

# THE INHIBITION OF FLOWERING BY WATER STRESS

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## Summary

Plants of *Lolium temulentum* L., a single-cycle, long-day plant, and *Pharbitis nil* Chois. cv. Violet, a single-cycle, short-day plant, were subjected to osmotic stress during the inductive cycle. An osmotic potential of  $-18$  atm (using polyethylene glycol, mol. wt. 4000) during the 24-hr exposure to light completely prevented flowering in *L. temulentum*. Similarly,  $-6$  atm osmotic potential during the 16-hr dark cycle suppressed flowering in *P. nil*. Water stress during induction, achieved by withholding water to soil-grown plants, also prevented flower induction in *Xanthium strumarium* L.

With *L. temulentum* and *X. strumarium*, stress accompanied by defoliation during the period immediately following the inductive cycle also prevented flowering. The data were consistent with a stress-imposed inhibition of translocation of the floral stimulus from the leaf. *L. temulentum* plants which were stressed but not defoliated during this period formed flowers, suggesting that the floral stimulus itself is relatively stable within the leaf during a period of stress.

## I. INTRODUCTION

Specific effects of episodes of water stress on the development of plants have been frequently described (Salter and Goode 1967) and it has been suggested that such specific effects are due to the increased sensitivity of processes occurring rapidly at the time in which the stress is operative (Williams and Shapter 1955). This is particularly apparent in the cereal plant where, as an example, water stress during internode elongation results in greatly reduced culm extension (Aspinall, Nicholls, and May 1964). Effects of water stress on apical morphogenesis and flower formation in cereals (Nicholls and May 1963; Husain and Aspinall 1970) and in *Lupinus* (Gates 1968) suggest that the apex is particularly sensitive to water stress during both vegetative and floral (Skazkin and Fontalina 1951) development. Part of these effects on apical growth may be mediated through an inhibition of the processes of photoperiodically controlled floral induction, which can be studied most readily with plants that can be promoted to flower by a single inductive treatment. The present investigation explores the effects of water stress on the process of floral induction using the single-cycle plants *Lolium temulentum* L., *Pharbitis nil* Chois., and *Xanthium strumarium* L. In these plants the inductive treatment can be clearly separated from consequent floral development, allowing direct investigation of the response of this process to water stress.

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## II. METHODS

In the experiments with *L. temulentum*, the plants were grown for approximately 5 weeks in a controlled-environment cabinet in 10-cm plastic containers, using a vermiculite : sand mixture as the rooting medium (Aspinall and Paleg 1963). Five plants were grown in each pot which was watered daily with a complete nutrient solution. This preliminary growth period in an 8-hr photoperiod, 2000 f.c. light intensity, 20°C environment was extended until the blade of the sixth leaf was fully expanded. The plants were then exposed to one inductive cycle by extension of the 8 hr of high intensity light with 16 hr of incandescent illumination of 80 f.c. at plant height. The plants were returned to the 8-hr photoperiod regime for 3 weeks before evaluation of the response. All leaves except the sixth leaf on the main stem were removed immediately before the extended photoperiod (Evans 1960*a*, 1960*b*). Where effects on transport of the floral stimulus were studied, the lamina of leaf 6 was removed at various times during and subsequent to the inductive treatment.

These photoinductive treatments were combined with periods of osmotic water stress imposed with polyethylene glycol (mol. wt. 4000) solutions. Water stress was initiated by flooding the rooting medium with sufficient polyethylene glycol solution at the required osmotic potential to completely replace any nutrient solution in the pot. Water stress was relieved by flooding the pot with distilled water and allowing it to drain seven times, thus removing all traces of polyethylene glycol from the rooting medium. Polyethylene glycol has been widely used as an osmotic agent in water-potential studies (Lagerwerff, Ogata, and Eagle 1961; Jarvis and Jarvis 1963; Janes 1964; Barrs 1966). Injurious effects unrelated to its function as an osmotic agent (Leshem 1966) and which could be due to impurities (Lagerwerff, Ogata, and Eagle 1961) were not found in the present study, even in plants exposed for 72 hr to a -10 atm osmotic potential solution. The entry of polyethylene glycol into the plant was also examined indirectly (Slatyer 1961) and it was concluded that the compound was largely excluded from the plant, at least during exposure for 24 hr.

