Wheat Special Report No. 22

Vernalization Requirement and Response to Day Length in Guiding Development in Wheat

Peter Stefany

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Preface

This Wheat Special Report deals with wheat flowering, a central issue to any crop improvement activity. Among the factors affecting environmental fitness, flowering time is overriding and tightly linked to many other physiological responses.

The paper analyzes the response of a diverse set of genotypes to vernalization and daylength. An effort is made to separate these two major genotypic responses such that our understanding of the flowering of wheat can be improved. We hope that eventually the manipulation in size and timing of the sink (spike) could lead to increased yields.

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Abstract

Vernalization requirement and response to day length are the major factors controlling development in wheat (*Triticum aesitvum* L.). This study was to determine how they integrate in the field in Obregon, Sonora, Mexico to result in development phenotype. In addition to a natural day-length treatment, day length was shortened in a second treatment by covering the crop from 0.5 h before twilight until 1.0 h past sunrise, extended in a third treatment by illumination from 0.5 h before until 3.0 h after sunset for the entire season, and extended by the same amount in a fourth treatment beginning 47 days after planting. Development of one facultative, one winter, six spring cultivars, and ten F_3-derived F_5 lines from the spring-spring cross Pfau/Weaver was followed by dissection of plants every two days. In addition to the nonvernalized treatment, cultivars were also subjected to six weeks of vernalization in darkness at 6°C prior to planting in the field. Beginning two days after germination in the field, the spring, facultative, and winter cultivars Oasis, TAM 200, and Centurk/Veery 5, respectively, were also moved to a cold chamber and subjected to 6°C and day lengths simulating those outdoors for three weeks before being returned to the field. After germination, all entries were insensitive to day length. During this phase, development was vegetative and no progress was made towards flowering. Without vernalization, this juvenile phase was 68 and 40 d long in winter and facultative cultivars, respectively, and ranged from between 20 and 33 d in spring genotypes. The subsequent day length sensitive phase was always associated with the shift from vegetative to reproductive development. All cultivars, when vernalized for six weeks and subsequently transplanted to the field on the same day when nonvernalized plants received their initial irrigation, shifted from vegetative to reproductive development earlier than their nonvernalized counterparts. A vernalization treatment after normal germination in the field, either extended or did not effect the duration of the juvenile phase. After the juvenile phase, all entries developed more quickly towards flowering the longer the day. Whenever an entry had initiated the spike, spikelet, or floret prior to day 47, when the second extended day-length treatment was imposed, the development of the respective organ was not influenced. The later flowering of winter and facultative than that of spring wheats is due largely to their long juvenile phases. Vernalizing temperatures do not shorten the juvenile phase through a response to cold per se, but rather by allowing part of it to be transgressed during a time of minimal growth. After the juvenile phase, all genotypes move into the reproductive phase with a concomitant response to day length. They do not vary in being either sensitive or insensitive to day length, but rather in the rate of development towards flowering which any given length of day provokes. Response to day length determined the duration of spikelet initiation and how quickly each spikelet progressed towards flowering.

Introduction

Wheat is grown around the world in environments which vary widely in amount and seasonal distribution of rainfall, as well as temperatures and temperature ranges experienced during the growing season (28). Adaptation is often dependent on the crop reaching anthesis at an optimum time with respect to environmental limitations such as terminal drought (32), late season rainfall (28), or extreme heat during spike development (15). Development before anthesis is often of adaptive significance as well. Rapid development after germination can result in damage from late frost (19, 24). A long rapid spike growth phase prior to anthesis may increase yield potential through greater radiation input (8, 10). Vernalization requirement and response to day length are the two major mechanisms through which development rate in wheat is controlled (5, 17, 18, 23, 36). In attempting to improve adaptation and performance of wheat genotypes, it would be advantageous to understand how the genes for each of these response contribute to guiding development. However, complex interactions between these two responses often make it difficult to separate their effects (11, 36). With this study, I hope to gain insight into the way in which vernalization requirement and response to day length interact in the field to result in development phenotype. This may, in conjunction with yield trials, provide some clues as to which, if any, combination of expression of these two responses contributes to higher yield potential in the Yaqui Valley. Furthermore, if the effects of these two responses could be clearly separated, further progress may also be made towards understanding the genetics of vernalization and day length response. Although much is known about the location of loci controlling both responses, information about the mechanisms of inheritance, especially in the case of day length response, is still vague (1, 11, 16, 21, 26, 30, 33, 34). Only if vernalization requirement and day-length response can be separated can sound interpretations about the genetics governing each trait be made from populations segregating for anthesis date. On a more applied level, if genotype for each response could be readily identified, it may be that germplasm could be classified for developmental adaptation to specific environments based on genes or gene combinations for vernalization and day-length response.

Materials and Methods

Trial layout.

This trial was planted in the field in Obregon, Sonora (27°22' N lat) in northern Mexico on 12 December 1992. Prevernalized plants (see below) were moved to the field on the same day and an irrigation of approximately 70mm given the whole trial. Germination of nonvernalized seed was on 13 December 1992. Subsequent irrigations of approximately 90 mm were given on 20 January, 6 April, and 16 April, when soil moisture was depleted by 50%. The area had been fertilized with 150 kg N and 46 kg P_2O_5 ha^{-1} before planting.

The trial was planted in six flood irrigation basins (melgas) measuring 15 x 17 m each. The basins were in a line from north to south, bordering each other on the 15 m side. Each of four of these basins were subjected to a unique day-length treatment (see below). The remaining two basins were planted as border and acted as a buffer on either side of day-length treatments requiring lighting. In each basin subjected to a day-length treatment, each entry was planted in a 1.5 m row in each of two replications in a randomized complete block design. Rows were 0.2 m apart. Planting density was 300 seeds m^{-2}, except in prevernalized rows, where planting density was 333 seeds m^{-2}. In each basin, the area not planted with experimental material was planted to border.

Entries.

One facultative, one winter, and six spring cultivars, as well as ten lines from the spring-spring cross Pfau/Weaver were used in the trial (Table 1). In the lines, single plants were harvested in the F_3. They were bulked through to the F_5 used in the trials.

Day-length treatments.

In the northern most basin, day length was not altered (0h treatment). In this, as well as the extended day-length treatments (basins four and six, below) the 6.2 x 3.5 m area planted to the trial entries was centered in the 15 x 17 m basin. In the second basin from the north, the rows planted to experimental material were covered from 0.5 h before dawn until 1.0 h after sunrise to shorten the day (-1h treatment). At dawn the soil holds no heat which could be reradiated and trapped under the cover as it would at dusk. Dawn was defined as the time of day when the sun was 6° below the horizon, when radiation becomes photoperiod effective (13, 37). At Obregon, this occurs between 27 and 31 min before sunrise, depending on the time of year (calculated using *Astre* program of the French Meteorological Service). Black polyethylene sheeting was drawn back and forth over the experimental rows between two ridged end walls at the appropriate times of day by an

Table 1. Wheat genotypes used in the study.

Cultivar	Abr.	Origin	Adaptation	Growth habit
Centurk/Veery 5	C/V	CIMMYT	Mexico	Winter
TAM 200	TAM	Texas A&M	Texas	Facultative
Weaver	Wev	CIMMYT	Mexico	Spring
Seri	Ser	CIMMYT	Mexico	Spring
Rayon	Ray	CIMMYT	Mexico	Spring
Super Kauz	SKz	CIMMYT	Mexico	Spring
Oasis	Oas	CIMMYT	Mexico	Spring
Las Rosas	LRs	Argentina	Argentina	Spring
P/W 95	95	CIMMYT	Unselected†	Spring
P/W 424	424	CIMMYT	Unselected†	Spring
P/W 554	554	CIMMYT	Unselected†	Spring
P/W 891	891	CIMMYT	Unselected†	Spring
P/W 1249	1249	CIMMYT	Unselected†	Spring
P/W 1278	1278	CIMMYT	Unselected†	Spring
P/W 1325	1325	CIMMYT	Unselected†	Spring
P/W 1436	1436	CIMMYT	Unselected†	Spring
P/W 1611	1611	CIMMYT	Unselected†	Spring
P/W 1892	1892	CIMMYT	Unselected†	Spring

† These lines were selected as having diverse flowering dates and similar heights, but not for adaptation to any particular environment.

electric motor controlled by an automatic timer. Due to size constraints, two such "light-out shelters" were used, one for each replication. The shelters were centered in the basin, but offset rather than next to each other to prevent mutual shading. Whenever the shelters were closed, an electric fan in one of the ridged end walls of each shelter would pull air through an intake in the opposite wall to further reduce the chance of heat buildup under the cover. The hole of the air intake as well as the hole for the fan were covered with a black box opening to the inside and the outside of the shelter but containing a series of internal baffles which blocked the passage of light but allowed the flow of air. Soil and air temperatures outside and inside the shelters were measured just as the covers opened several times during the season and were never found to be significantly different from each other. The third basin was border only. In the fourth basin, the area planted to the trial entries was illuminated from 0.5 h before sunset to 3.0 h past sunset from day 47 until physiological maturity ($+3h_{47}$ treatment) by ten 300 W halogen lamps installed 2 m above the soil surface. The lamps were angled down so that the surface of the cover glass was at about a 45° angle to the surface of the soil. Five lamps flanked each of the 6.2 m sides of the experimental area. The bottoms of the lamp posts were 0.5 m from this border and spaced on 1.25 m from each other. Light intensity was 6 and 11 μmol m^{-2} s^{-1} at 0 and 40 cm above the soil surface, respectively. The lamps were turned on and off by automatic timer. To prevent heating of the trial by the lamps, the original cover glasses were replaced by double pane glass between which water was circulated to dissipate the heat. Soil and air temperatures outside and inside the illuminated area were measured just before the lights were extinguished several times during the season and were never found to be significantly different from each other. The fifth basin was border only. In the sixth, southern-most basin, days were lengthened as in the fourth basin, but the treatment was imposed from the day before the initial irrigation until physiological maturity (+3h treatment).

Vernalization treatments.

Three different vernalization treatments were imposed. In the first treatment, plants were not vernalized. In the second, prevernalized treatment, plants were germinated in and stored at 6°C and complete darkness for six weeks. To make subsequent planting in rows easier, seeds for this treatment were glued to strips of paper towel in a straight line spaced at 1.5 cm with *Artwork Spray Repositionable Mounting Adhesive* (Mecanorma Co., France). The towels were folded along the same line, the strip covered with plastic along its length, and rolled up. The roles were placed in plastic cups, thoroughly wetted, and subjected to vernalization as described. In the third, postvernalized treatment, seeds were planted in the field exactly as in the nonvernalized treatment. However, a 1.5 m length of 6 cm diameter PVC pipe, which had been cut in half along its length, was buried just below the soil surface along the length of the rows which were to be postvernalized. Two days after the initial irrigation, the pipes, along with soil and germinated seeds, were removed from the field and placed in a cold room at 6°C. Illumination of the cold room by 75 W fluorescent tubes, providing a light intensity of 120 μmol m^{-2} s^{-1} at the soil surface, was set to match the length of the day, including twilight, outdoors. After three weeks, these rows were returned to the

field by sliding the soil with plants from the pipes back into the divots left by their removal. Within each replication, entries and vernalization treatments were randomized. Only cultivars were prevernalized. Only Oasis, TAM 200, and Centurk/Veery 5 were postvernalized.

Tracking development.

Beginning 9 days after germination, two plants from each row were dissected every Monday, Wednesday, and Friday, and stage of development of the apex determined. Stage of the two plants was averaged to one value for that row on any given day. Development stages were assigned the numerical values as listed in Table 2.

To determine the number of spikelets initiated, the number of rachis nodes of four main stem spikes per row was counted at the end of the season. The four numbers were averaged to give one value for the row.

Analysis.

