Water stress during reproductive stages affects seed quality and yield of pea (Pisum sativum L)

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Abbreviations: IBSF, irrigated before seed filling and not during seed filling; IDSF, irrigated during seed filling and not during the period from the start of flowering to the

initiation of seed filling; NI, non-irrigated treatment; WI, irrigated as needed during the whole growing season.

ABSTRACT

Physiological pea (*Pisum sativum* L.) seed quality depends on various factors affecting the plant, including water supply, the true effect of which has not been characterized. The effects of different periods of water stress during reproductive stages on the seed yield and seed physiological quality were investigated in field studies over three years (1991, 1992 and 1993) in Brain-sur-l'Authion, France, on a Mollisol, Rendoll, eutrochreptic soil. Irrigation during seed filling (IDSF) and irrigation during the period from the start of flowering to the start of seed filling (IBSF) were compared to a non-irrigated (NI) and a well-irrigated (WI) treatments. The physiological quality of pea seeds was assessed by the germination percentage, conductivity test, and cold test. The germination percentage averaged 98% and was not modified by water stress. In 1993, rainfall during the reproductive stages was high, and there were no differences in seed yield or quality between treatments. In 1991 and 1992 the rainfall was much lower, and the NI treatment showed the lowest seed yield and quality as far as the conductivity test and cold test were concerned. The WI treatment showed the best yields. Water stress during the flowering period (IDSF) did not reduce seed quality compared to WI when it was followed by an optimal water supply during seed filling, and reduced seed yield slightly. Water stress during seed filling (IBSF) decreased seed yield but the effect on seed quality was not significant. Mean seed weight was higher and less variable in IDSF treatments than in WI treatments. Changing irrigation strategies for pea seed production

towards irrigation during seed filling may improve the physiological quality of the seedlots without decreasing the seed yield.

Seed germination quality in pea depends on the pathological, physical and physiological state of the seed (Powell et al., 1984). While the pathological state (Powell et al., 1984) and physical properties (Deneufbourg, 1992) of the seed are increasingly well known, little is known about the factors that are responsible for differences in physiological quality between seed lots at harvest. At present, the physiological quality of the seed is not really taken into account by pea seed growers. Moreover, the water supply to pea crops for seed production varies greatly in France according to the cropping area and how irrigation is managed. But the consequences of water supply on the physiological quality of the seed are not known.

The effect of the water supply of the plant on seed quality has been investigated in some large-seeded legumes, especially in soybean. In field experiments, Smiciklas et al. (1989) observed that water stress during the period of seed filling in soybean induced a reduction in seed quality as assessed by germination and conductivity results, compared with those where there was no or earlier water stress. In contrast, Vieira et al. (1992) working on greenhouse and field experiments on soybean observed no or little effect of drought stress on seed quality. Dornbos and Mullen (1991) observed a negative effect of drought stress which was enhanced by high air temperatures. Heatherly (1993), in a three-year field study, observed that drought stress resulted in reduced germination of harvested soybean, but the daytime temperature during the seed filling period exceeded 30 °C for all experiments.

In pea, literature about the effect of drought stress is less abundant. Nichols et al. (1978), working with potted plants, observed no effect of drought stress on seed conductivity or germination. However, in a two-year field experiment, Raymond et al. (1988) found reduced pea seed quality when water was withheld during seed filling. They concluded applying the final irrigation at 500 degree-days after blooming (about two weeks) was necessary to produce viable seed yields similar to those obtained with continuous irrigation through early senescence.

The effect of the maturity level of the seed at harvest has been reported in soybean (TeKrony et al., 1980) and in peas (Bedford and Matthews, 1976; Rachidian and Le Deunff, 1986) to be an important factor affecting seed quality. For pea, a harvest moisture content of 40 % appears to be the optimum maturity stage for the best expression of the physiological quality of the seed (Fougereux et al., 1995). Periods of drought stress, climatic conditions, and maturity levels are not always specified in the reported experiments. This could explain why results do not all agree. Although a tendency for a deleterious effect of drought stress during the seed filling period on seed quality is becoming apparent, further experiments are needed for more reliable conclusions about the effect of drought stress at different reproductive stages of the crop. The objective of this work was to study the effects of plant water stress at different stages on pea seed quality, distinct from the pathological and mechanical aspects of seed quality.

