

# Germination of Range Plant Seeds at Alternating Temperatures<sup>1</sup>

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## Highlight

The germination behavior at alternating temperatures of range plants suitable for seeding semi-arid range was consistent with their behaviour at the fixed temperatures of the alternation cycle, but not with weighted mean daily temperature. Unfavorable temperatures produced a greater retardation of germination than would be expected from their relative influence on the weighted mean. Alternating temperatures did not stimulate germination in the spe-

cies studied. These data support conclusions from previous work regarding low seedbed temperatures as a factor in the failure of semi-arid range seeding operations.

In the first part of this investigation (Ellern and Tadmor, 1966; hereafter referred to as part I), germination behaviour of pasture plants at fixed temperatures under laboratory conditions was interpreted in the light of soil temperatures recorded in the field.

In the semi-arid Negev, diurnal temperature fluctuations in the seedbed zone of shallow seeded range plants normally reach an amplitude of about 20C

on bright dry days and about 10C during cloudy and rainy periods (Tadmor et al., 1964). The bluegrasses (*Poa* spp.), orchardgrass (*Dactylis glomerata* L.), Bermuda grass (*Cynodon dactylon* L.) and others have been shown to respond to such fluctuations and to germinate only or better at alternating temperatures (Harrington, 1923; Morinaga, 1926; Lehmann and Aichele, 1931). The question therefore arose whether the species investigated also respond in this way; whether their germination at alternating temperatures is consistent with that at fixed temperatures; to what extent germination is a function of hour-degrees and how it is affected by the amplitude between temperature extremes. Investigations at fixed temperatures only might be insufficient to explain plant establishment in the field.

<sup>1</sup>This research has been financed in part by a grant made by the U.S. Department of Agriculture, under P.L. 480, contract No. A10-CR-45. Contribution from the National and University Institute of Agriculture, Rehovot, Israel, 1966, Series No. 1017 E.

The contributions of Harrington (1923) and Morinaga (1926) to this topic as well as Lehmann and Aichele's (1931) comprehensive review of work on gramineae are still of importance today. Stotzky and Cox (1962) and especially Cuddy (1963) and Nakamura (1962a, b) working on pasture species, employed alternating temperatures along with other techniques primarily as a means of forcing germination, rather than of investigating their role as an environmental factor. Went (1949), Juhren, Hiesey and Went (1953), and Hylton and Bement (1961) have made comprehensive studies of germination and early growth of range plants, conducting parallel trials in the field and in a variety of fully controlled environments; these investigations however do not include many of the species and environmental conditions investigated in the present study.

#### Methods and Materials

*Experimental procedure*—Temperature alternations were within the temperature range commonly encountered in the seedbed zone (2-5 cm soil depth) during the winter (sowing) season in the semi-arid Negev. They included most of the possible combinations between temperatures of 4, 8, 10, 15, 20 and 25C and were applied by transferring petri dishes containing seeds to and fro between humidified incubators, representing "day" (8 hr) and "night" (16 hr) temperature. All seeds were kept in the dark except for daily counts, and "day" or "night" in this paper refers to periods of 8 hr and 16 hr only. The methods and the seeds employed were identical with those used in part I: the perennial grasses, *Agropyrum desertorum* (Fisch.) Schult. (crested wheatgrass, vars. Fairway and Nordan—1962 harvest); *Phalaris bulbosa* L. (hardinggrass, local ecotype, 1962 harvest); *Oryzopsis holciformis* (M. B.) Hack. (hairy ricegrass,

**Table 1. Summary of germination behavior at fixed temperature of range plants: Adverse effect of temperature extremes as indicated by days to onset, to full germination, and final germination percentage at low (4-10C) and high (25-30C) temperatures. Minus = adverse effect; plus = no adverse effect.**

Species	Susceptible to adverse effect of:					
	Low temp. (4-10C)			High temp.(25-30C)		
	onset	full	final	onset	full	final
1. <i>A. desertorum</i> (Fairway)	-	-	-	+	+	+
2. <i>A. desertorum</i> (Nordan)	-	-	+	+	+	+
3. <i>Phalaris bulbosa</i>	-	-	+	+	+	+
4. <i>Oryzopsis holciformis</i>	-	-	-	+	+	-
5. <i>Hordeum bulbosum</i>	+	-	+	-	-	-
6. <i>Avena sterilis</i>	-	-	+	+	-	+
7. Barley (Beecher)	+	+	+	+	+	+
8. Wheat (Florence Aurore)	+	+	+	+	+	+
9. <i>Medicago hispida</i>	+	+	+	+	-	-
10. <i>M. truncatula</i>	+	+	+	+	-	+
11. <i>Trifolium purpureum</i>	+	+	-	+	+	-