An analysis of variance for development stage on each dissection day and number of spikelets initiated was performed separately for each day-length treatment. Day length was considered to be influencing the development of any one entry, within a vernalization treatment, when development stage differed significantly from that in the next shortest day length, e.g. the day on which the development stage in +3h treatment was significantly different from that in the 0h treatment (Fig. 1).

Table 2. Stages of apical development.

Stage	Associated morphology	Photograph in literature
1 ↓ 30	Number of primordia initiated. Emerged leaves are also counted. Spikelet primordia (double ridges) not yet perceptible.	Kirby (20), Figs. 5.16 & 5.17, Gardner (12), Figs. 1 to 4, Nerson (27), Figs. A to D.
31	Spikelet primordium first perceptible as **double ridges**. The most advanced spikelet primordium (also referred to in stages 32 to 38) forms a ridge as yet smaller than that of the degenerating leaf primordium immediately below it.	None. However, see bottom spikelets in Kirby Fig. 5.18, and Gardner Fig. 6.
32	The spikelet primordium forms a ridge the same size as that of the leaf primordium immediately below it.	Kirby, Fig. 5.18.
33	Spikelet primordium extrudes just beyond the leaf primordium.	Gardner, Fig. 6, Nerson, Fig. F.
34	The most advanced spikelet primordia are swollen so that leaf primordia are just barely still visible between them.	Nerson, Fig. G.
35	The most advanced spikelet primordia are swollen so that adjacent primordia touch each other.	Nerson, Figs. H to K.
36	**Glume primordia** perceptible as a single ridge on each side of the base of the spikelet.	Kirby, Figs. 5.20 & 5.21, Gardner, Figs 7 & 8.
37	**Lemma primordia** perceptible as multiple ridges on the sides of the spikelet.	Kirby, Figs. 5.22 & 5.23, Gardner, Figs. 9 & 10.
38	Viewing the spike so that the symmetrical plane of the spikelets is best seen, the initiation of **floret primordia** at angles to the left and right of the spike axis, alternately among subsequent spikelets, is perceptible.	Kirby, Figs. 5.24 & 5.25, Gardner, Fig. 12, Nerson, Figs. M & O.
39	Initiation of the last **(terminal) spikelet** at the top of the spike on a plane of symmetry at a right angle to those of previous spikelets is perceptible.	Kirby, Fig. 5.26 & 5.27, Gardner, Fig.15, Nerson Fig.R,
40	Two floret primordia perceptible on terminal spikelet.	Kirby, Fig. 5.26.

Table 2. (continued)

Stage	Associated morphology	Photograph in literature
41	Three floret primordia perceptible on terminal spikelet.	None.
42	Four floret primordia perceptible on terminal spikelet.	Kirby, Fig. 5.28.
43	Five floret primordia perceptible on terminal spikelet.	Gardner, Fig. 18.
44	Six floret primordia perceptible on terminal spikelet.	None.
45	In the most advanced floret of the terminal spikelet (also referred to in stages 46 to 54) the stamens and carpel reach to the same height.	Esau (7), Plate 93A†.
46	Stamens extend beyond the top of the carpel. Horn-like precursors to styles not elongated.	Kirby, Fig. 7.1.
47	Stamen filaments are first perceptible but not extended. Styles not elongated.	None
48	Stamen filaments elongate. Styles begin to elongate. Tips of styles are now sharply pointed rather than rounded.	Briggle (4), Fig. 14F†. Kirby, Fig. 7.10.
49	Styles are slightly pubescent on their inner surface. Ovary begins to swell.	Kirby, Fig. 7.11.
50	Pubescence on styles begins to elongate. Ovary pubescent.	None
51	Styles hairy, elongated, thread-like at tip. Ovary hairy.	None
52	Styles thread-like along entire length.	None
53	Stigmas feathery, anthesis imminent.	Kirby, Fig. 7.16.
54	**Anthesis**. Pollen grains stick to stigmas.	None

† The photographs in the cited texts have been reprinted from Bonnett (2,3).

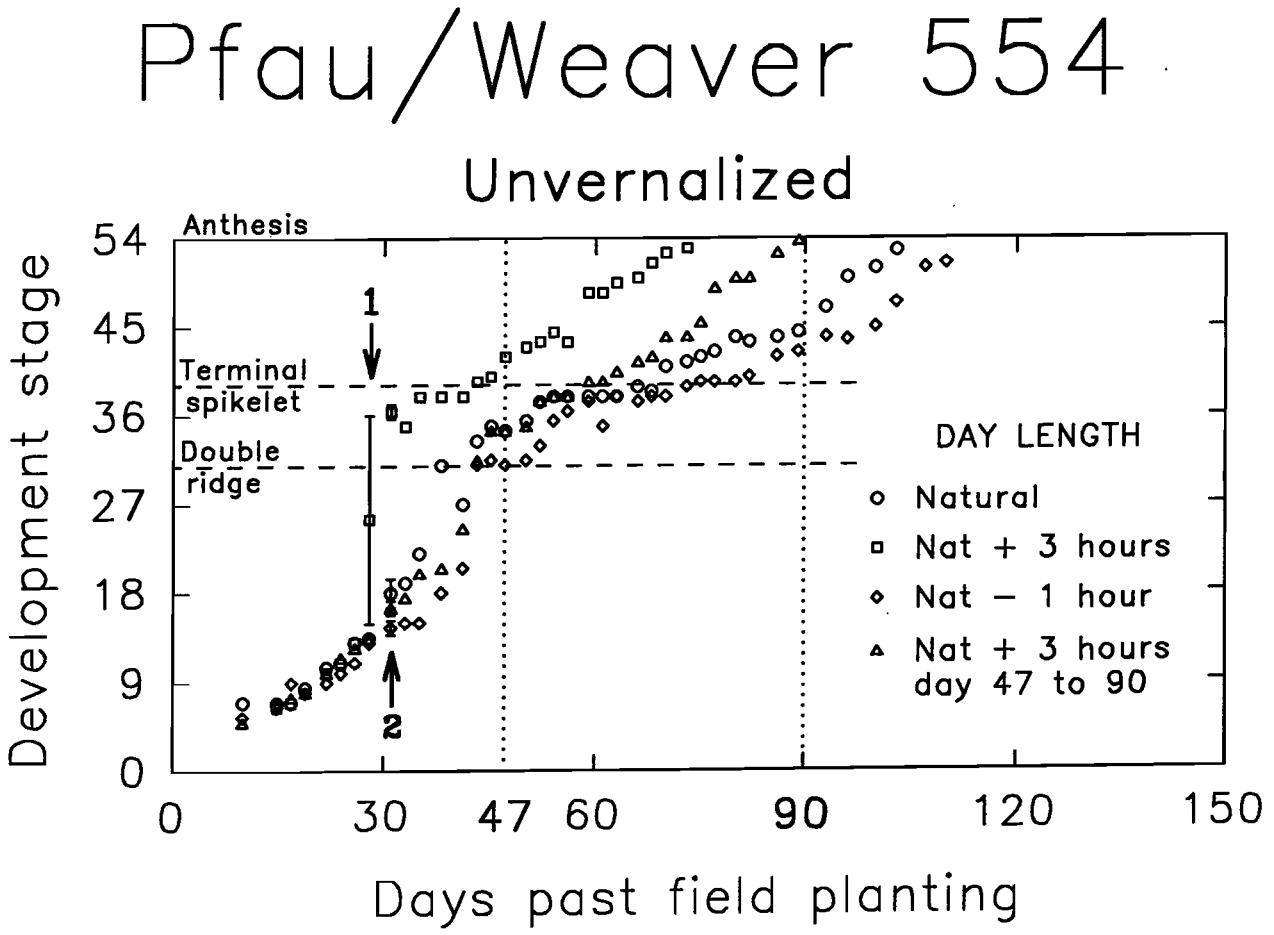

Fig. 1. Development of P/W554 at four day lengths. Arrow 1 marks the day on which development in the +3h treatment (□) became significantly faster than in the 0h treatment (○). Arrow 2 marks the day on which development in the 0h and $+3h_{47}$ (△) treatments became significantly faster than in the -1h treatment (◇).

Results

Day-length insensitive phase.

After germination, all entries passed through a period during which development was the same in all day-length treatments. To determine if any one day-length treatment was accelerating the development of an entry, its development stage on each dissection day was compared to that in the next shortest day-length treatment (Fig. 1). Across entries, the days on which development between the +3h and 0h, between the 0h and -1h, and between the $+3h_{47}$ (which was identical to the 0h treatment until day 47) and -1h treatments diverged did not differ significantly from each other (Table 3). The three days of divergence were therefore averaged to give one estimate of the duration of the day-length insensitive phase for each genotype (Figs. 2 and 3). The duration of that period varied among genotypes. Without vernalization, it was 65 and 40 d long for the winter wheat Centurk/Veery 5 and the facultative wheat TAM 200, respectively. Among spring wheats, it varied significantly from between 21 and 32 d. After a six week vernalization, the period of insensitivity to day length in the field was shorter for all cultivars, although not significantly for Las Rosas. Prevernalization did not shorten the period of day-length insensitivity to the same degree for all cultivars. Three weeks of vernalization after germination in the field prolonged the duration of the day-length insensitive phase of Oasis by 17 d, but did not significantly effect its duration in TAM 200 and Centurk/Veery 5.

Day-length sensitive phase.

Influence of day length.

All entries in all vernalization treatments responded to differences in day length among the +3h, 0h, and -1h treatments before double ridge (Figs. 4 and 5). With the exception of unvernalized and postvernalized Centurk/Veery 5 in the 0h treatment, development was always faster the longer the day. Ranking among entries in days to double ridge varied among day-length treatments.

Influence of a delayed increase in day length.

There were generally three types of response to a 3 h increase in day length after day 47. In those entries which initiated the terminal spikelet before the lights in the $+3h_{47}$ treatment were turned on, the terminal spikelet flowered on the same day in the 0h and $+3h_{47}$ treatments (Fig. 6). In entries which initiated the terminal spikelet after the lights in the $+3h_{47}$ treatment were turned on, did not respond to day length before the floret primordia stage, but the first floret of the terminal spikelet flowered significantly earlier in the $+3h_{47}$ than in the 0h treatment (Fig. 6). Entries whose day-length insensitive phase extended past day 47 reached double ridge, terminal spikelet, and anthesis sooner in the $+3h_{47}$ than in the 0h treatment (Fig. 7).

Table 3. Day after planting on which development first differed significantly among three pairs of day-length treaments.