MATERIALS AND METHODS

Crop procedures

Field studies were conducted in 1991, 1992 and 1993 at Brain sur l'Authion (Anjou, France), on a clay limestone soil (Mollisol, Rendoll, eutrochreptic soil using the US classification). 'Solara', a semi-leafless pea cultivar, was used in all experiments. Seeds were sown on 14, 12 and 11 March, respectively for the three years. Inter-row spacing was 0.175 m in 1991 and 0.35 m in 1992 and 1993. Individual plots were 3 x 10 m in 1991 and 5 x 10 m in 1992 and 1993. Buffer areas (2 m wide) separated individual plots. Weeds were well controlled by applications of preemergence pendimethalin plus neburon and postemergence pendimethalin plus bentazone. Fungi and insects were well controlled by applications of carbendazim plus chlorotalonil mixed with endosulfan plus thiomethon, every ten days from the beginning of flowering to the end of grain filling. Plant densities were 60, 78 and 88 plant.m^{-2}, for 1991, 1992 and 1993 respectively.

Irrigation management

Water was applied by drip lines placed on the soil surface with emitters at 30-cm intervals. There were two rows of peas between lines in 1991 and one row in 1992 and 1993. The amount of water applied was controlled with volumetric counters, one per plot. Drought stress was imposed by withholding water at the start of drought stress periods. In 1991, irrigation during unstressed periods was managed according to the climatic demand. Each day, the water balance was calculated from emergence, taking into account the inputs and outputs of water. The inputs included soil water reserve, rainfall and irrigation. Outputs included the evapotranspiration (ETP, Penman method, Penman, 1948), corrected by a crop coefficient k (Deumier et al., 1991). The values used were 0.5 from emergence to the 5-leaf stage, 0.7 from

5-leaf to 7- leaf stage, 0.9 from 7-leaf to 9-leaf stage, 1 from 9-leaf stage to the beginning of flowering, and 1.2 after the beginning of flowering. Twenty mm of water were applied when the water deficit exceeded 20 mm.

In 1992 and 1993, irrigation during unstressed periods was managed according to tensiometric measurements. In each plot, three tensiometers were installed at a depth of 0.2, 0.4 and 0.6 m. Twenty mm of water were applied when the mean value of the three tensiometer readings at 0.4 m was below - 40 MPa.

Water treatments and rainfall

In 1991, three irrigation treatments were imposed, and four in 1992 and 1993. All treatments included optimal irrigation before flowering. In 1991, treatments consisted of a non-irrigated (NI) control (irrigation stopped at the beginning of flowering), and two treatments irrigated until the initiation of seed filling (Ney and Turc, 1993), or the end of seed filling which is defined as physiological maturity according to Ney and Turc (1993). These last two treatments are denoted as IBSF for « irrigated before seed filling » and WI for « well-irrigated » respectively. In 1992 and 1993, the 4 treatments consisted of a non-irrigated (NI) control, two treatments irrigated until the beginning (IBSF) or the end (WI) of seed filling, and a treatment where irrigation was stopped at the beginning of flowering and began again at the initiation of seed filling until the end of seed filling (IDSF for « irrigated during seed filling »). Treatments were arranged in a randomized complete block with three replications in 1992 and 1993. In 1991 each treatment was replicated three times but not in a block design due to the irrgation system used. Analysis of variance was conducted separately on each year's data (significant result if $p<0.05$, highly significant if $p<0.01$) and means were separated by Newman-Keuls test at the 5% level.

Figure 1 shows rainfall and evapotranspiration during the crop cycle for the three years. In 1991, evapotranspiration was high and rainfall was low during both the flowering and seed filling period, whereas, in 1992, rainfall was low during the flowering period but higher at the end of the seed filling period. In 1993, rainfall was high during the flowering period and low during the seed filling period.