Treatment effects were determined from the growth stage and length of the apex of the main shoot. Twenty-five plants were used in each determination.

These procedures were simplified with *P. nil* as the plant is sensitive to photoinduction in the cotyledon stage. Seeds were treated with sulphuric acid to allow germination (Zeevaart 1964), washed, and planted in trays of vermiculite maintained at 30°C in the dark. After 48 hr, uniform seedlings were selected and planted singly into 2 by 1 in. specimen tubes containing half-strength Hoagland's solution. The plants were supported by fibre-glass mesh and were grown for a further 48 hr in a 27°C, 16-hr day before being subjected to a single inductive 16-hr dark period. Water stress was imposed by substituting the appropriate concentration of polyethylene glycol (dissolved in half-strength Hoagland's solution), mannitol, or sucrose during the stress period. The solution was removed by repeated washing with distilled water. In those experiments in which the solutions were changed during the dark period, this was effected through tubes leading out of the sealed cabinet. Following induction, the plants were transplanted singly into pots containing the vermiculite : sand mixture and were watered daily with Hoagland's solution. The plants were grown in a 27°C, 16-hr photoperiod environment for 4 weeks when the number of flower buds, the presence or absence of a terminal bud, the number of nodes on the stem, and the internode lengths were recorded.

*X. strumarium* plants were grown for 6 weeks in pots of soil in a glasshouse with the photoperiod extended to 24 hr with low intensity incandescent light. They were then transferred to a controlled-environment room maintained at 25°C with continuous illumination for 1 week before the 16-hr dark inductive treatment. All the leaves were retained except on plants in treatments designed to explore the effect of water stress on stimulus translocation which were defoliated to one sensitive leaf 24 hr before induction. Water stress was imposed by withholding water from the plants for various periods commencing at intervals before induction. Plants were rewatered immediately before the inductive period, immediately after the inductive period, or 48 hr after the end of the inductive period.

In all three species the water status of the plant was assessed by measurement of leaf relative turgidity (Barrs and Weatherley 1962) either before or during the inductive or translocation phases. The water potential of *P. nil* cotyledons was measured at intervals through a stress period in one experiment, using a Spanner psychrometer (Spanner 1951).

## III. RESULTS

(a) *Water Stress and Floral Induction*

Preliminary experiments with *L. temulentum* indicated that an osmotic potential in the rooting medium of  $-10$  atm or above reduced leaf relative turgidity to 89% but did not affect flower induction. Consequently the osmotic potential was decreased further to  $-18$  and  $-24$  atm in the subsequent experiment. In this case the relative turgidity of the retained sixth leaf was measured. The inductive cycle consisted of a 16-hr incandescent extension of the basic 8-hr photoperiod. Osmotic stress was imposed 2 hr before this extension commenced and was released 2 hr before the end ( $T_1$ ) or at the end ( $T_2$ ) of the light extension period.