Entry	Day-length treatments compared		
	+3h/0h	0h/-1h	+3Dh/-1h
Unvernalized			
Centurk/Veery 5	66	61	67
TAM 200	43	35	41
Weaver	26	28	31
Seri	24	26	24
Rayon	24	26	24
Super Kauz	22	24	24
Las Rosas	19	24	22
Oasis	17	22	22
P/W 891	31	33	33
P/W 554	28	31	31
P/W 424	33	31	24
P/W 1892	31	24	24
P/W 1249	28	24	24
P/W 1325	24	24	24
P/W 1436	26	22	24
P/W 1278	22	22	24
P/W 95	22	22	24
P/W 1611	22	22	24
Mean	28	28	28
Significant treatment differences		P>0.45	

Entry	Day-length treatments compared		
	+3h/0h	0h/-1h	+3Dh/-1h
Prevernalized			
Centurk/Veery 5	28	22	24
TAM 200	19	15	15
Weaver	19	17	17
Seri	14	17	15
Rayon	9	14	17
Super Kauz	15	10	10
Las Rosas	24	17	17
Oasis	14	14	17
Mean	18	16	17
Significant treatment differences		P>0.64	
Postvernalized			
Centurk/Veery 5	63	56	65
TAM 200	38	38	47
Oasis	41	31	38
	47	42	50
		P>0.08	

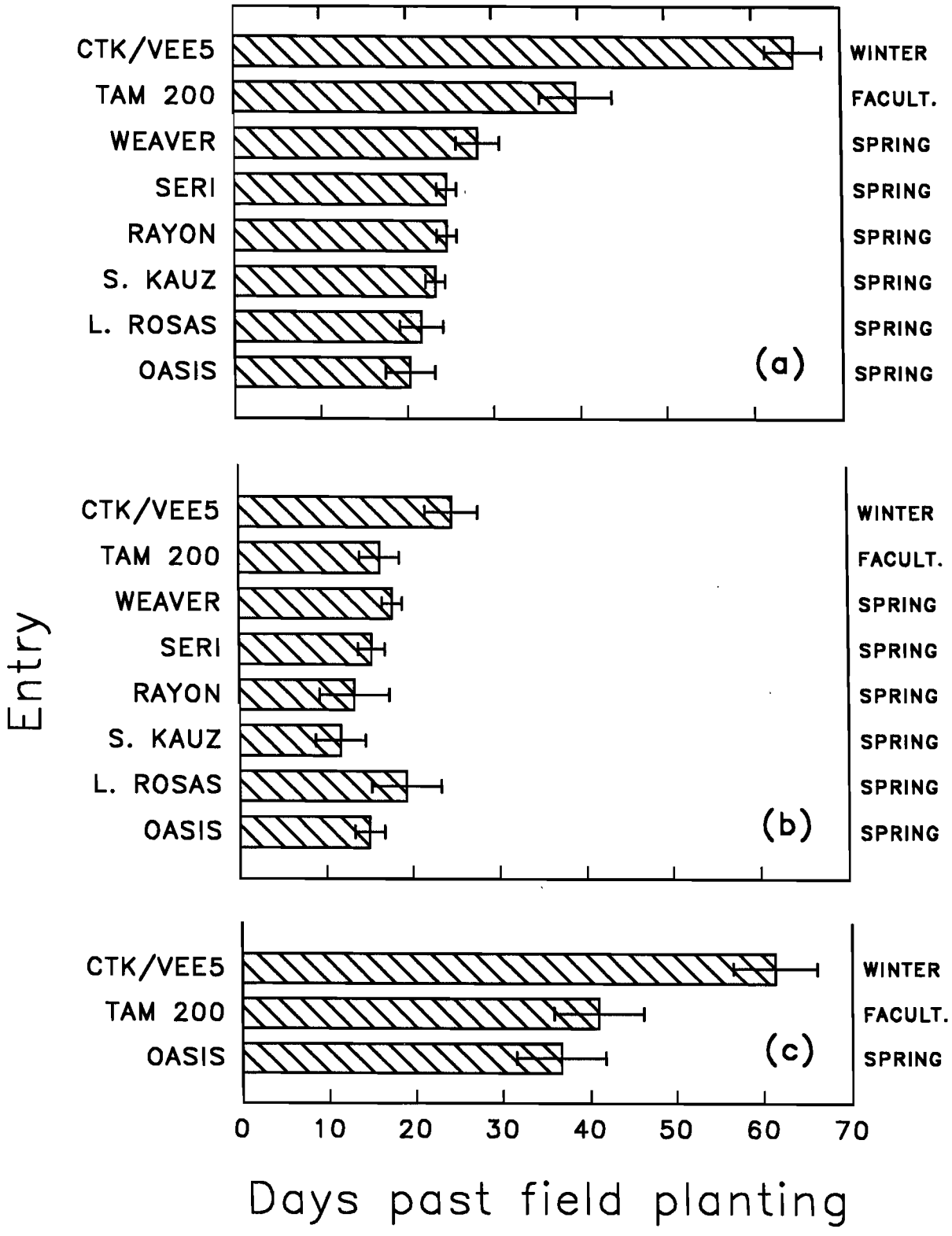

Fig. 2. Number of days until first response to day length when cultivars were unvernalized (a), prevernalized (b), and postvernalized (c).

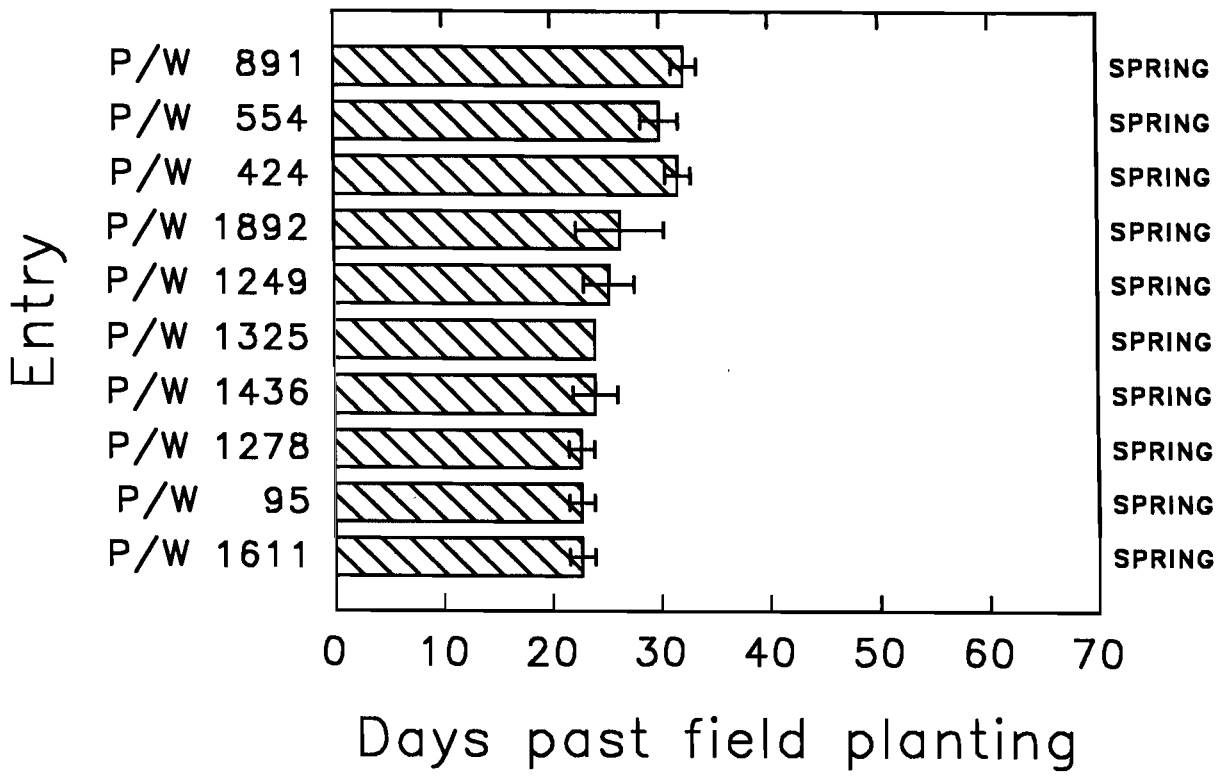

Fig. 3. Number of days until first response to day length among lines from the cross Pfau/Weaver.

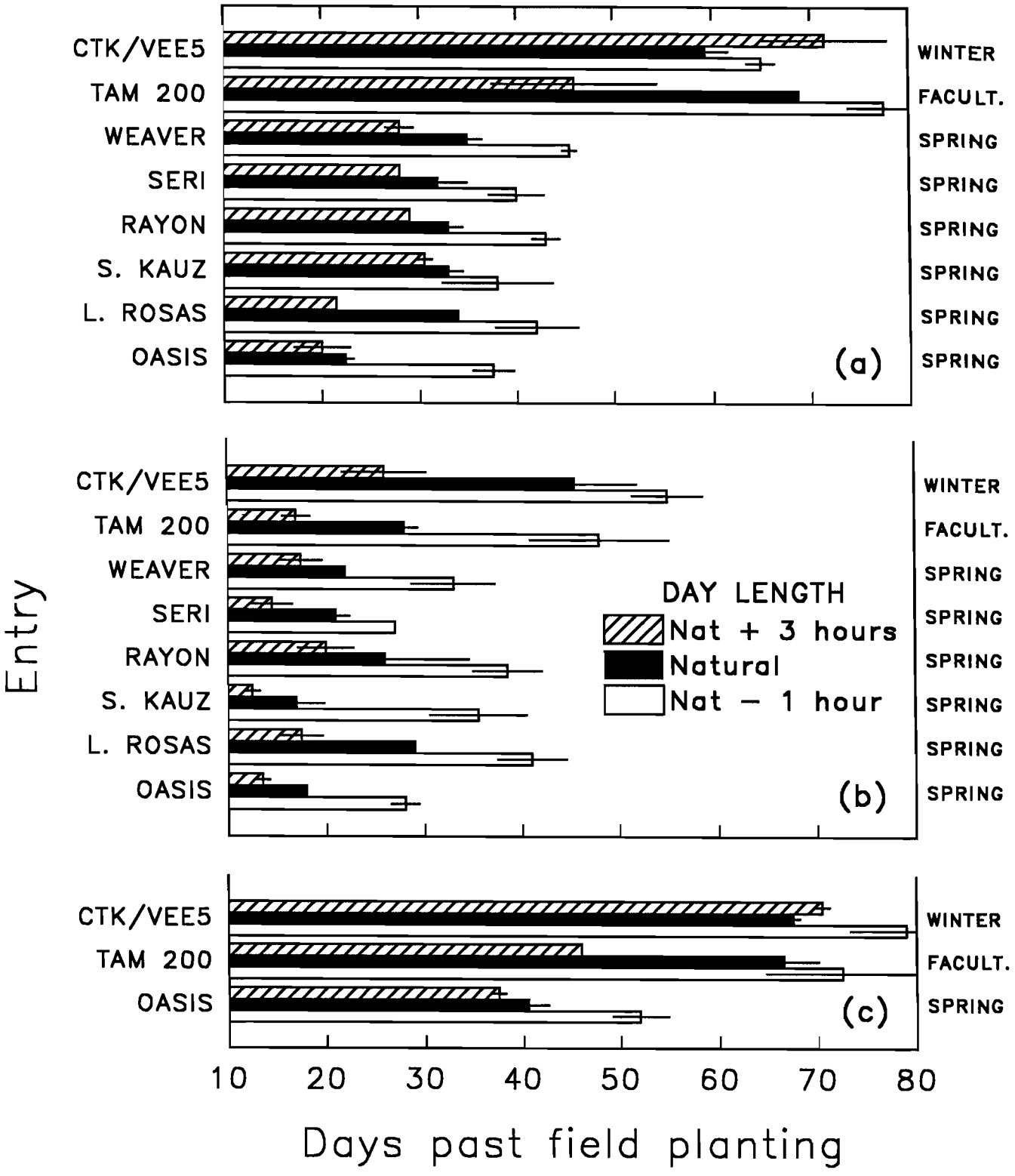

Fig. 4. Days to double ridge of cultivars at three day lengths when they were unvernalized (a), prevernalized (b), and postvernalized (c).