Crop development evaluation

For irrigation management, the « beginning of flowering » stage was visually determined. The « initiation of seed filling » and « end of seed filling » stages were evaluated with a method based on monitoring seed moisture content. Fifty plants per plot were collected every two or three days between the beginning of pod setting and harvest. Seeds were extracted manually from pods and assembled according to their node number. Seed moisture content was determined for each node according to the method described below. On the basis of the observations of Rachidian and Le Deunff (1986), a node was considered to be at the initiation or the end of seed filling when the moisture content of the seeds was 80 or 55 %, respectively. Thus, the « initiation of seed filling » stage, at the crop level, was defined as the time when seed moisture content at the first node reached 80 %, while the stage « end of seed filling » stage was defined as the time when seeds of the upper node reached 55 % moisture content.

Harvesting methods

Harvests were performed when moisture content of the first node reached 15 %. For each plot, 50 consecutive plants were collected manually well within the edges. Seeds were extracted manually from the pods to constitute a seedlot, and stored in an air-conditioned chamber (15 °C - 72 % relative humidity) until quality assessment.

Yield and yield component measurements

For each plot of each treatment the mean number of flowering nodes per plant, yield and yield components (seed number and mean seed weight) were measured on a sample of 80 plants in 1991 and 50 plants in 1992 and 1993. In 1992, 300 seeds from each treatment were individually weighed, in order to assess the within-lot variability of this component.

Physiological quality assessment

Two tests were added to the germination percentage, which is the most common measure of seed quality. The first one was a conductivity test, whose relevance for predicting field emergence and identifying low-quality seedlots in peas has been shown in many reports (for example Bedford, 1974; Ladonne, 1992). As some external factors may strongly increase the susceptibility of the seeds to imbibition damage, particularly cold and wet sowing conditions (Simon and Wiebe, 1975; Ladonne, 1992), a cold test was added to assess physiological quality. Ladonne (1992) showed that such a test makes it possible to identify low vigor seedlots which had acceptable germination levels in the laboratory, but resulted in poor field emergence. Germination tests were performed according to ISTA recommendations (ISTA, 1985). Two hundred seeds randomly chosen from each seedlot, in four replicates of 50 seeds, were sown in boxes containing sand moistened to 10 % versus dry weight with deionized water. The boxes were then covered with polyethylene films to avoid evaporation and placed for 8 days in a germination room (20°C - photoperiod of 9h/24h). Normal and abnormal seedlings were counted at the end of the germination period and the germination percentage (percent normal seedling) of the four boxes from each seedlot were averaged. Conductivity tests were performed on 100 seeds per seedlot with an automatic seed analyzer (ASAC 1000, Neogen Corporation, Lansing, Michigan, U.S.A.). Before the test, seed moisture content was equilibrated at about 15 % to avoid the presence of non-imbibed seeds. To take into account variations in seed size between lots, results are expressed per gram of seed, as recommended by ISTA (ISTA, 1987). Cold test procedures were the same as those of the germination test, except that boxes were placed at 1°C for 24 h before being placed for 8 days at 20° C. For this test, seed moisture content for all seed lots was equilibrated to about 11% by placing seeds for two weeks at ambient air conditions. Linear regression was used to determine the relationship between conductivity test and cold test results.

RESULTS

Seed yield and yield components

Measures of seed yield and yield components were used to evaluate the effects of water deficits for the different years and treatments on seed yield and size distribution. The number of flowering nodes provides information on the effects of water deficits during the «beginning of flowering-initiation of seed filling » period and the mean seed weight gives information on the effects of water deficits during the whole period of seed filling. For both 1991 and 1992, non-irrigation reduced the corresponding yield components values (Table 1). In 1993 there was no difference between treatments until the initiation of seed filling. This was probably due to the high rainfall during flowering which eliminated water stress. However mean seed weight was lower than controlfor the non-irrigated treatments during the seed filling period. In 1991 and 1992 the highest seed yield was obtained with the WI treatment, and the lowest with the NI and IBSF treatments. The IDSF treatment had the second highest value for seed yield in 1992 and was similar to the WI treatment in 1993. The IDSF treatment gave the highest mean seed weight in 1992 and 1993.