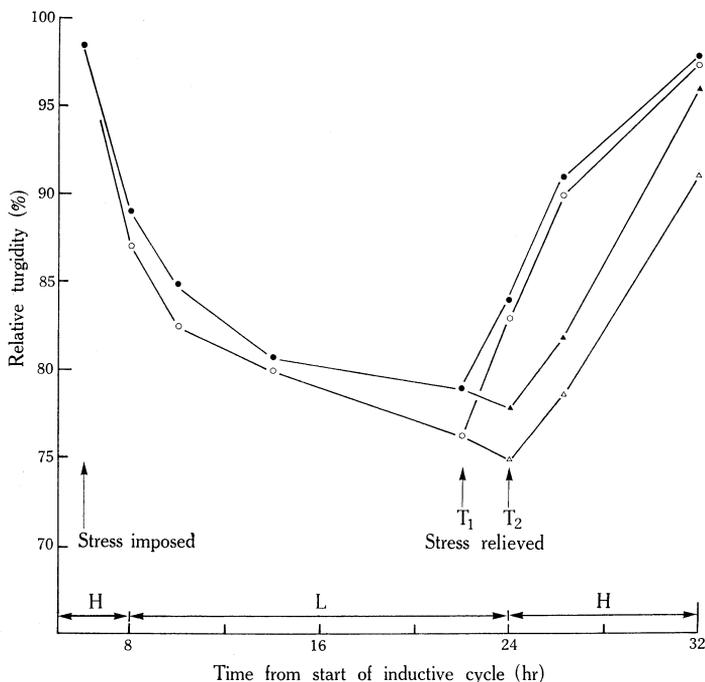


Fig. 1.—Relative turgidity (Barrs and Weatherley 1962) of the sixth leaf of *L. temulentum* plants subjected to osmotic stress during the inductive cycle. Polyethylene glycol solutions with osmotic potentials of  $-18$  atm (●) and  $-24$  atm (○) were employed to impose osmotic stress.  $T_1$ ,  $T_2$ , different times at which stress was relieved. H, high light intensity; L, low light intensity.

Leaf relative turgidity decreased rapidly when stress was imposed (Fig. 1) and reached a minimum of 78–75% in 18 hr. Recovery of turgidity upon rewatering was rapid. Water stress retarded apical development at both levels (Table 1) and, as the majority of stressed plants had not initiated flowers, it appears that stress inhibited floral induction. The time of terminating the osmotic stress had no differential effect, indicating that floral stimulus synthesis in the final 2 hr of the light extension was of no greater importance than in the earlier period. Apex length was similarly affected (Table 1), except that the longer exposure to severe stress inhibited

apex elongation more than any other treatment. This may have been related to the slower recovery of leaf relative turgidity in this treatment.

TABLE 1  
WATER STRESS, FLORAL DEVELOPMENT, AND APEX LENGTH IN  
*L. TEMULENTUM*

Plants were subjected to osmotic stress during the inductive period (0 to +24 hr) and the effect on apical growth assessed 3 weeks later. The stage of apical development was scored according to an arbitrary scale (Vince 1965) in which 2 denotes a vegetative apex, 3 an apex showing double-ridge development, and 5 an apex with glume initials visible

Osmotic Potential (atm)	Periods of Stress (hr)	Stage of Development	Apex Length (mm)
0		4.8	1.58
-18	+6 to +22	2.3	1.26
-24	+6 to +22	2.4	1.27
-18	+6 to +24	2.3	1.29
-24	+6 to +24	2.0	1.18
L.S.D. ( $P = 0.05$ ):		0.6	0.08

In the initial experiment with *P. nil*, seedlings were subjected to osmotic potentials of -6, -12, -18, or -24 atm during the 16-hr dark inductive period.