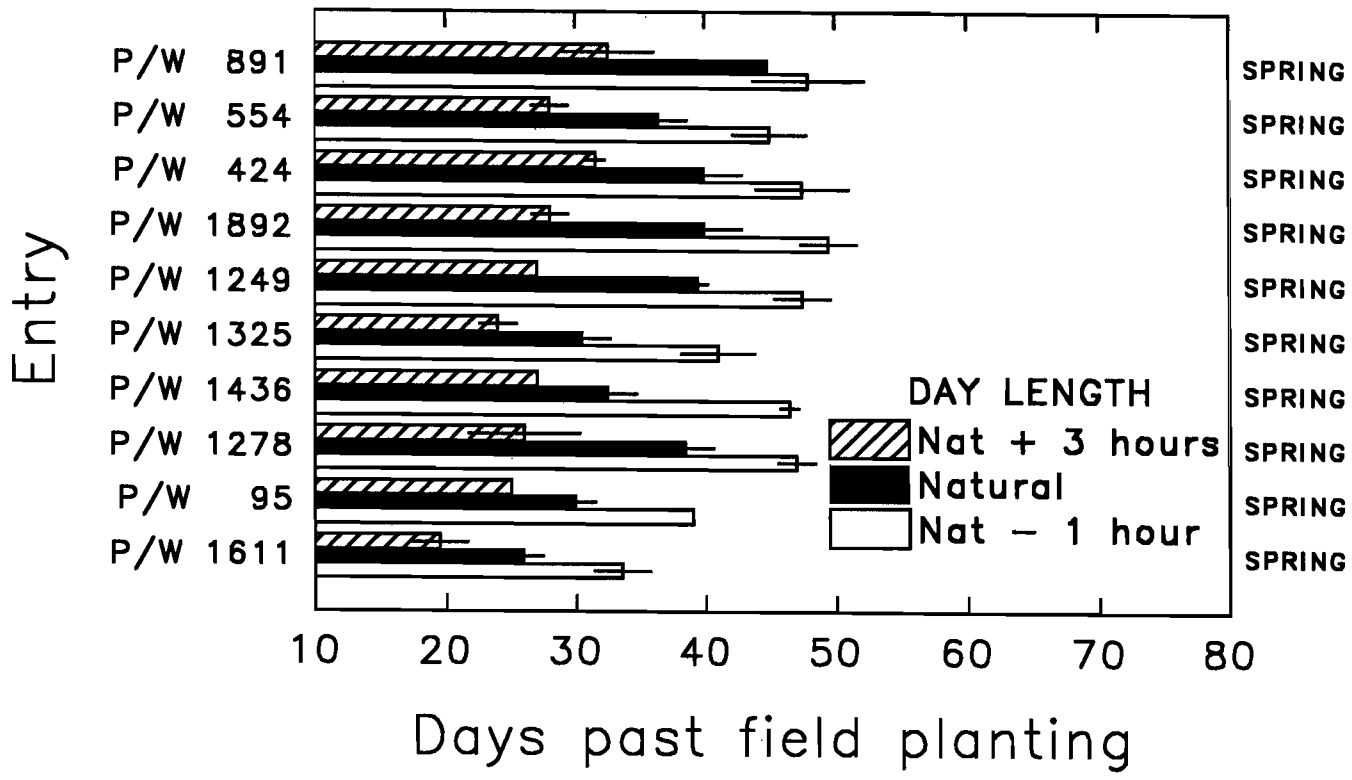

Fig. 5. Days to double ridge of lines from the cross Pfau/Weaver at three day lengths.

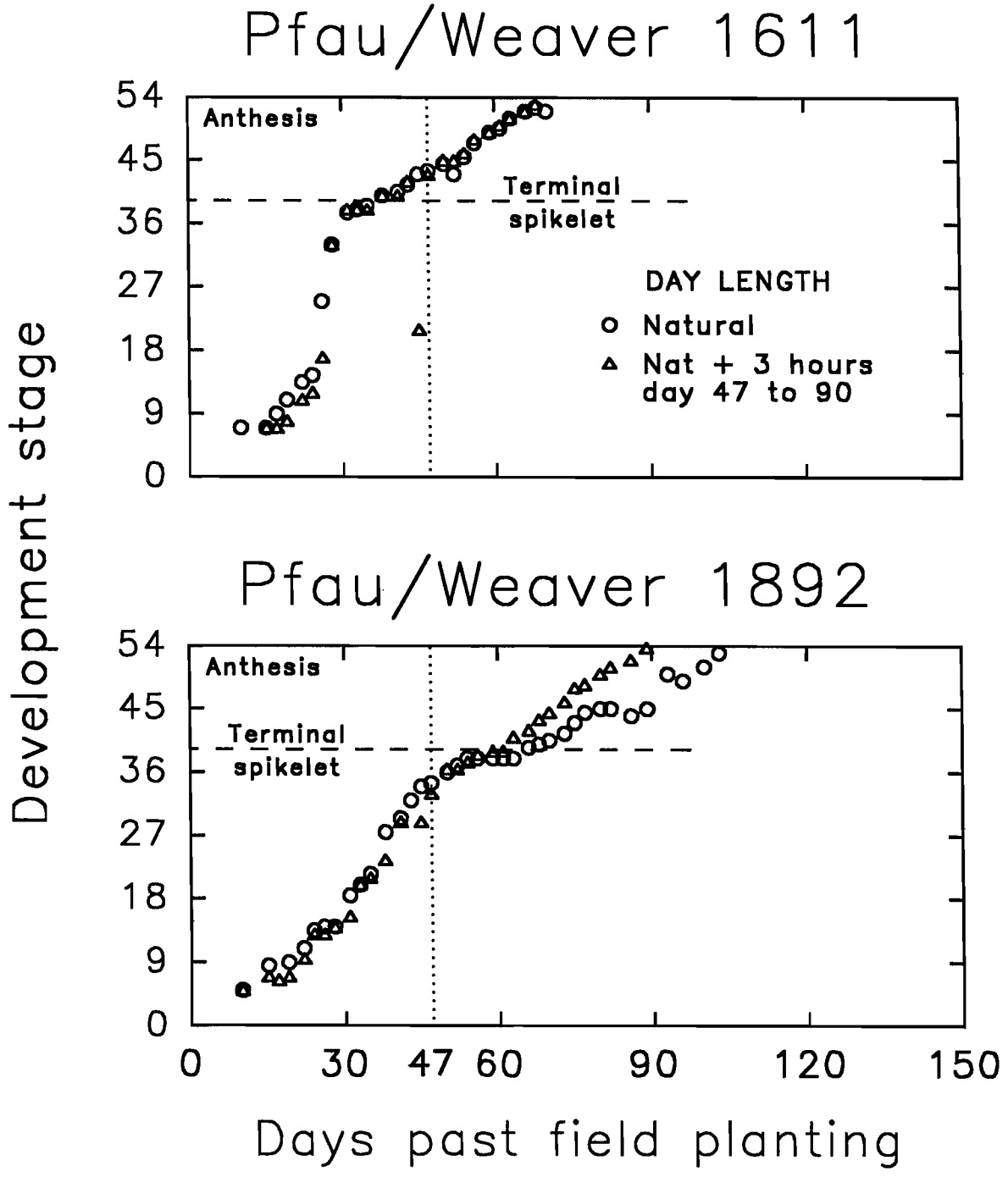

Fig. 6. Two types of response in development of the terminal spikelet to a 3 h extension of the day beginning 47 d after planting.

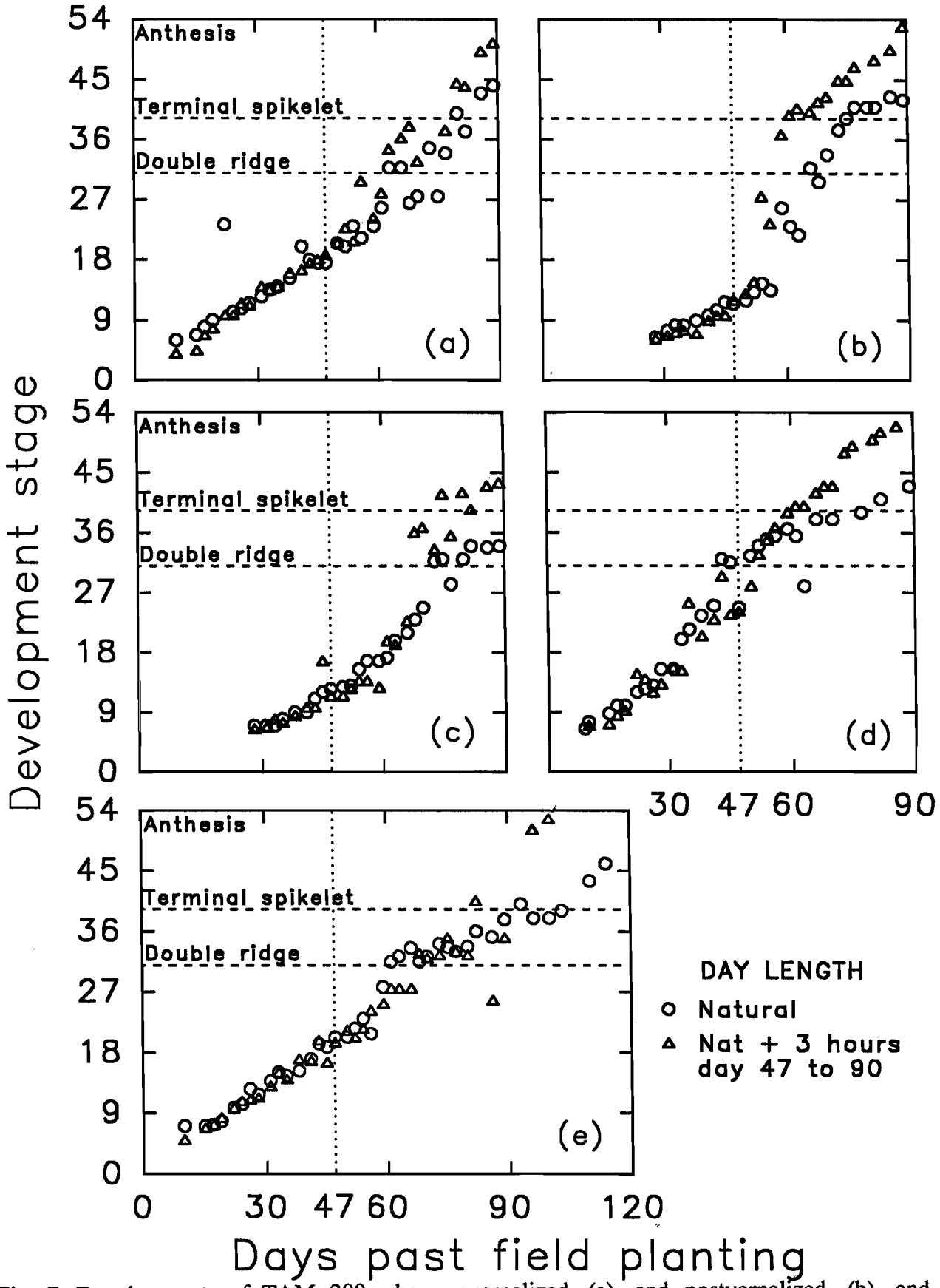

Fig. 7. Development of TAM 200 when unvernalized (a), and postvernalized (b), and Centurk/Veery 5 when postvernalized (c), prevernalized (d), and unvernalized (e) when days were lengthened by 0 and 3 h beginning 47 days after planting.

Physiological aspects.

Development patterns.

Varying combinations of vernalization requirement and response to day length generated a great variety of development patterns (Figs. 8 and 9). Variability among entries in flowering date was less in the +3h than in the 0h treatment.

Morphology.

The number of spikelets initiated was related to the number of days from first response to day length until terminal spikelet under natural but not under extended day lengths (Fig. 10). Variability in spikelet number among entries was similar at both day lengths, but variability in the duration of spikelet initiation was considerably lower under long days.

Genetic aspects

The day-length insensitive phases of lines from the cross Pfau/Weaver were generally of the same duration as one of the two parents (Fig. 11). Those of P/W891, P/W554, and P/W424 were slightly longer than that of Weaver, but not significantly. The duration of the day-length sensitive phase can not be compared between entries with day-length insensitive phases of different durations. Their respective first responses were on different days and therefore to different day lengths. However, among entries which first responded to day length on the same day, there was a great deal of variation in the rate development towards flowering. In the +3h treatment, differences in the duration of the day-length insensitive phase and differences in day-length response were often masked by the time anthesis was reached (Figs. 8 and 9).