Within-lot variability of mean seed weight in 1992 is shown in Figure 2. Individual seed weights were generally higher and more uniform for the IDSF treatment than for the other treatments. Coefficient of variation (CV) values corresponding to this figure are 11.5, 12.2, 19.3 and 16.3 for WI, IDSF, IBSF and NI, respectively.

Physiological quality

The results of the three measurements of physiological quality (conductivity test, germination percentage, and cold test) are presented in Table 2. For the three years, the germination percentage was very high (mean value for the three years was 98%), and not significantly different between treatments. In 1993, none of the three methods for measuring germination quality revealed differences between treatments. In 1991 and 1992, differences existed between treatments as far as conductivity tests were concerned. Treatments without any irrigation after the start of flowering showed a poorer quality compared to other treatments. In 1991, although the differences were not significant, the later the irrigation was stopped, the higher the quality was. In 1992, the IDSF treatment showed that stopping irrigation between the beginning of flowering and the initiation of seed filling did not reduce physiological quality. The results of conductivity test for the IBSF treatment did not differ significantly in 1991 and 1992 from those for treatments including irrigation during seed filling (WI, IDSF). The cold test indicated that although the IBSF treatment did not differ significantly from the non-irrigated control neither did it differ from the WI and IDSF treatments. Moreover, there were large differences in the conductivity test and cold test results for different years, especially between 1992 and 1993 during which the irrigation systems were the same, taking into account the WI treatment. Results for the three years showed a negative linear relationship between the cold test percentage and conductivity (Fig. 3).

DISCUSSION

As differences in the conductivity test and cold test results occurred between years for WI treatment, the effects of drought stress on pea seed physiological quality must first be discussed year by year. Results from 1991 showed that drought stress starting at the beginning of flowering and maintained during seed filling was sufficient to decrease seed physiological quality. Water stress during seed filling only seemed to decrease seed quality compared to that of well-irrigated plants, but this statement can not be made with definity because the values did not differ significantly. Experiments from 1992 confirmed these results and showed that physiological quality was maintained compared to the WI treatment if drought stress was limited to the period from the start of flowering to the start of seed filling (IDSF treatment), and plants were kept well-watered during the seed filling period. Experiments from 1993 could not confirm these results due to high rainfall. The IBSF treatment from this year did not show any decrease in physiological quality and this could be explained by a lower stress intensity or a later stress period during seed filling compared to the same treatment from 1991 and 1992 (Fig. 1). The results for the three years show that the whole reproductive period is a period of sensitivity of pea seed physiological quality to drought stress, and that the decrease in quality is lower when the stress does not occur during seed filling. These results are in accordance with the results of authors (Raymond et al., 1988 in pea, Smiciklas et al., 1989 in soybean) who observed a deleterious effect of drought stress on pea seed quality when water was withheld during seed filling. Our observations may also explain why drought stress during the reproductive period might have been reported as non effective on pea seed quality, if the stress preceded the seed filling period.

Differences in seed quality assessed by the conductivity test and cold test for the WI treatments from 1992 and 1993 managed with the same irrigation system showed that drought stress was not the only factor responsible for the seed physiological quality during our experiments. The effects of the environment during seed development on the germination quality of seeds have been investigated by several authors for some large-seeded leguminous species. In beans (*Phaseolus vulgaris* L.), Siddique and Goodwin (1980) found a deleterious effect of high maturation temperatures on the percentage of normal seedlings. In soybean (*Glycine max* (L.) Merr.), Keigley and Mullen (1986) found that exposure to increasing periods of high temperature during the seed filling period resulted in a linear decline in seed germination and vigor. In peas, Nichols et al. (1978) observed no differences in seed quality when the plants were cultivated at 21 or 24°C. However, these authors concluded that there is a deleterious effect of high drying temperatures on seed quality, especially for immature seeds.