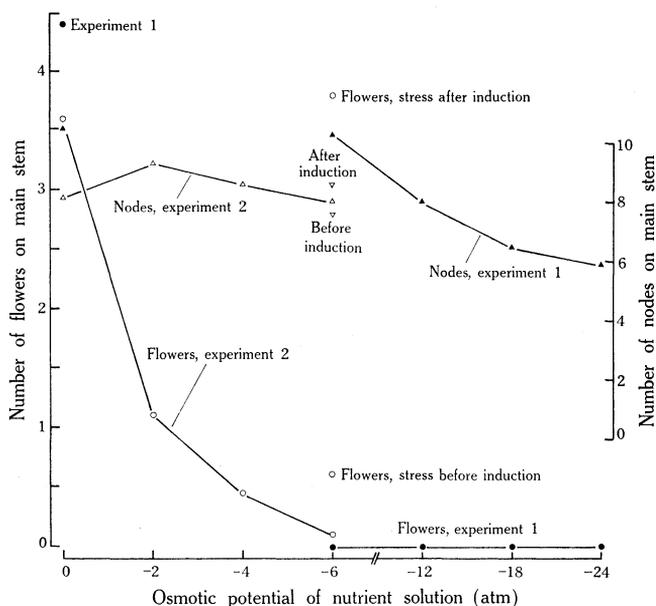


Fig. 2.—Flowering response and node production by *P. nil* cv. Violet plants subjected to osmotic stress during a 16-hr dark inductive period. The figure includes the data from two experiments.

All four osmotic stress treatments completely prevented flower production although an average of 4.4 flowers were formed on plants not subjected to stress (Fig. 2).

The number of nodes produced on the main stem of the plants was unaffected by the  $-6$  atm stress (control, 10.5;  $-6$  atm stress, 10.2) but more severe stress reduced both the number of nodes and internode extension.

The apparent sensitivity of *P. nil* to osmotic stress was further investigated by subjecting seedlings to osmotic stress of  $-2$ ,  $-4$ , or  $-6$  atm during the period of floral induction. In addition, treatments were included in which a  $-6$  atm stress was given either during the 16 hr immediately before induction or the 16 hr immediately after. The level of flowering in the control was slightly less than in the previous experiment, but again a  $-6$  atm stress completely prevented flowering (Fig. 2). Even the  $-2$  atm stress substantially reduced flowering. None of these mild stress treatments reduced vegetative growth, either as node number or internode length. At the end of the 16-hr inductive period, the relative turgidity of the cotyledons of seedlings subjected to the  $-6$  atm stress had fallen to 65% whereas that of control seedlings was 98%.

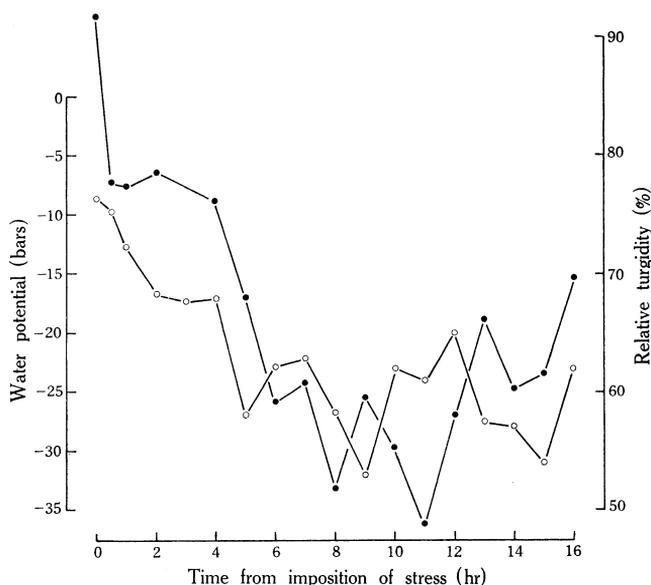


Fig. 3.—Water potential (○) and relative turgidity (●) of the cotyledons of *P. nil* seedlings which had their roots immersed in a  $-6$  atm osmotic potential solution of D-mannitol during 16 hr of darkness.

The inhibition of flowering due to this exposure to osmotic potentials below  $-6$  atm in the root zone was not a specific effect of the polyethylene glycol molecule as solutions of D-mannitol and sucrose of the same osmotic potential also completely prevented flowering when given throughout the 16-hr dark period (control, 3.7 flowers per plant;  $-6$  atm potential, no flowers). These solutions also had no influence on the vegetative growth of the plants (control, 18.8 nodes; sucrose, 18.9; D-mannitol, 19.9; polyethylene glycol, 18.7). This strongly suggests that the inhibition was due entirely to the water potential developed in the plant during the dark period. The actual water potential developed in *P. nil* cotyledons under these conditions was measured hourly through the 16-hr dark period with plants subjected to a  $-6$  atm osmotic potential using D-mannitol (Fig. 3). Variation between individual plants was considerable, but it is clear that the water potential of the cotyledons fell

rapidly during the first half of the dark period to stabilize at a level of  $-25$  to  $-30$  bars for the remainder of the dark period.