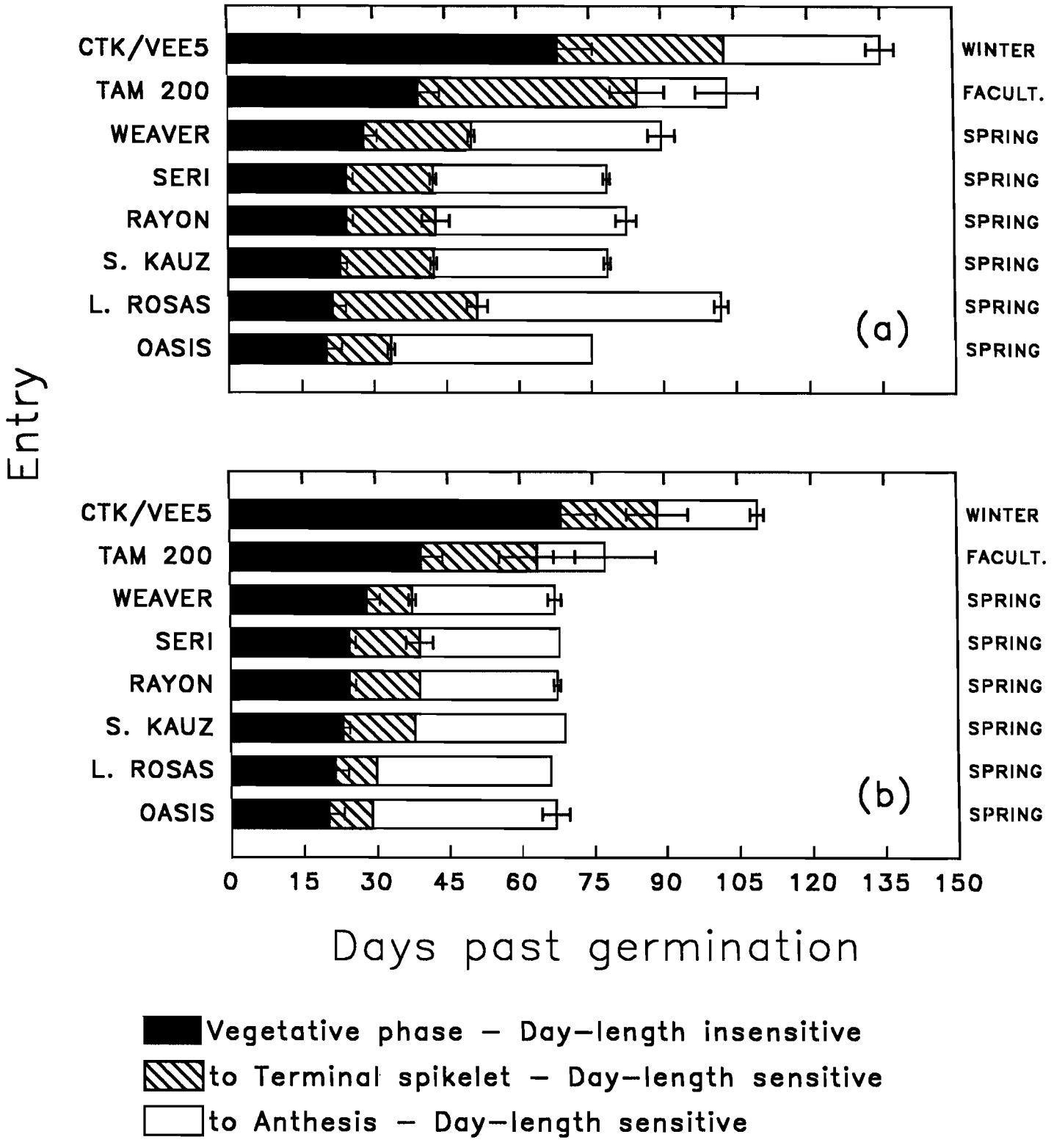

Fig. 8. Development of unvernalized cultivars when days were extended by 0 (a) and 3 h (b).

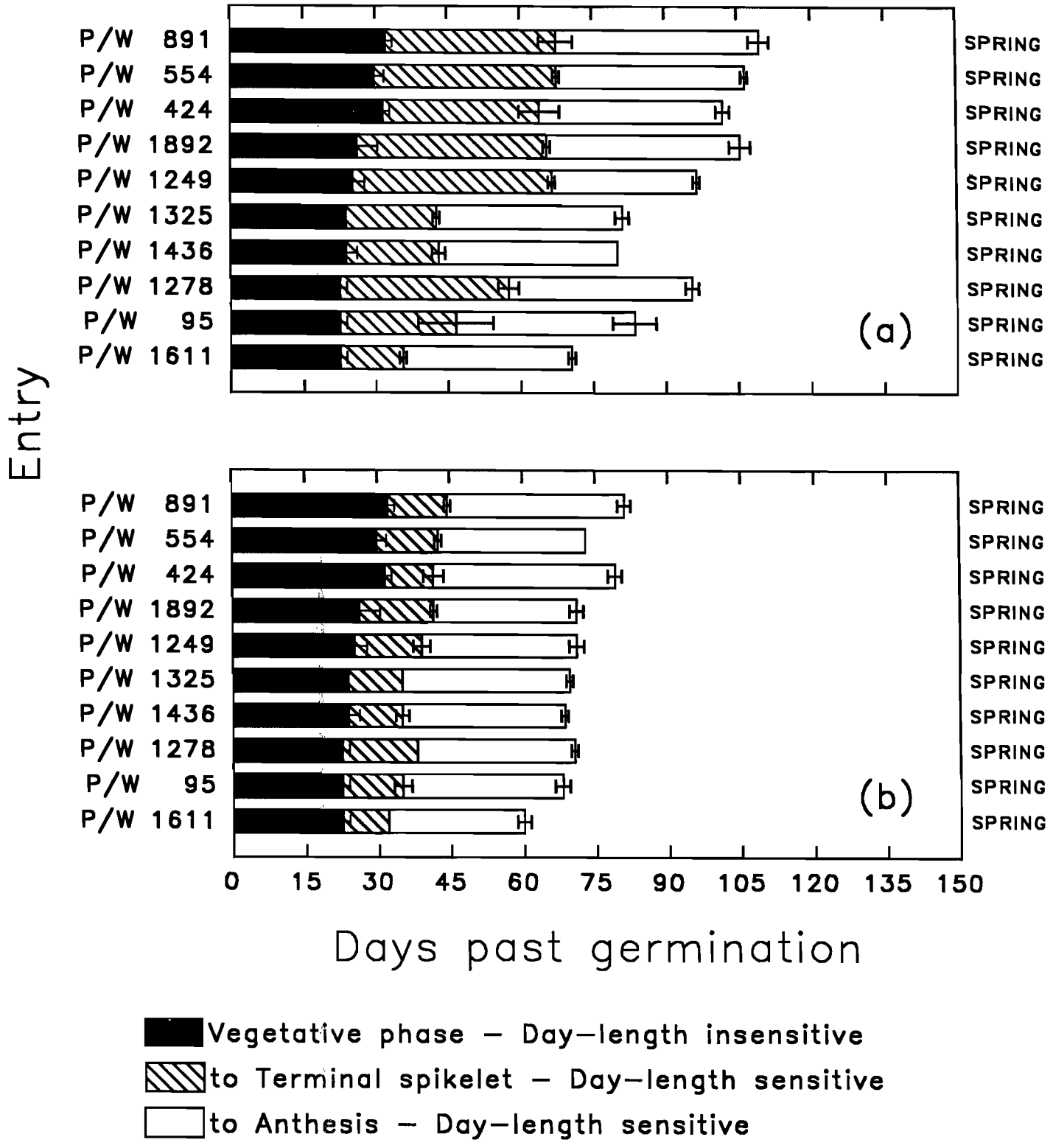

Fig. 9. Development of lines from the cross Pfau/Weaver when days were extended by 0 (a) and 3 h (b).

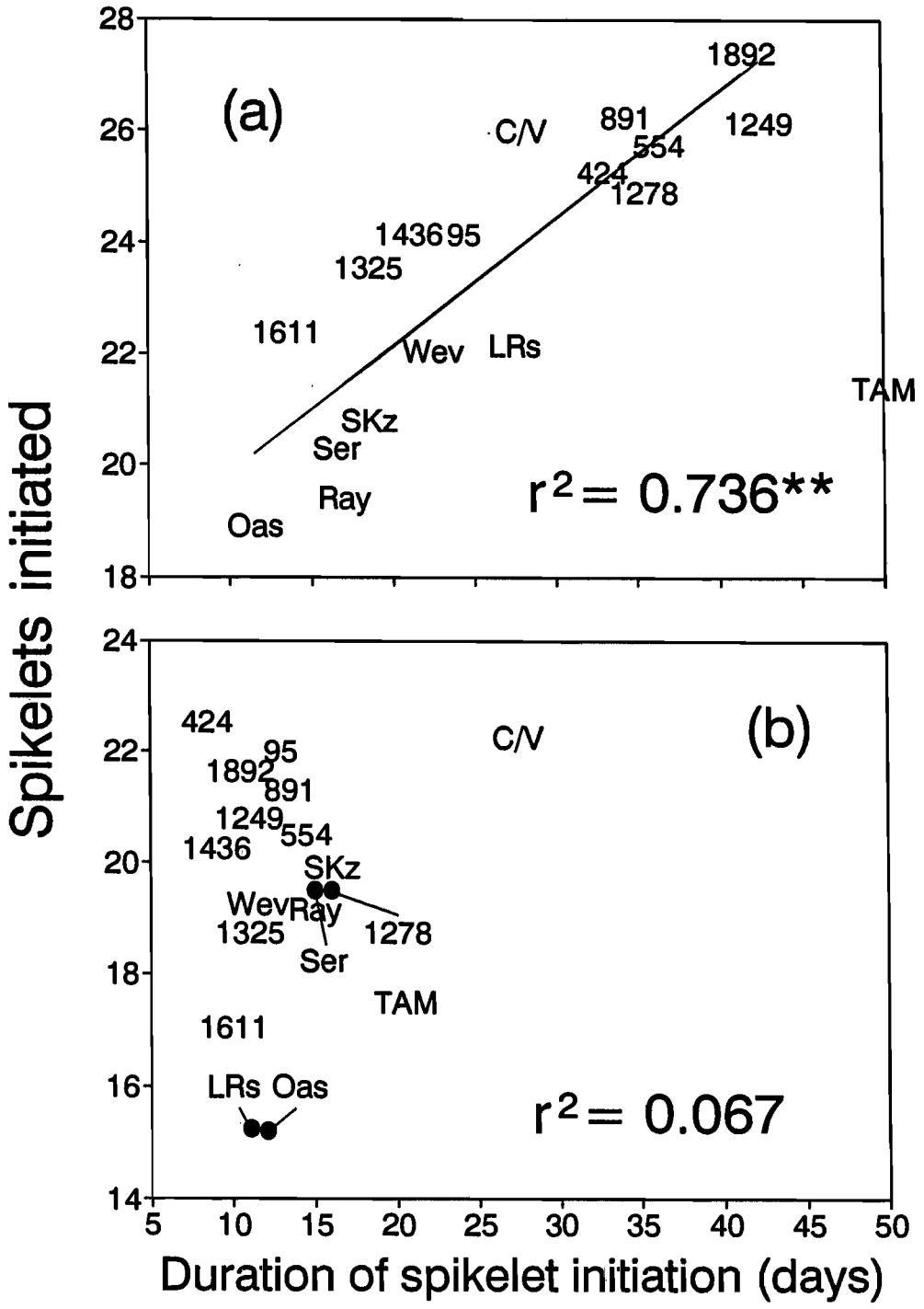

Fig. 10. Correlation between days from initiation of the first spikelet (end of the vegetative phase) to initiation of the last (terminal) spikelet and the number of spikelets initiated when days were extended by 0 (a) and 3 h (b). For abbreviations see Table 1.