The effect of mineral nutrition on the germination quality of pea seeds has also been reported in a few papers. Hadavizadeh and George (1988), working on plants grown in pots under glass, observed no effect of potassium, but they found an increase in seed vigor (assessed by the conductivity test) for the situations where high nitrogen was combined with medium phosphorus supply. Keiser and Mullen (1993) showed under hydroponic conditions that poor seed Ca concentration was associated with a low percentage of normal seedlings. Smiciklas et al. (1989) obtained the same results in soybean. In our experiments, no significant differences in mineral nutrition between treatments and between years were observed. But there was a difference (2.5 to 3 °C) in mean temperature during seed dessiccation, especially between 1992 and 1993. These differences could be partly responsible for the quality differences among years for the WI treatments.

Our results should also be discussed regarding irrigation strategies. The WI treatment showed the best results, as assessed by seed yield, and a high seed physiological quality. The late irrigations needed in this strategy could, however, lead to pathological decreases in quality in field conditions where aspersion is used. But the strategy for pea seed production practiced at present in France is based on irrigation until the beginning of seed filling. This strategy, corresponding to IBSF treatments in our experiments, led to failures in seed yields mainly due to low mean seed weights and to uncertain physiological quality. The strategy involving irrigation limited to the seed filling period (IDSF treatment) gave low seed numbers.m^{-2}, which was consistent with other authors' results (Silim et al., 1992; Ney et al., 1994), but not low seed yields due to higher mean seed weights. The seed physiological quality with this strategy was as high as in the well-irrigated treatment. Mean seed weight was also less variable, which might lead to higher quality of seedlings at emergence (Deneufbourg and Duchêne, 1994). An adequate water supply during seed filling without irrigation during the flowering period could therefore be tested as an alternative strategy to obtain high quality seedlots with high seed yields.

In our results, seed viability was never affected by water management, as shown by the high levels obtained in the germination tests. However, the results of the two vigor tests showed strong differences in seed vigor between the different treatments. Moreover, the relationship between these two tests is rather high (Fig. 3). This illustrates that both tests measure the same property of the seeds, i.e. susceptibility to imbibition damage, which is not assessed by germination tests carried out in optimal germination conditions.

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Fig. 1. The climate during the three years of a field irrigation timing experiment (1991 = a; 1992 = b; 1993 = c) on ' Solara ' pea. S = sowing date, BF = beginning of flowering, IGF = initiation of seed filling (----- for WI treatment and — for NI treatment), EGF = end of seed filling (----- for WI treatment and — for NI treatment). D1, D2 and D3 are the first, second and third decade of each month, respectively.