1962 harvest) and *Hordeum bulbosum* L. (bulbous barley, 1963 harvest); the annuals, *Triticum aestivum* L. (wheat var. Florence Aurore, 1963 harvest); *Hordeum vulgare* L. (barley var. Beecher, 1963 harvest); and *Avena sterilis* (animated oats, 1963 harvest); the annual legumes *Medicago hispida* Gaertn. (bur medic, 1962 harvest); *Medicago truncatula* Gaertn. (barrel medic, 1962 harvest); and *Trifolium purpureum* Loisel (purple clover, 1963 harvest). The work was done in the summer of 1964 when after-ripening was expected to be complete. Germination was regarded as complete when both radicle and coleoptile had emerged, except with *Hordeum bulbosum* and *Avena sterilis*, where a radicle size of 2 mm was taken to indicate germination.

*Presentation and analysis of data*—Three parameters were chosen for analysis: a) days to "onset" of germination, defined as the day on which 10% of "final" germination was reached under any one temperature regime, b) days to "full" germination (80% of "final" germination), and c) "final" germination, defined as the cumulative germination percentage reached on the 30th day on which counts were usually terminated. These parameters have been fully discussed

in part I (Ellern and Tadmor, 1966).

The diagrammatic presentation was adapted from Harrington (1923), Morinaga (1926), and Lehmann and Aichele (1931). Adverse temperature regimes show as peaks of time and/or as troughs of percentage. Weighted mean temperature (W.M.T.) has here been calculated as "day" temp. + 2 · "night" temp.

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#### Results

The germination responses to fixed and alternating temperatures for the eleven species studied are presented in Fig. 1-11. For Fig. 3-11, only the data relating to "day" temperatures of 4, 15, 25 and 30C are shown; those for 8, 10 and 20C have been omitted. Results obtained with the same species in Part I have been summarized in Table 1 for comparison. Weighted mean temperature (W.M.T.) corresponding to each temperature alternation is shown for Fig. 1 and 2 only.

*Onset and full germination.*—In the species sensitive to low fixed temperature (the perennial grasses, nos 1-4 in Table 1 and Fig. 1-4), the time required for onset and full germination shortens as "night" temperatures rise in each set of

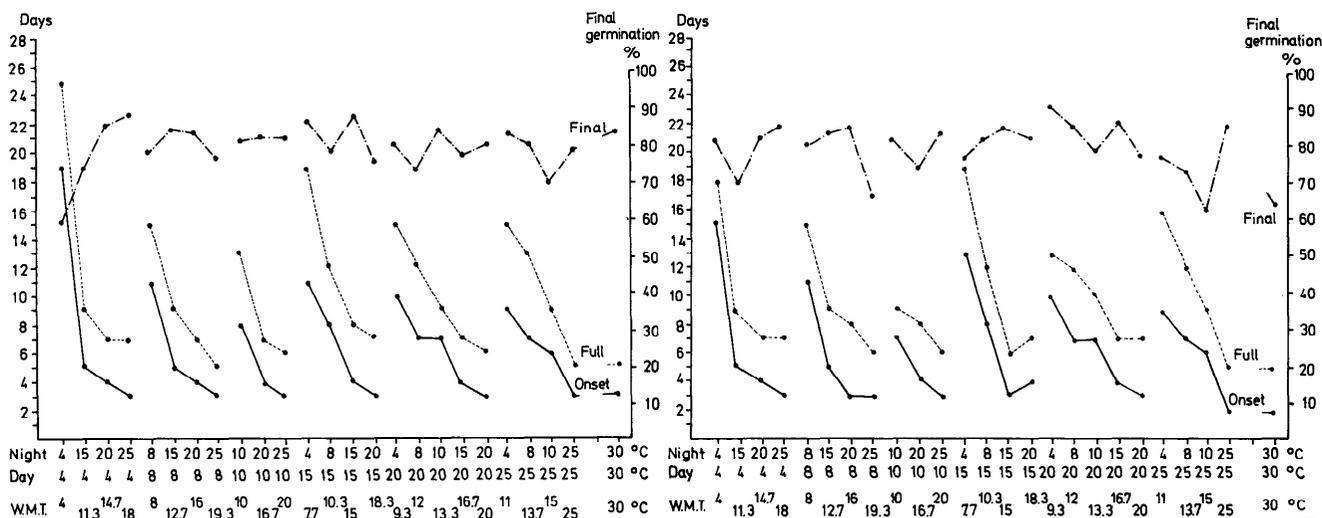


FIG. 1 and 2. Days to onset and to full germination and final germination percentage of *Agropyron desertorum* (var. Fairway), left; and *A. desertorum* (var. Nordan), right at fixed and alternating temperatures. Abscissa scale in °C. "Onset" = 10% of "final". "Full" = 80% of "final". "Final germination" = percentage reached on 30th day.