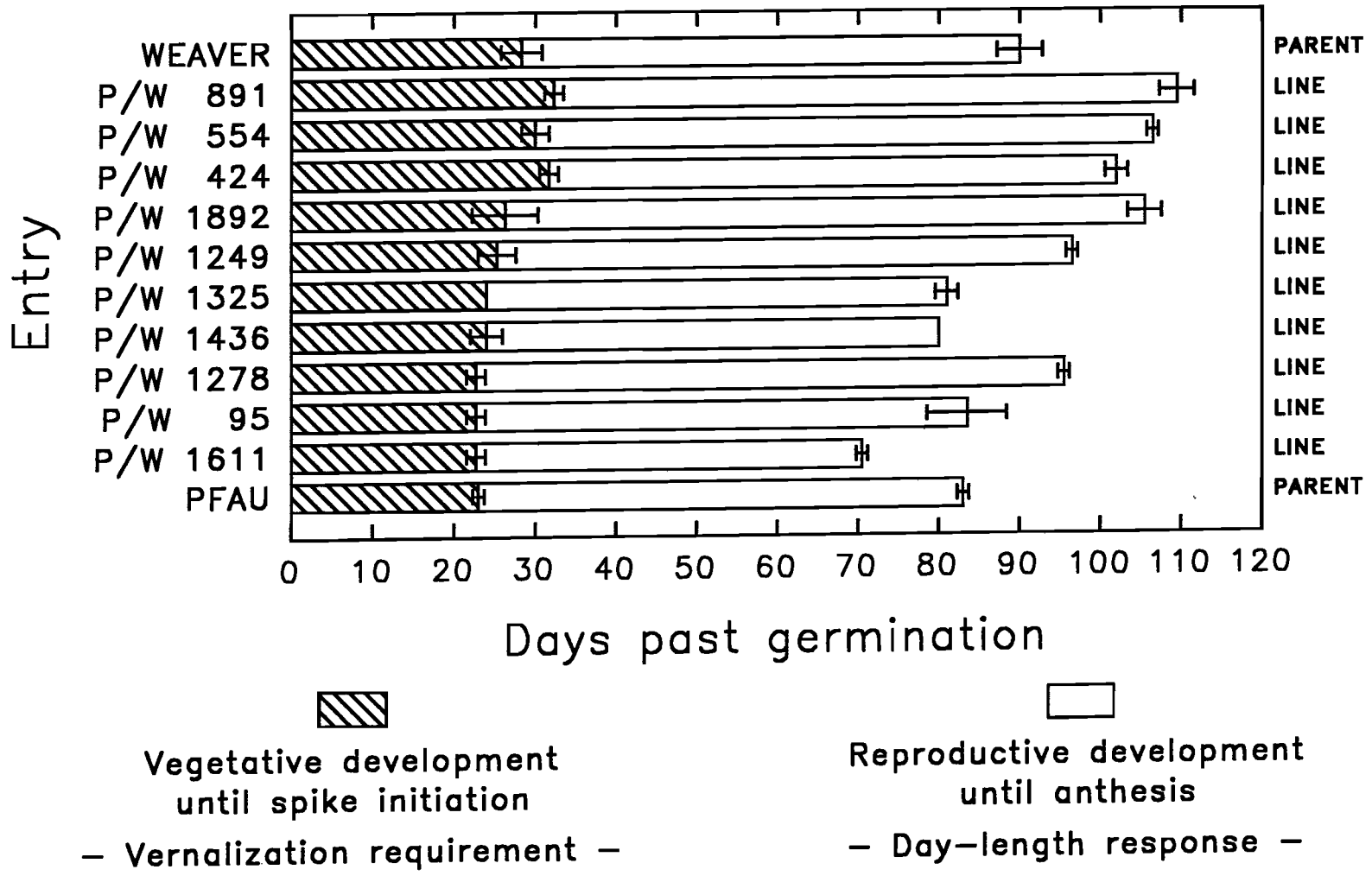

Fig. 11. Separation of development of lines from the cross Pfau/Weaver into the phase controlled by vernalization requirement and the phase controlled by response to day length. (Data for Pfau estimated from dissection of plants from neighboring trial of same germination date.)

Discussion

Day-length insensitive phase.

After germination, wheat plants were insensitive to day length (Fig. 1). During this day-length insensitive phase, only leaf primordia were initiated. Development was vegetative and the plants made no progress towards flowering. Once the day-length insensitive phase had transpired, plants changed from vegetative to reproductive development and began to initiate spikelets. The length of the day on which spikelets were first initiated determined how rapidly they developed towards flowering. Passage to the day-length sensitive, reproductive phase was therefore most easily and immediately perceptible in the +3h treatment, where rapidly developing spikelet primordia became perceptible as double ridges more or less on the day on which they were initiated. However, even before double ridge, the response to day length was observable in the 0h and $+3h_{47}$ treatments through greater elongation of the spike (12, 20, 27) and more rapid primordia initiation (20) than in the -1h treatment (Fig. 1). **During a day-length insensitive period after germination, development is vegetative (initiation of leaves). Thereafter, development is reproductive (initiation of spikelets) and progresses towards flowering at a rate dependent on day length.** A juvenile phase, during which plants are unresponsive to day length, has been reported for rice by Vergara and Chang (35) and Yuan *etal.* (38), for wheat by Major (23), and for barley by Roberts *etal.* (29).

The 65 and 40 d vegetative phases of Centurk/Veery 5 and TAM 200 were considerably longer than those of all spring types studied (Figs. 2 and 3). **The late flowering of winter and facultative wheats appears to be due, in part, to a substantially longer juvenile phase than in spring wheats, during which there is no response to day length and no progress towards flowering.** Roberts *etal.* (29) found that, at 15°C, spring-sown barleys responded to day length 8 to 10 d after germination, while autumn-sown barleys were unresponsive to day length for up to 32 d. Manupeerapan *etal.* (24) found that slower progress towards ear initiation (measured as the appearance of double ridges) was the main cause for late flowering in winter wheats. Griffiths *etal.* (14) found that vernalization allows the apex to begin initiating spikelets by making it sensitive to long days. She proposes that the exposure to cold sensitizes the apex to a substance formed in the leaves which is known to control the response to day length. Manupeerapan *etal.* (24), however, found that all wheats eventually form spikelets, even without vernalization. It is suggested, therefore, that at vernalizing temperatures in a cold room or after a fall planting in temperate climates, while growth is minimal, some or all of the juvenile phase elapses, making the plant sensitive to day length soon after its removal from the cold room or the arrival of spring.

This hypothesis was investigated by exposing the cultivars in this study to a vernalization treatment of 6°C for six weeks. After this treatment, all responded to day length earlier (Fig. 2) and flowered sooner after planting in the field (Table 4) than without vernalization. Still, low temperatures could have, for example, triggered some hormone which made the plant responsive to day length. To investigate this possibility further, rows

Table 4. Days from field planting to anthesis at four day-length treaments.

Entry	Day-length treatment				Entry	Day-length treatment			
	-1h	0h	+3h	$+3h_{47}$		-1h	0h	+3h	$+3h_{47}$
	Unvernalized					Prevernalized			
Centurk/Veery 5	152	135	68	103	Centurk/Veery 5	-	115	73	88
TAM 200	142	104	78	95	TAM 200	107	89	75	78
Weaver	101	90	67	84	Weaver	100	81	62	75
Seri	96	79	68	77	Seri	86	67	57	69
Rayon	97	83	68	78	Rayon	89	73	65	71
Super Kauz	94	79	69	76	Super Kauz	93	73	59	68
Las Rosas	118	102	66	89	Las Rosas	119	103	82	87
Oasis	103	75	67	74	Oasis	96	67	62	73
P/W 891	124	110	81	94					
P/W 554	118	107	73	90	Mean	97	83	67	76
P/W 424	113	102	79	89	Treatment $LSD_{.05}$			4	
P/W 1892	122	106	71	89					
P/W 1249	102	97	71	88					
P/W 1325	100	81	70	79		Postvernalized			
P/W 1436	103	80	69	81					
P/W 1278	109	96	71	88	Centurk/Veery 5	157	140	95	114
P/W 95	91	84	68	79	TAM 200	129	123	90	95
P/W 1611	85	71	60	69	Oasis	108	94	87	88
Mean	110	93	73	85		126	119	91	99
Treatment $LSD_{.05}$		2					7		

of Centurk/Veery 5, TAM 200, and Oasis which had been planted along with nonvernalized seed were removed from the field and subjected to a vernalization treatment of 6°C for three weeks after normal germination. This treatment had no significant effect on the duration of the juvenile phase of Centurk/Veery 5 and TAM 200 and extended it in Oasis (Fig. 2). This suggests vernalization after germination does not speed development towards flowering through a biochemical response of the apex to cold, but rather allows part of the juvenile phase to elapse during a period of minimal growth. **Vernalization is a biological clock phenomenon rather than a response to the feeling of cold *per se*.** Soon after temperatures rise and active growth begins, following removal from the cold room or with the advent of spring, winter wheats are ready to respond to day length and begin reproductive development. If they are not exposed to a cold period, active growth begins immediately, but they do not pass to the reproductive mode with its associated noding for an extended period (65 d in this study), hence the grassy appearance of nonvernalized winter wheats. The juvenile phase of spring wheats is shorter (21 to 32 days in this study). When planted in spring, active growth begins and they initiate spikes and begin noding soon thereafter, never exhibiting the prodigious leafy growth of winter wheats. After a fall planting, the same rapid shift to reproductive development would result in winter kill in spring wheats (19). **It is the duration of the day-length insensitive, vegetative, juvenile phase which defines the vernalization requirement of a genotype.**

The duration of the juvenile phase also varied among spring wheats (Figs. 2 and 3), suggesting that some spring types have a weak vernalization requirement. The juvenile phase of spring wheats is always shorter than in facultative and winter wheats, although with the advent of spring winter crosses, these classifications may erode more and more into a continuum. A weak vernalization requirement such as that of Weaver and P/W 554, if measured in days to flowering, can be partially or completely masked by rapid development during the day-length sensitive phase if days are sufficiently long (Figs. 8 and 9, respectively). Conversely, genotypes with a very short juvenile phase, i.e weakest vernalization requirements, such as Las Rosas and P/W 1278 may appear to have a weak vernalization requirement due to slow progress towards flowering during the day-length sensitive phase (Figs. 8 and 9, respectively).

Day-length sensitive phase.

Differences among entries in day-length response.

All genotypes responded to day length before double ridge, reaching it more quickly the longer the day (Figs. 4 and 5). The only exception was Centurk/Veery 5, which reached double ridge last in the +3h treatment when unvernalized and postvernalized. However, after day 40 a drainage canal was put into service immediately next to this trial which tended keep the +3h treatment wetter and slightly cooler than other day-length treatments. Other genotypes had already passed double ridge in the +3h treatment by the time the canal went into service and would not have been effected. The response of all entries in

this study to day length before double ridge indicates that **there is no such thing as a "day-length insensitive" genotype.**

Genotypes responded differently to different day lengths. In the 0h treatment there was a great deal of variability in days to flowering, even among genotypes with juvenile phases of similar duration (Figs. 8 and 9). There was much less variation in the +3h treatment. Major has shown that **genotypes vary in the day length below which they develop at a minimum rate, the day length above which they develop at a maximum rate, and perhaps the minimum and maximum rates themselves** (23). It appears that genotypes which require very long days to develop at their maximum rate, such as Las Rosas and P/W 1278, are distinguishable by their late flowering in the 0h treatment. Days in the +3h treatment appear to have been long enough to push the development rates of most entries to their maximum. Genotypic differences in day-length response among most genotypes were not perceptible when days were very long.

The nature of the response to day length.

Spikelet initiation lasts from the end of the juvenile phase to initiation of the terminal spikelet. **After the juvenile phase had passed, response to day length determined how long the spike would continue to initiate spikelets (Fig. 1). The longer the day, the shorter the period of spikelet initiation** (Table 5), i.e. the sooner the last spikelet was initiated.

In the $+3h_{47}$ day-length treatment, days were extended by 3 h beginning 47 days after planting. The response of entries whose juvenile phase ended after day 47, was as discussed in the previous paragraph (Fig. 7, Table 6; group 1). Since there was no response to day length during the juvenile phase, it made no difference to spike development if day length was increased at germination or just before the end of the juvenile phase.

