and mature over a period of time. The stage of maturity of individual seeds within an early harvested lot is therefore very variable, but less so with delayed harvest, since *P. pratensis* seeds do not shed easily. The failure of some seeds to germinate in the immature seed lots can, therefore, be due to marginally viable and non-germinable embryos while some exhibite true dormancy. This may be a factor in the strong interactions reported here.

Seed harvesting before physiological maturity can not be recommended. Besides causing technical problems due to high moisture levels, immature seed are low in vigour and sensitive to deviations from the ideal storage and curing environment. Even though the post-mature lots exhibited high levels of dormancy, harvesting at that stage is more desirable since these lots possess seeds of more uniform quality and higher vigour. Proper curing and storage combination should remove or minimize dormancy before use.

The interesting feature that seed dormancy is enhanced with delayed harvest conflicts with findings reported from studies with non-Icelandic material where dormancy is reduced with delayed harvest. This contradiction is probably due to differences in environmental factors. The studies were made with seed grown under more favorable climatic conditions and, hence, effects on dormancy and germination of harsh environment, like low temperature and frequent precipitation during seed maturation, are not expressed. However, whether this unique environmental response is typical for *P. pratensis* as a species or whether it is just a population characteristic remains to be elucidated.

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