

Cucumber Seed Germination: Effect and After-effect of Temperature Treatments

Eugeniya F. Markovskaya • Elena G. Sherudilo • Marina I. Sysoeva*

Institute of Biology, Karelian Research Centre of Russian Academy of Sciences, Pushkinskaya st. 11, Petrozavodsk, 185910, Russia

Corresponding author: * sysoeva@krc.karelia.ru

ABSTRACT

In this review an attempt has been made to analyze the results of the studies on the problem of cucumber seed germination under different temperature treatments published since the 1950s, including papers that have been available in Russian only. The effects of daily alternating temperatures on cucumber seed germination have been studied for decades. There are different types of temperature pre-germination seed treatments, i.e. by constant low temperature and daily alternating temperatures (daily temperature gradients and temperature drop). This review shows that temperature treatments affect cucumber seed germination and have long after-effects on subsequent plant growth and development. Temperature pre-germination treatments of cucumber seeds can enhance plant development, increase plant productivity and resistance. The level of plant response depends on the type of treatment.

Keywords: *Cucumis sativus* L., daily alternating temperatures, low temperature, phytochromes, temperature drop

CONTENTS

INTRODUCTION.....	25
EFFECTS AND AFTER-EFFECTS OF CONSTANT LOW TEMPERATURES.....	25
Pre-germination seed treatments and germination.....	25
Pre-germination seed treatments and plant growth and development.....	26
Seed freezing.....	27
Seed cooling.....	27
EFFECTS AND AFTER-EFFECTS OF DAILY ALTERNATING TEMPERATURES.....	27
Pre-germination seed treatments and germination.....	27
Pre-germination seed treatments and plant growth and development.....	28
Seed freezing.....	28
Seed cooling.....	28
Temperature drop.....	28
TEMPERATURE AND PHYTOCHROME CONTROL.....	29
FUTURE PERSPECTIVES.....	29
ACKNOWLEDGEMENTS.....	29
REFERENCES.....	29

INTRODUCTION

Seeds play a very important role in nature, agriculture and horticulture. Seeds are a special plant organ with specific properties and functions. Simple in their structure and design, seeds are very species-specific. Seed germination is a complex process and it is regulated by many factors such as nutrient, temperature, water, light and substrate (Shinomura *et al.* 1996; Nikolaeva *et al.* 1999). Environmental factors affect seeds during their maturation (Spears *et al.* 1997; Bettey and Finch 1998), storage (Barton 1964; Rakowski *et al.* 1998), germination (Simon *et al.* 1976; Felipe 1980; Mayer and Poljakoff-Mayber 1989) and also have an after-effect on subsequent plant growth and development (Kandina 1958; Buduryan 1962; Genkel' and Kushnirenko 1966).

In this review we focus on temperature effects on cucumber seed germination and subsequent plant growth and development. Different types of temperature pre-treatments of seeds are described in the literature: constant temperature and daily alternating temperature (daily temperature gradients and temperature drop).

EFFECTS AND AFTER-EFFECTS OF CONSTANT LOW TEMPERATURES

Pre-germination seed treatments and germination

Initial low temperature enhances the seed germination of many species (Lewak and Rudnicki 1977; Nikolaeva 1967, 1979, 1982). Several hours or a few days of low temperature incubation, referred to as prechilling, promote the germination of non-deep dormant seeds (Nikolaeva 1999). Cucumber seeds have an endogenous, non-deep physiological dormancy that disappears with dry storage during normal handling (Genève 1998). Dormancy of cucumber seeds can be induced by imbibing in -1.8 MPa polyethylene glycol solution and pulsing with far red light for 15 min prior washing and drying. When re-imbibed with water at 20°C, dormancy is broken by raising the temperature to 30°C for 6 h. Cucumber seeds with broken dormancy were found to germinate in water over a smaller temperature range than seeds in which dormancy had not induced (Amritphale *et al.* 2000). Cucumber seed germination does not require expo-