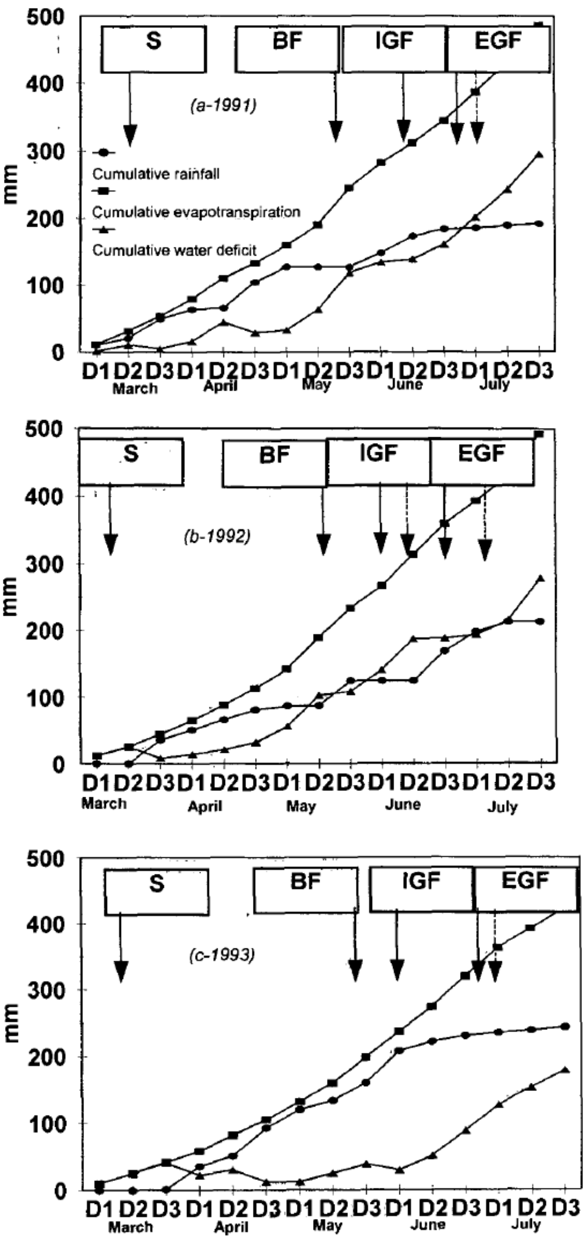

Fig. 2. Within-lot variability of mean seed weight of « Solara » pea for water stress imposed at different stages of plant development (data for 1992 only).

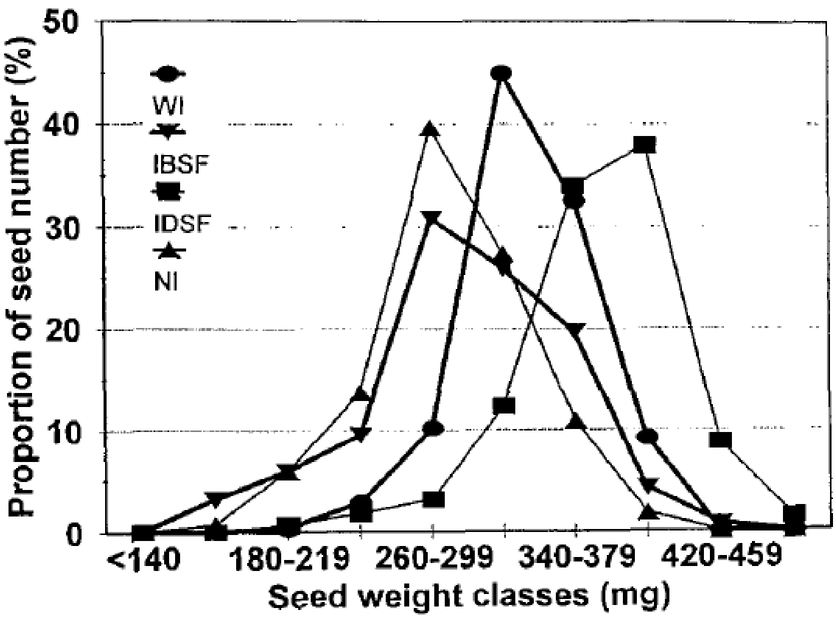

Fig. 3. Relationship between the conductivity test (X-axis) and germination percentage with cold test (Y-axis) in pea. Each point is the mean value for a water treatment for a given year. Treatments correspond to water stress imposed at different stages of plant development. The line represents the linear regression ($Y=-0.86X+208.44$, $r^2=0.75$)