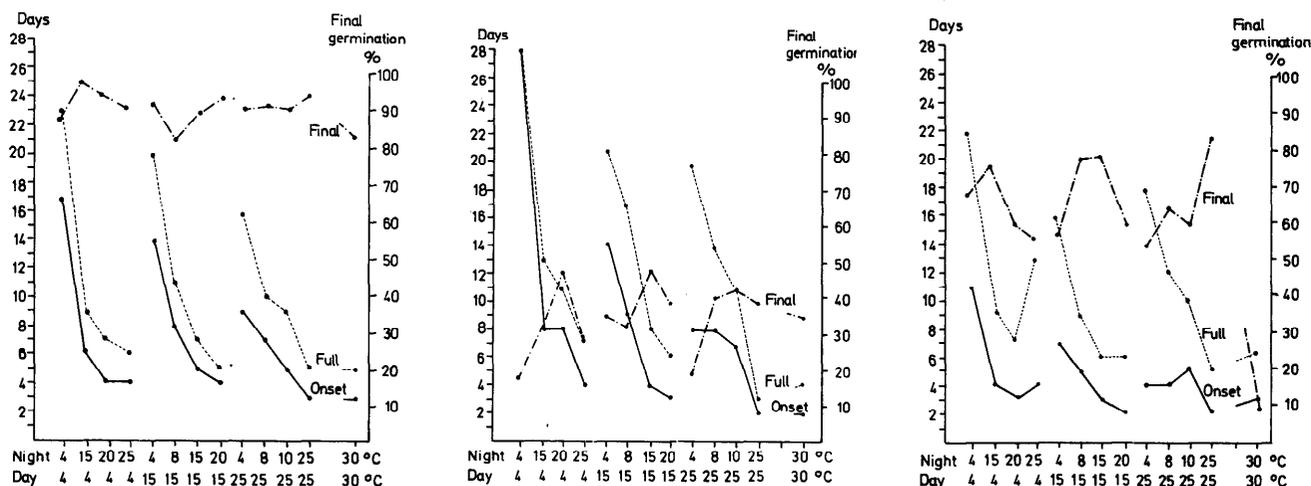


FIG. 3, 4, and 5. Days to onset and to full germination and final germination percentage of *Phalaris bulbosa*, left; *Oryzopsis holciformis*, center; and *Hordeum bulbosum*, right at fixed and alternating temperatures.

alternations having the same day temperature. Almost irrespective of the "day" temperature (4-25 C) severe retardation of germination is caused by the 16-hr night period at 4C and germination is fastest with 25C night period.

The annual grain and legume species—barley, wheat and *Medicago hispida* (Fig. 7-9)—least sensitive to fixed low temperatures were least retarded. *Avena sterilis*, *Medicago truncatula* and *Trifolium purpureum* (Fig. 6, 10 and 11) were somewhat more

delayed and these species thus occupy an intermediate position between the least sensitive crop plants and the cold-sensitive perennial grasses.

The sensitivity of *Hordeum bulbosum* and *Medicago* spp. to high temperatures is less readily apparent. Comparing Fig. 5, 9 and 10 with the others, however, reveals retardation between the 20C and 25C 16-hour thermo-periods (left side of figures) where these alternate with the 4C 8-hour one. The increasing retardation for the 15, 20 (not

shown), and 25C day temperatures when alternated with the 4C night temperature is another indication of the high temperature sensitivity of the *Medicago* spp.

The differential between days to onset and to full germination, i.e. the slope of the cumulative germination curve (not shown), actually measures the uniformity of the seed lot regarding time to germination (Heydecker, 1965). This is comparable to Koller's (1957) "percent per day" concept, and seems to be faster