Among entries whose juvenile phase ended before day 47, there were two basic types of response (Fig. 6). Genotypes such as P/W1611, which initiated the terminal spikelet well before day 47, did not respond to the $+3h_{47}$ treatment (Table 6; group 2). **Once the terminal spikelet was initiated, any subsequent change in day length did not further alter floret initiation rate or the flowering date of the oldest floret.** There were four exceptions. Oasis, when prevernalized, which reach floret primordia on day 27, did flower earlier in the 0h treatment, but differences in development between the 0h and $+3h_{47}$ treatments became apparent immediately after the juvenile phase and could not have resulted from a response to day length, since the $+3h_{47}$ had not yet been imposed (Fig. 12). Flowering of Super Kauz was substantially different between the two treatments, but due to a large error for days to anthesis in both treatments, the differences were not significant. Development of TAM 200 was very variable among plants and development curves were difficult to interpret (Fig. 12). This cultivar adapted to Texas may segregate for day length response at more southern latitudes. Development of Weaver, when prevernalized, was similar between the

Table 5. Duration of spikelet initiation measured in days from the end of the juvenile phase to terminal spikelet.

Entry	Day-length treatment			Entry	Day-length treatment		
	-1h	0h	+3h		-1h	0h	+3h
	Unvernalized				Prevernalized		
Centurk/Veery 5	28	38	24	Centurk/Veery 5	-	59	19
TAM 200	66	45	24	TAM 200	-	23	16
Weaver	37	22	9	Weaver	29	15	9
Seri	18	18	14	Seri	26	15	10
Rayon	36	18	14	Rayon	36	23	17
Super Kauz	30	19	14	Super Kauz	39	22	13
Las Rosas	47	30	8	Las Rosas	44	27	8
Oasis	37	13	9	Oasis	25	12	7
P/W 891	47	35	12				
P/W 554	45	38	13	Mean	32	25	12
P/W 424	53	42	20	Treatment $LSD_{.05}$		2	
P/W 1892	48	39	15				
P/W 1249	49	41	14				
P/W 1325	32	19	11		Postvernalised		
P/W 1436	40	19	11				
P/W 1278	44	35	15	Centurk/Veery 5	-	43	14
P/W 95	33	24	12	TAM 200	47	34	12
P/W 1611	23	13	9	Oasis	34	14	10
Mean	40	28	14		41	30	12
Treatment $LSD_{.05}$		2				4	

Table 6. Effect of a three hour extension of the day beginning 47 days after planting on days to floret primordia, terminal spikelet and anthesis of the first floret of the terminal spikelet.

Entry	Vernalization treatment†	Days to floret primordia when day was extended by...		Days to terminal spikelet when day was extended by...		Days to anthesis when day was extended by...	
		0 hours	3 hours	0 hours	3 hours	0 hours	3 hours
			Group 1				
Ctk/Vee 5	Prev	64	58	77	59	115	88
TAM 200	Postv	72	60	75	61	123	95
TAM 200	Unv	84	72	85	75	104	95
Ctk/Vee 5	Unv	92	92	103	93	135	104
Ctk/Vee 5	Postv	99	75	104	79	140	141
Mean		82	71	89	73	123	105
			Group 2				
Oasis	Prev	25	29	27	33	67	73
Seri	Prev	27	31	29	35	67	69
Weaver	Prev	29	37	33	41	81	75
Super Kauz	Prev	28	26	34	32	73	68
Oasis	Unv	31	34	34	37	75	74
P/W 1611	Unv	32	31	36	36	71	69
Rayon	Prev	34	36	37	41	73	71
TAM 200	Prev	36	42	39	43	89	78
P/W 1325	Unv	38	38	43	43	81	79
Super Kauz	Unv	41	41	43	44	79	76
Seri	Unv	41	41	43	42	79	77
P/W 1436	Unv	43	42	43	43	80	81
Rayon	Unv	42	44	43	45	83	80
P/W 95	Unv	41	41	46	43	84	80
Mean		35	37	38	40	77	75
			Group 3				
Las Rosas	Prev	42	46	47	53	103	89
Weaver	Unv	47	45	51	53	90	84
Oasis	Postv	49	51	51	53	94	88
Las Rosas	Unv	43	45	52	52	102	89
P/W 1278	Unv	50	47	58	59	96	88
P/W 424	Unv	57	54	64	58	102	89
P/W 1892	Unv	53	55	66	58	106	89
P/W 1249	Unv	53	55	67	61	97	88
P/W 554	Unv	53	53	68	58	107	90
P/W 891	Unv	59	57	68	64	110	94
Mean		51	51	59	57	101	89
$LSD_{.05}$		7	8	6	9	6	12

† Prev = Prevernalized, Unv = Unvernalized, Postv = Postvernalized.

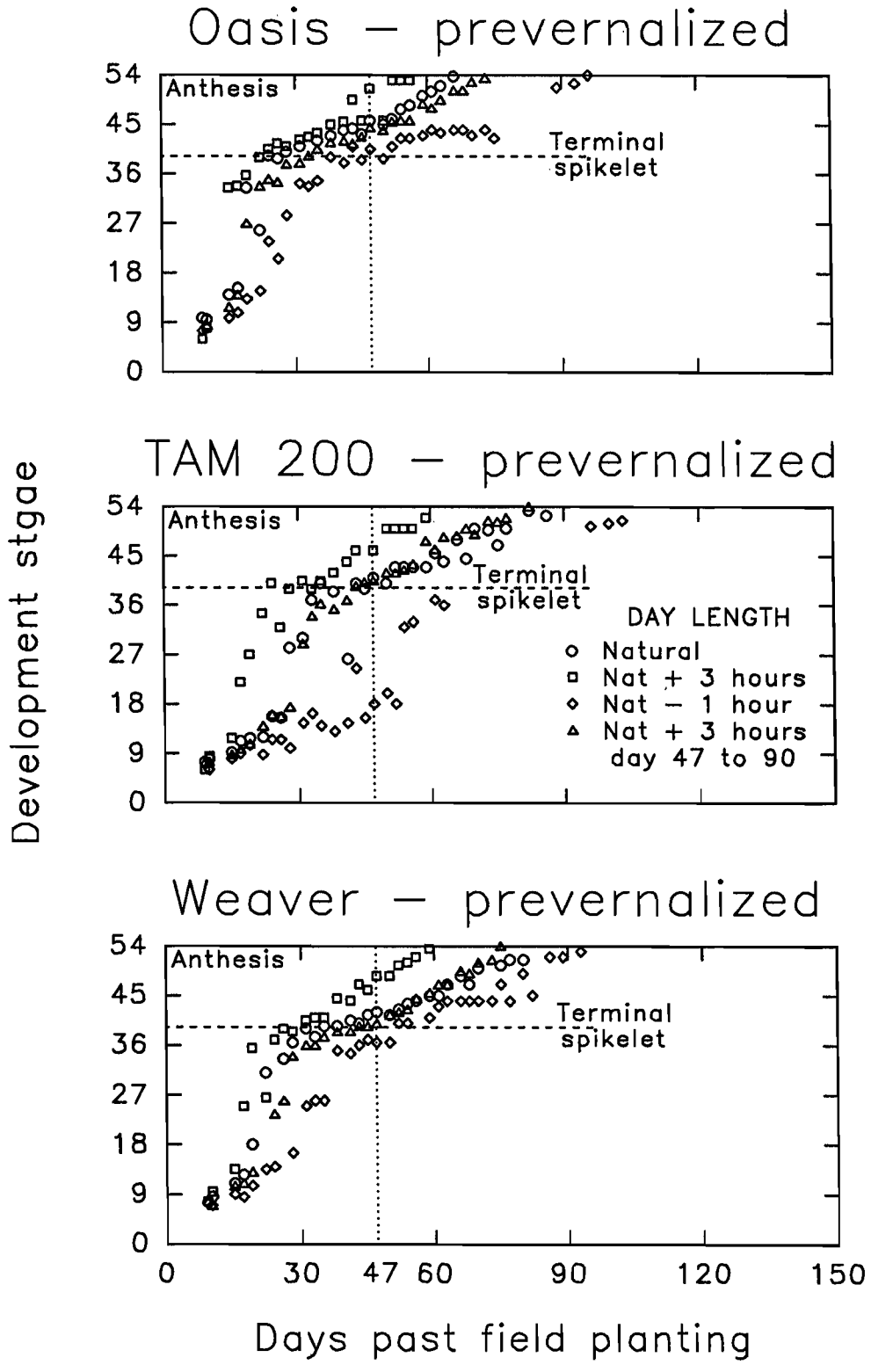

Fig. 12. Development of Oasis, Tam 200, and Weaver at four daylengths after prevernalization.

0h and $+3h_{47}$ until just before anthesis (Fig. 12). The difference in flowering date between the two treatments may be due to experimental error. In genotypes which initiated the terminal spikelet after day 47, such as P/W 1892, development of first spikelets was not effected, at least up to initiation of florets (stage 38), after which their development was no longer followed (Table 6; group 3). However, they did flower earlier. **Response to day length at the initiation of the terminal spikelet determined how quickly it progressed to flowering.**

Among entries in which development of the terminal spikelet was effected by the $+3h_{47}$ treatment, there appeared to be two classes of response. Entries which reached floret primordia several days after day 47 initiated the terminal spikelet earlier and initiated florets more quickly in the $+3h_{47}$ treatment than in the 0h treatment (Fig. 13). **The longer the day, the sooner the terminal spikelet was initiated and the faster it initiated florets.** In entries which initiated the terminal spikelet close to day 47, the oldest floret of the terminal spikelet flowered earlier in the $+3h_{47}$, but the date of terminal spikelet initiation and floret initiation rate were not (Fig. 14). It may be that, in these cases, the terminal spikelet had been initiated by day 47 and rate of floret initiation was not effected by a subsequent change in day length. Florets are initiated after the spikelet. This may have taken place after day 47 and so their development rate towards flowering differed in the 0h and $+3h_{47}$ treatments. **The response to day length appears to determine how quickly florets progress towards flowering.** The difficulty in making exact interpretations lies in the precision with which the day of initiation of spikelets and florets can be determined. The day on which the first cell differentiated into the respective organ can not be perceived with the eye.

Physiological ramifications.

This and the following section on genetics deal not so much with analyses of data, but rather the possible implications and applications of the results discussed so far.

Development patterns.