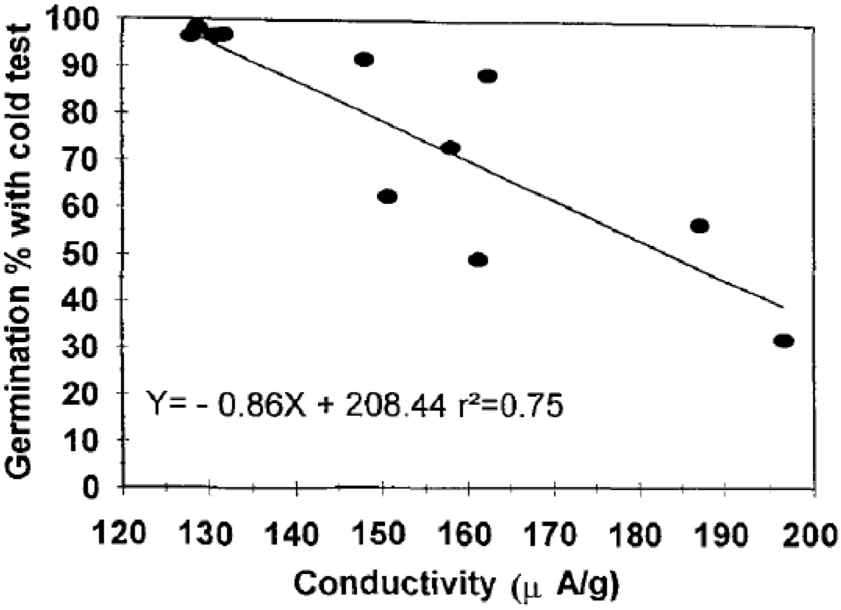

Table 1. Yield and yield components of ' Solara ' pea as affected by water treatment imposed at different stages of plant development for the three years.

Year	Treatment	Flowering nodes plant $^{-1}$	Mean seed weight	seed number m^{-2}	Seed yield
			mg, 0% moisture		$t.ha^{-1}$, 0% moisture
	NI†	5.1	253	1533 b‡	3.89 b
1991	IBSF	7.1	245	1918 ab	4.70 b
	WI	7.6	264	2368 a	6.26 a
		NS	*NS*	*	*
	NI	5.3 b	232 c	1882 b	4.37 c
1992	IDSF	5.7 b	293 a	2057 b	6.03 b
	IBSF	8.7 a	238 c	2109 b	5.02 c
	WI	9.5 a	262 b	2868 a	7.51 a
		***	***	***	***
	NI	8.3	257 b	2360 a	6.05 a
1993	IDSF	8.2	288 a	2477 a	7.14 a
	IBSF	8.7	240 c	2441 a	5.88 a
	WI	9.1	274 a	2603 a	7.13 a

	NS	**	*	*

*, ** and *** Significant at the 0.05, 0.01 and 0.001 levels, respectively.

† IBSF= pea irrigated before seed filling and not during seed filling; IDSF = pea irrigated during seed filling and not during the period from the start of flowering to the initiation of seed filling; NI = non-irrigated; WI = pea irrigated during the whole growing season.

‡ Treatments within a column and year followed by the same letter are not significantly different with the Newman-Keuls test at the 5% level.

Table 2. Mean physiological quality of ' Solara ' pea as affected by water treatments imposed at different stages of plant development for the three years.

Year	Treatment	Germination percentage	Conductivity test	Cold test
		% normal seedlings	µA.g^{-1}	% normal seedlings
	NI†	99.0	196.7 a‡	32.3 b
1991	IBSF	98.3	161.2 b	49.3 ab
	WI	98.3	150.7 b	62.7 a
		NS	**	*
	NI†	91.2	187.1 a	57.0 b
1992	IDSF	98.8	148.0 b	92.0 a
	IBSF	96.7	158.0 b	73.3 ab
	WI	96.2	162.3 b	88.7 a
		NS	**	*
	NI	98.3	128.0	96.7
1993	IDSF	98.0	128.7	98.3
	IBSF	98.0	131.7	97.0
	WI	97.7	130.7	96.7
		NS	*NS*	*NS*

*, ** Significant at the 0.05 and 0.01 levels, respectively.

† IBSF= pea irrigated before seed filling and not during seed filling; IDSF = pea irrigated during seed filling and not during the period from the start of flowering to the initiation of seed filling; NI = non-irrigated; WI = pea irrigated during the whole growing season.

‡ Treatments within a column and a year followed by the same letter are not significantly different with the Newman-Keuls test at the 5% level.