This experiment suggests that considerable water deficits were developed in the cotyledons of *P. nil* seedlings subjected to moderate osmotic stress. Exposure to such water deficits for long periods was not essential, however, in order to inhibit the flowering response. Submerging the roots of the plants in  $-6$  bars osmotic potential mannitol solution for either the first or the second 8 hr of the dark period completely prevented flowering. Moreover, exposing the plants to a similar osmotic potential for as short as 2 hr in the centre of the dark period significantly reduced flowering: control (no stress), 1.2 flowers per plant; 2-hr stress, 0.4; 4-hr stress, no flowers per plant [significant difference ( $P = 0.05$ ), 0.5].

In contrast to the effect of water deficit during the dark period, a  $-6$  atm potential applied immediately after floral induction had no effect on either flowering or vegetative growth (Fig. 2). Stress immediately before induction substantially reduced flowering without affecting vegetative growth, however, and it was initially presumed that this was due to the effect of stress at this time on the expansion of the cotyledons. In unstressed plants, the cotyledons were fully expanded at the time of floral induction, but previous stress inhibited the unfolding of the cotyledons which were still partially folded at the time of induction.

This supposition was tested by delaying the inductive dark period by 48 hr and then subjecting the seedlings with expanded cotyledons to a  $-6$  atm osmotic potential D-mannitol solution for 16 hr either immediately before, during, or immediately after the dark period. Once more the pre-dark water stress was inhibitory [control, 1.4 flowers per plant; stress before dark period, 0.7; stress during dark period, 0.2; stress after dark period, 1.7; significant difference ( $P = 0.05$ ), 0.4]. This experiment eliminated the hypothesis that cotyledon expansion was the important factor in the inhibition due to osmotic stress before the inductive dark period. It remains possible that water stress at this time inhibits some pre-induction processes which are essential for the inductive process itself. The sensitivity of the flowering response to osmotic stress at this time was compared with that during the dark period by subjecting plants (with fully expanded cotyledons) to a series of osmotic potentials, using D-mannitol, during these two periods. The processes occurring during the dark period itself appear to be considerably more sensitive than those occurring before the inductive treatment (Fig. 4).

The effects of water stress on flower induction in *Xanthium* were assessed by withholding water from soil-grown plants for 48, 40, or 24 hr before the start of a 16-hr dark inductive period. This resulted in leaf relative turgidities of 74, 85, and 88% respectively 1 hr before the dark period. Half of the plants were rewatered immediately before the dark period and the remainder immediately after. Water stress terminating before the inductive period had only a minor effect on flower formation (Fig. 5) but when continued through the dark period had a much more marked effect. The most severe stress completely prevented flowering in many plants and retarded it in all others. A subsequent experiment with more prolonged and severe stress (down to 67% relative humidity) confirmed these results in that flowering was prevented in nearly all plants when stress continued through the inductive period (control mean flowering stage 4.4; severe stress 1.1). With this

severe stress, however, termination of the stress immediately before the dark period did not prevent a considerable inhibition of flowering (mean flowering stage 1.8). This may have been due to the slow recovery of plants from such a severe stress, as the leaves were not fully turgid 16 hr after rewatering.