Various combinations of vernalization requirement and response to day length yield a large variety of development patterns (Figs. 8 and 9). Which, if any of these, contribute to higher yield was not investigated in this trial. The cultivars included in this study were planted in yield trials with the same germination date as this vernalization/day-length trial in Obregon, Sonora, Mexico, but those results had not been analyzed by the time of this writing. However, it has been found that under irrigated conditions it might be advantageous to prolong the terminal spikelet to anthesis phase. This allows greater radiation inputs (PTQ) during rapid spike growth and minimizes spikelet abortion (8). Under rainfed conditions in arid environments, such as in Syria, early flowering, before stored soil water is depleted, is the prime requirement for higher yield (32). **If there are optimum development patterns, they most likely vary with environment.** It is also important to note that development patterns shift with environment in very complex ways. This can

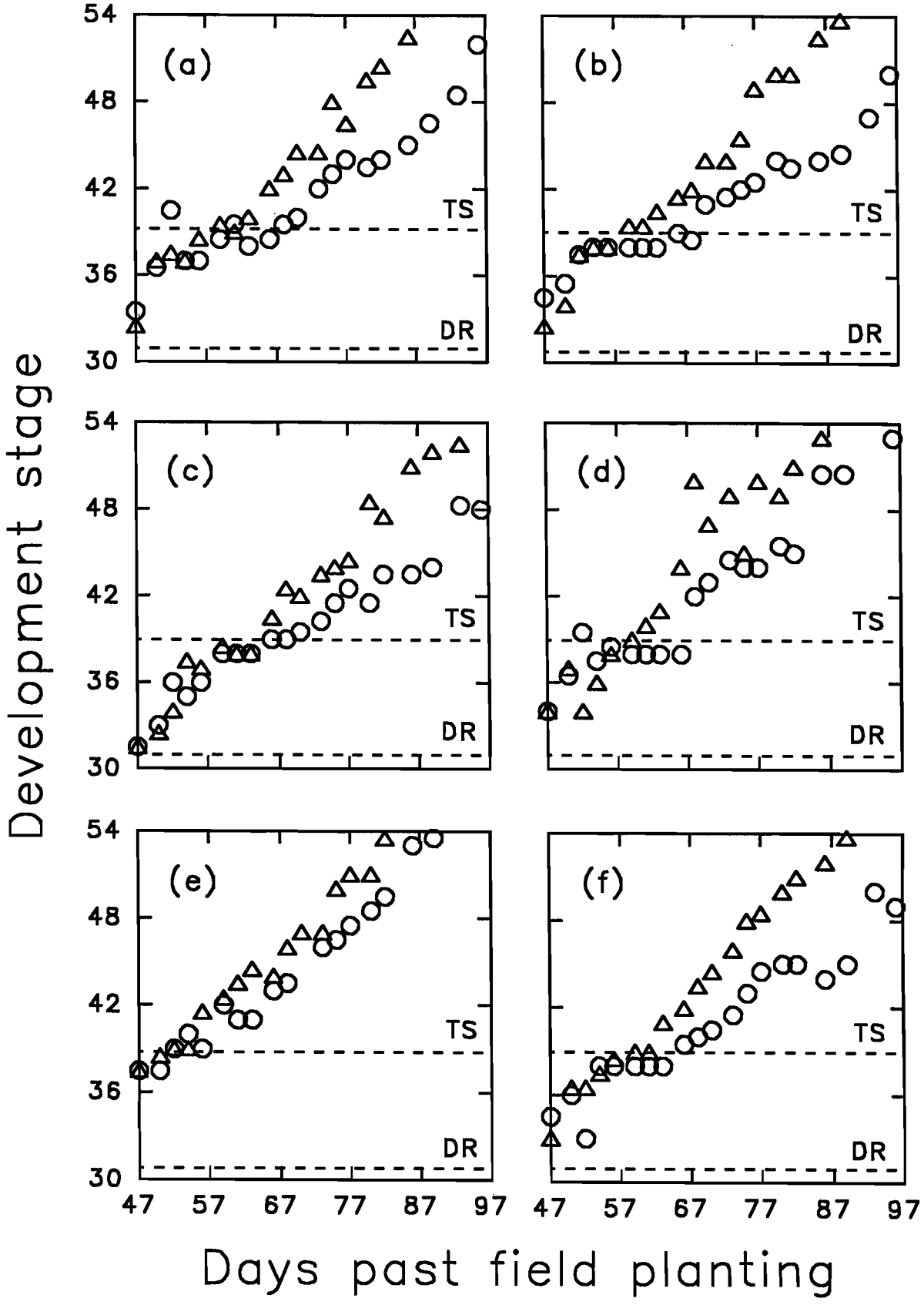

Fig. 13. Development of P/W424 (a), P/W554 (b), P/W891 (c), P/W1249 (d), Weaver when unvernalized (e), and P/W1892 (f), when days were not lengthened (○) and lengthened by 3 h beginning 47 days after planting (△).

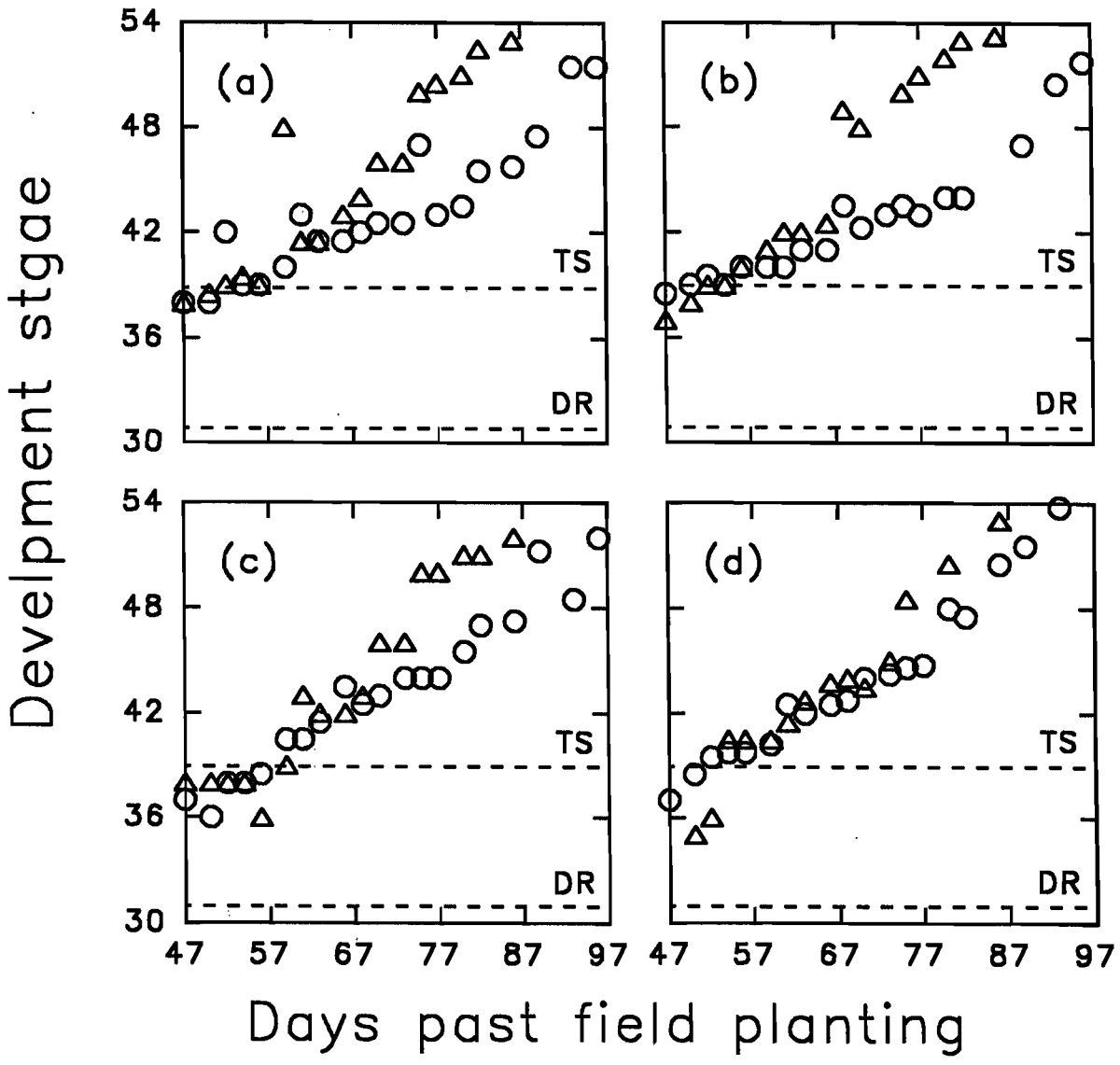

Fig. 14 . Development of Las Rosas when unvernalized (a), and prevernalized (b), P/W1278 (c), and Oasis when postvernalized (d), when days were not lengthened (○) and lengthened by 3 h beginning 47 days after planting (△).

be seen by comparing the patterns in the 0h and +3h treatments in Figures 8 and 9. **By moving a genotype from one environment to another, its development pattern will most likely change.** Such a shift is most dramatically exemplified by the Argentinean cultivar Las Rosas, which is wholly unadapted to the short days of the Obregon winter. Genotypes which are commonly considered "day-length insensitive", are most likely those which respond to any day length, no matter how short, by developing towards flowering at their maximum rate.

Morphology.

Besides possible direct adaptive advantages, **development patterns also determine, at least partially, plant morphology.** Generally, **the longer the spikelet initiation phase, the greater the spikelet number.** This has been widely reported (6, 9, 17, 20, 25) although the relationship may not be quite so clear-cut. In this study, the variation among entries in duration of the spikelet initiation phase was drastically reduced when days were long. Although spikes tended to be smaller, the variation in spikelet number was largely maintained (Fig. 10), suggesting that under certain conditions, the rate of spikelet initiation may be more important the duration of spikelet initiation.

A shorter juvenile phase has been reported to result in fewer leaves (6, 14, 20, 36), possibly effecting both source size and tillering ability. Again, whether or not these characteristics are of use in increasing yield or yield potential is not the point of this study.

Genetic ramifications.

This was not a genetic study. However, in the following discussion, preliminary ideas about possible modes of inheritance and investigations into their nature are discussed.

Vernalization requirement.

Most vernalization studies attempt to classify genotypes according to vernalization requirement by observing the effect of vernalizing temperatures on flowering date. However, such classification is often difficult because of the confounding effects of genotypic variation in optimum vernalizing temperature, day-length response, and growth habit, and changing response to vernalizing temperatures with plant age (11). **It is proposed that the duration of the day-length insensitive (juvenile) phase, may define the vernalization requirement**, as discussed above. This would allow the vernalization requirement to be quantified and segregating populations to be analyzed accordingly. However, determining the duration of the juvenile phase required destructive methods in this study and is, as yet, of no use in segregating populations, but work on nondestructive methodologies is in progress.

As discussed above, some spring wheats appear to have a weak vernalization requirement. Although only ten, nonrandomly chosen F_3-derived F_5 lines from the cross

Pfau/Weaver were used in this study, preliminary speculation about the genetics of the weak vernalization response may be possible. With some ambiguity, it appears that the duration of the juvenile phase of the progeny and parents fall into groups (Fig. 11); those with a relatively long day-length insensitive phase (Weaver, P/W891, P/W554, P/W424) and those with a shorter day-length insensitive phase (Pfau, P/W1892, P/W1249, P/W1325, P/W1436, P/W1278, P/W95, and P/W1611). This suggests that the weak vernalization response may be inherited through simple dominance, as most vernalization genes appear to be (33, 34). However, since there is some evidence for the possibility of multiallelism for some vernalization genes (11, 31) this can not be ruled out.

Day-length response.

Response to day length, expressed as the rate of development towards flowering after the end of the juvenile phase, can only be compared among entries whose juvenile phases are of similar duration. Entries with longer juvenile phases, e.g. P/W891, first responded to day length later in the year than did entries with shorter juvenile phases, e.g. P/W1611, (Fig. 11). Days later in the year were longer and therefore responses among the two groups can not be compared. However, among entries with juvenile phases of similar duration (e.g. P/W1892, P/W1249, P/W1325, P/W1436, P/W1278, P/W95, and P/W1611 or P/W891, P/W554, P/W424), there is considerable variation in response to day length. Within these groups, several classes of day length response were observed, with the development of many lines being accelerated to a greater or a lesser extent than either parent. This hints at additive effects of genes for response to day length at multiple loci. Although three loci for response to day length have been identified (1, 16, 21, 26, 30, 36), their mode of inheritance and mode of action are not understood.

In the +3h treatment, where the variability in day-length response among most Pfau/Weaver lines is generally not perceptible when measured as days to anthesis, P/W1611 flowered earlier than other lines with juvenile phases of similar duration (Fig. 11). The question of how P/W1611 differs in the genetics of day-length response from those line remains. If still longer days than those in the +3h treatment would have accelerated the development of P/W95, P/W1278, P/W1436, P/W1325, P/W1249, and P/W1892, to that of P/W1611, then these lines differ in the day length required to reach the maximum development rate, i.e. P/W1611 was developing at its maximum rate, the other lines required longer days than those of the +3h treatment to do so. If all lines were developing at their respective maximum rates in the +3h treatment, these lines differ in the maximum rate of development towards flowering which they can achieve. Whichever is the case, long days can mask genotypic differences in day-length response (Figs. 8b and 9b).

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