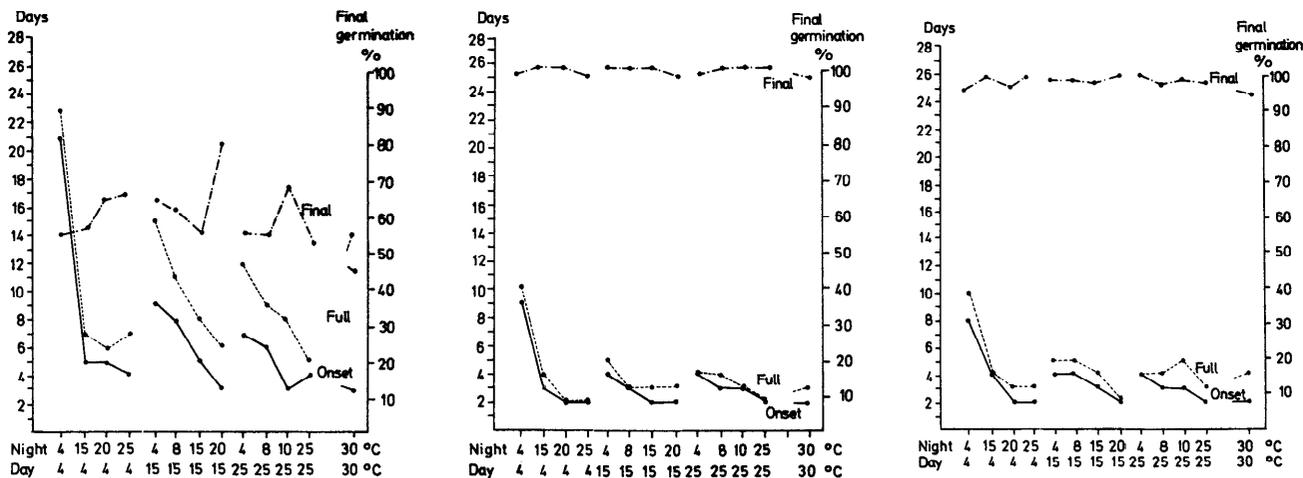


FIG. 6, 7, and 8. Days to onset and to full germination and final germination percentage of *Avena sterilis*, left; Beecher barley, center; and Florence Aurore wheat, right at fixed and alternating temperatures.

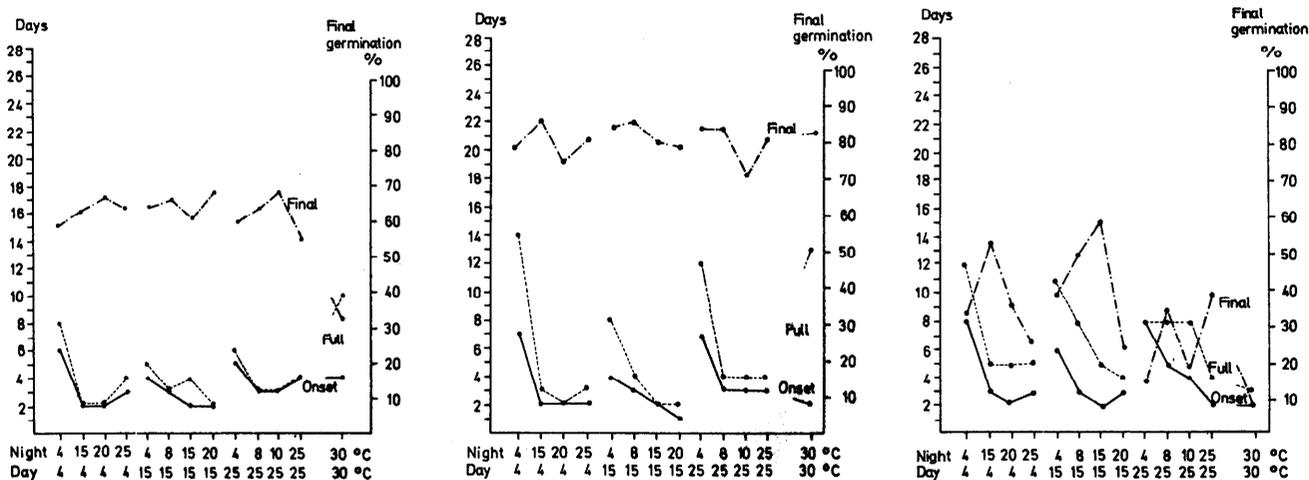


FIG. 9, 10, and 11. Days to onset and to full germination and final germination percentage of *Medicago hispida*, left; *M. truncatula*, center; and *Trifolium purpureum*, right at fixed and alternating temperatures.

in the species less sensitive to one or both temperature extremes (barley, wheat, *Medicago hispida* and *Phalaris*; (Fig. 3, 7, 8 and 9) than in the more sensitive species (*Oryzopsis holciformis* and *Hordeum bulbosum* (Fig. 4 and 5). However, some legumes (Fig. 10 and 11) do not conform with this trend. It is also faster at favourable temperature alternations (troughs) than at unfavorable ones (peaks) although this trend is less definite.