(b) *Water Stress and Translocation of the Floral Stimulus*

Indirect evidence suggests that a floral stimulus is translocated from the induced leaf of *L. temulentum* to the apex in the 24 hr immediately following floral induction (Evans 1960a, 1960b). The effect of osmotic stress during that period was investigated

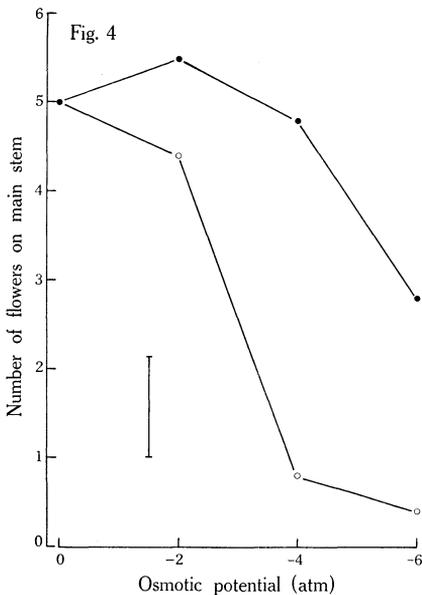


Fig. 4.—Flowering response of *P. nil* plants subjected to various degrees of osmotic stress for 16 hr during the inductive dark period (○) or immediately before it (●). Significant difference at  $P = 0.05$  indicated by vertical line.

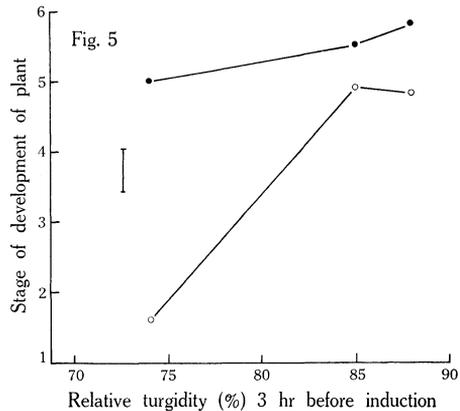


Fig. 5.—Water stress and apical morphogenesis in *X. strumarium*. Plants were grown in pots of soil and watering was terminated 48, 40, or 24 hr before the start of the inductive dark period and recommenced immediately before or immediately after the 16-hr dark period. ● Stress before induction. ○ Stress before and during induction. Significant difference at  $P = 0.05$  indicated by vertical line. Stage of plant development is after Salisbury (1963).

with plants reduced to the sixth leaf and given a single inductive cycle. Polyethylene glycol solutions of  $-18$  or  $-24$  atm potential were applied to the rooting medium 2 hr before the end of the inductive cycle and were washed out 2, 6, or 10 hr later. The leaf which had generated the floral stimulus was removed at the time the stress was relieved. Leaves of non-stressed plants were removed at the same time. Water stress reduced leaf relative turgidity to 88% in 2 hr and 80–82% in 10 hr; when the stress was removed the relative turgidity (in leaves retained for measurement) returned to 95% within 4 hr.

The non-stressed plants demonstrated the pattern of response attributed to translocation of a floral promoter (Table 2) in that floral development was greater

TABLE 2

WATER STRESS AND TRANSLOCATION OF THE FLORAL STIMULUS IN *L. TEMULENTUM*

Plants, previously reduced to one leaf, were subjected to osmotic stress for varying times during the period of floral stimulus translocation. The induced leaf was removed at the time the osmotic stress was relieved, and the effect on apex length and floral development (assessed as in previous table) was measured 3 weeks later

Osmotic Potential (atm)	Period of Stress +22 to +24 hr		Period of Stress +22 to +28 hr		Period of Stress +22 to +32 hr	
	Stage	Apex Length (mm)	Stage	Apex Length (mm)	Stage	Apex Length (mm)
0	2.2	1.18	2.6	1.29	3.1	1.39
-18	2.0	1.14	2.1	1.14	2.1	1.17
-24	2.0	1.12	2.0	1.15	2.0	1.19
L.S.D. ( $P = 0.05$ ):	0.01	0.06	0.01	0.06	0.01	0.06

the longer the leaf was retained. In contrast, water stress completely prevented any such response and there was no development of flowers. Apex length was influenced in a completely parallel manner. Water stress appears, therefore, to inhibit translocation of the floral stimulus.

A similar experiment was conducted with *X. strumarium* except that stress was induced by withholding water. It was impossible in this case to avoid subjecting the plants to mild water stress during the inductive period. Although stress during induction reduced the flowering response, it could be demonstrated that stress during the translocation phase, coupled with subsequent leaf removal, reduced flowering still further (75% vegetative, Table 3).

TABLE 3

WATER STRESS AND TRANSLOCATION OF THE FLORAL STIMULUS IN *X. STRUMARIUM*

Plants were given an inductive dark period from 0 to +16 hr and were grown for a further 4 weeks before the development of the apex was assessed according to the scale of Salisbury (1963) in which 1 marks the first visible signs of floral development. Each value is the mean of 12 plants

Treatment	Stage of Flowering
Control—stressed only before induction (-48 to 0 hr), leaf not removed	4.4
Water stress during induction but not translocation (-48 to +16 hr), leaf not removed	2.0
Water stress during induction but not translocation (-48 to +16 hr), leaf removed after translocation (+64 hr)	2.3
Water stress during induction and translocation (-48 to +64 hr), leaf removed after translocation (+64 hr)	0.7
L.S.D. ( $P = 0.05$ ):	1.1

These experiments suggest that both the process of floral induction and the subsequent translocation of the floral stimulus from leaf to apex are inhibited by

water stress. There remains the possibility that previously formed floral stimulus may be dissipated during an episode of water stress. This was investigated in a further experiment in which *L. temulentum* plants were subjected to a  $-24$  atm osmotic stress during the translocation phase and rewatered or rewatered with simultaneous defoliation at intervals thereafter. The osmotic stress reduced leaf relative turgidity to 80% in 6 hr and a minimum of 63% in 34 hr.

As in the previous experiment, defoliation at the time of stress removal inhibited the flowering response indicating inhibition of transport of the flowering stimulus during stress (Fig. 6). The non-stressed plants responded to defoliation such as to

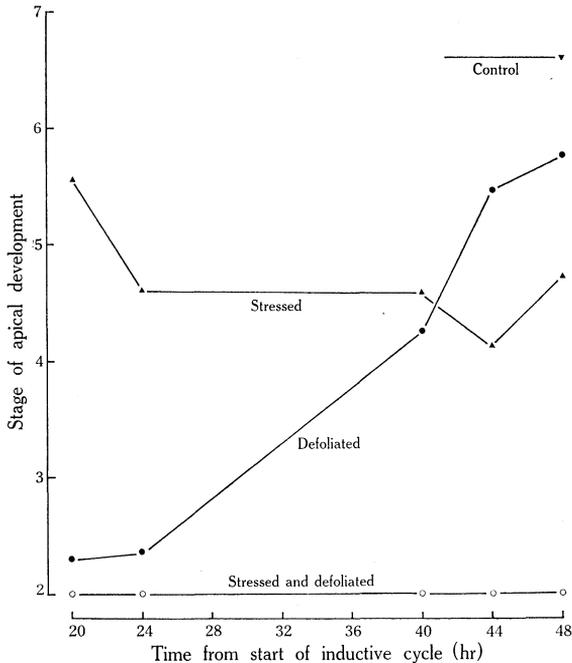


Fig. 6.—Influence of osmotic stress ( $-24$  atm, polyethylene glycol) on the translocation and stability of the floral stimulus in *L. temulentum*. Plants were exposed to an inductive 24-hr light treatment (0–24 hr) and osmotic stress was imposed at 22 hr and relieved at 28, 32, 48, 52, or 56 hr. Defoliation, where applicable, was carried out at the times stress was relieved. Apical development was assessed 3 weeks after induction according to the scale of Vince (1965) where 2 = vegetative, 3 = early floral, 7 = flower primordia swelling.

suggest that translocation of the floral stimulus occurred mainly between the hours  $+28$  and  $+52$  (beginning of inductive period = 0). Retention of the induced leaf after osmotic stress was relieved resulted in a substantial flowering response, even after 34 hr of stress. The floral stimulus cannot, therefore, be completely destroyed during water stress. Nevertheless, flower development was reduced when compared with the unstressed treatment. This reduction was maximal 4 hr after the end of induction and did not increase with more prolonged stress. Possibly stress was here inhibiting formation of the floral stimulus rather than promoting its breakdown.