**Final germination percentage.**—Final germination, though not consistently related to tempera-

ture alternations, generally exhibits wider fluctuations in species sensitive to temperature extremes (e.g. *Oryzopsis holciformis*, *Hordeum bulbosum* and *Trifolium purpureum*; Fig. 4, 5 and 11) than in the less sensitive species (e.g. wheat, barley and even *Phalaris*; Fig. 3, 7, 8). Those sensitive only to high or low fixed temperatures occupy an intermediate position (e.g. Fairway wheatgrass or *Medicago truncatula*; Fig. 1 and 10).

#### Discussion

**Response of species to alternating temperatures.**—From the data presented in Fig. 1-11, it is

clear that none of the species studied showed a favorable response to alternating rather than fixed temperatures as regards speed of germination (days to onset and full germination), final germination percentage, or to effect of amplitude between lower and higher temperature. Whereas in the data presented by Harrington (1923) and Morinaga (1926), germination at fixed temperature is much inferior to that at alternating temperature, in the present data the fixed temperatures fit into the overall pattern of germination response. The germination behavior of the

range plants investigated is therefore unlike that of the bluegrasses and other species in that they do not evince any response to alternating temperatures.

*Relation of germination to weighted mean temperature*—Germination does not appear to be a function of the weighted mean temperature (W.M.T.) of each alternation i.e. of hour-degrees. While rising W.M.T. was generally associated with increased speed of germination, the data show no consistent direct relationship between speed of germination at alternating temperatures and W.M.T. The retardation effect of adverse temperatures seemed to be stronger than would follow from their relative influence on the weighted mean of the alternation. The data are consistent with Harrington (1923), Went (1949), Wilsie and Shaw (1954), Wang (1960), and many others, who pointed out the dubious value of strict reliance on mean temperatures or day-degrees in bioclimatic work, especially as regards cyclic temperature fluctuations or alternations. No alternations with 30C and 35C were used in this work, since such temperatures are of less practical interest in the winter sowing season. This may explain why rising weighted mean temperature had, generally, a favorable effect.

*Other points.*—Germination response of the species to alternating temperatures was remarkably consistent with the response of the same species to the two fixed temperatures making up the alternation (Table 1). Unfavorable temperatures in the alternation reduced germination speed, but final or total germination percentage was comparatively unaffected. Adaptation of the species studied to survival in a natural environment is shown by the remarkable lack of effect on total germination of widely differing temperature alterna-

tions within the amplitude encountered in the field during the rainy season. At the same time, the data for alternating temperatures support the conclusion, arrived at in part I (Ellern and Tadmor, 1966), that low temperatures are a major underlying factor in the failure of range seeding operations in the semi-arid winter rainfall environment described, where the speed of germination rather than germination percentage is the critical factor for establishment of pasture plants. The absence of any consistent relationship between the data for germination speed (onset and full germination) and final germination percentage is in agreement with the findings of Hepton (1957), Harrington (1963), Cuddy (1963), and others.

The effect on germination of temperature alternations has here only been analysed qualitatively. Harries (1943) made an interesting study of the rate of acceleration in the time of embryonal development of insect eggs exposed to alternating temperatures, as compared with values calculated from the time required at fixed temperatures; Kotowski (1926) made a similar comparative analysis on the germination of vegetable seeds. Attempts made to subject these data to a comparable quantitative treatment will be reported separately.

#### Summary and Conclusions

Nine species of range plants, with wheat and barley for comparison, were germinated in darkened humidified incubators in petri dishes at seven fixed and 16 alternating temperatures, including most combinations between 4, 8, 10, 15, 20 and 25C liable to be encountered in seedbeds in the semi-arid south of Israel during the winter sowing season.

In none of the species was there a more favorable germination response to alternating than

to fixed temperatures. The application of alternating temperatures is therefore not a requirement in studying the temperature dependence of germination in these species.

While rising weighted mean temperature (hour degrees) was generally associated with increased speed of germination and, less consistently, with increased germination percentage, germination behavior at alternating temperatures seemed to be related to the separate effects of the two component temperatures and the time of exposure to each, rather than to be a direct response to hour-degrees such as W.M.T.

The results support conclusions reached in the first part of the work regarding low seedbed temperatures as a major factor in the failure of range seeding in semi-arid areas.

#### Acknowledgements

Grateful acknowledgement is made to Miss Ruth Hofbauer for her help in the laboratory; also to Dr. W. Heydecker, of the University of Nottingham School of Agriculture, for commenting on the manuscript.

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