#### IV. DISCUSSION

The results of these experiments suggest that the processes associated with the photoinduction of flowering in both long- and short-day plants may be inhibited by water stress. Indeed, the response of *P. nil* suggests that induction in that plant may be particularly sensitive to stress. The apparent difference in sensitivity between *P. nil* and *L. temulentum* may be an artefact, however, as in the one case the osmotic

solution was applied to a very small seedling in solution culture, whereas in the other the solution was supplied to a much larger plant supported in a particulate medium. At comparable times the relative turgidity of the cotyledons of *P. nil* seedlings exposed to  $-6$  atm solution was, in fact, lower than that of the sixth leaf of *L. temulentum* plants exposed to a  $-24$  atm stress. Whilst caution must be exercised in interspecific comparisons of relative turgidity, this does suggest that the two species may not differ markedly in sensitivity.

The close similarity of the inhibition of floral induction in *X. strumarium* by water stress to that in the other species provides strong evidence for the generality of the response. In addition, these results and the data from the use of different osmotic stresses confirm that the effect is due to water potential changes and not to any property of the osmotic stress.

The most probable site for the inhibitory effect of water stress on flower induction is the leaf. The facts that stress before the inductive period but not after it inhibits flowering in *P. nil* and that stress followed by defoliation prevents flowering but without defoliation is ineffective in *L. temulentum* strongly suggest that apical processes are not involved in the inhibition. The present uncertainty about both the effects of water stress on leaf metabolism, on the one hand, and the biochemistry of floral induction on the other renders any speculation on the nature of this inhibition unwarranted. Possible significant responses to a water deficit in this context include stomatal closure, inhibition of protein synthesis (Barnett and Naylor 1966), and changes in nucleotide metabolism (Kessler and Frank-Tishel 1962).

The inhibition of flowering produced by stress followed by defoliation during the period of stimulus transport can only be readily interpreted in terms of an inhibition of translocation. Information on the effects of water stress on translocation is confusing due to the close relationship between effects on photosynthesis, phloem transport, and activity of the importing organ (Wardlaw 1968). Although several authors have interpreted their data in terms of stress-induced inhibition of phloem transport (Hartt 1967; Plaut and Reinhold 1965, 1967), there is some evidence that translocation is itself relatively insensitive to stress when not affected by changes in photosynthesis or growth of the importing organ (Wardlaw 1967). These considerations also apply in the present case as growth of the importing organ, the apex, was undoubtedly reduced by water stress and this may have materially reduced the rate of translocation to the apex. Furthermore, it has been argued (Evans and Wardlaw 1966) that translocation of the flowering stimulus in *L. temulentum* is independent of assimilate transport and occurs at a different rate. If this is so, water stress may be inhibiting transport through a route other than the phloem cells. It would be inadvisable to use the present data as evidence for such a separate route, however, without supporting data on the transport of assimilates in the same system. It may well be that the effect of stress on apical growth is the controlling feature inhibiting the translocation of both assimilates and floral stimulus.

It is of interest to briefly consider the effects of water stress in the field situation in the light of the experimental evidence presented here. In the field, photoinductive conditions continue for long periods, not for a single cycle, but water stress is also likely to be extended into prolonged episodes. Thus, although flowering is unlikely to be completely inhibited by water stress, it may well be delayed. There

have been reports of delayed flowering associated with early water stress (Novikov 1952, 1954). Many of these effects on flowering could be associated with the influence of water stress on apical development subsequent to floral induction (Skazkin and Lerman 1952; Husain and Aspinall 1970) but some may be attributable to effects on induction itself.

#### V. ACKNOWLEDGMENTS

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