sure to low temperature, but the survival and performance of seeds after sowing are affected by many environment factors, including temperature. Low temperature applied after sowing not only reduces germination percentage in many cold-sensitive plants but also delays it (Thomas 1981). Cucumber seeds germinate rapidly at temperatures between 17 and 25°C, are able to germinate at temperatures below 14°C (Mancinelli and Tolkowsky 1968; Eisenstadt and Mancinelli 1974; Simon *et al.* 1976; Staub *et al.* 1989; Russo and Biles 1996), but the majority of cucumber seeds fail to germinate at temperatures below 11.5°C (Simon *et al.* 1976). Minimum germination temperature varied from 11.7 to 15.0°C for cucumber seeds (Røeggen 1987). The ability of cucumber seeds to germinate at low temperatures is cultivar dependent (Lower 1974; Staub and Wehner 1987). Research on the physiological aspects of low temperature germination was conducted by Nelson and Sharples (1980). In cucumber cultivars fresh seed dormancy can be overcome by removal of the seed coat, infusion of any of several regulators or dissipated during storage. Breeding programs have searched how to improve low temperature germination in cucumber (Nienhuis *et al.* 1983; Wehner 1984). Populations representing 4 cycles of recurrent half-sib selection for improved germinability at 15°C in a genetically broad-based population were evaluated for seedling emergence and other horticultural characteristics under field conditions. Results indicated that selection improved percentage emergence 7 days after sowing and mean number of days to emergence without affecting sex expression, seedling vigour or yield.

Germination at low temperatures could be improved by various pre-germination seed treatments. Edwards *et al.* (1986) increased germination by fermenting seeds for 4 days at 25°C. However, Nienhuis and Lower (1979) have shown that germination of cucumber seeds after fermentation was reduced at a suboptimal temperature of 15°C. Nelson and Sharples (1980) reported that the soaking of cucumber seed in fusicoccin increased germination, and that fusicoccin was more effective than gibberellic acid (GA_{4/7}, GA₃), or ethephon. On the other hand, growth regulators, which promote germination under prolonged exposure to suboptimal temperatures do not necessarily promote emergence in cool soil under field conditions (Staub and Wehner 1987).

Cucumber seed germination could also be promoted by seed pre-treatment with constant negative temperature (freezing of seeds). Vladimirova (1952) has shown that freezing of soaked cucumber seeds (cvs. 'Nerosimyi' and 'Nerosimyi-Havsky') at -2 to -5°C for 2 days strongly promoted germination at +10 to +12°C and increased cold hardening of cucumber seedlings. Freezing of soaked cucumber seeds for 12 h at -1°C increased cold and frost hardening of two-weeks-old seedlings (cvs. 'Muromsky', 'Vjaznikovskiy' and 'Nerosimyi') but not in cv. 'Klinsky' (Androsova 1940).

The hypothesis exists that changes in membrane order and lipid composition, reflected in a decrease in viscosity, are responsible for the pre-chilling phenomenon (van der Woude and Toole 1980). The concept that water entry into dry tissues leads to reorganization of membranes and that chilling temperatures interfere with this reorganization, was first suggested for yeast re-hydration by Herrera *et al.* (1956). The fact that chilling temperatures applied during the first water imbibition damage seeds of many species was noted by Pollok and Toole (1966). van Steveninck and Ledebor (1974) suggested on the basis of Arrhenius plots that the damage from chilling rehydrating yeast cells was possibly related to a phase transition which caused interference with lipid organization at low temperatures.

Simon *et al.* (1976) noted that denaturation of unspecified cucumber proteins was the most likely reason that seeds did not germinate well at low temperatures. If this is true, there may be problems in membrane reestablishment (Simon 1974), which may prevent the formation of organelles or compromise the integrity of plasma membranes.

They also found that lowered cucumber germination due to low temperatures was: 1) not due to imbibition of cold water or loss of membrane integrity, and 2) most likely due to denaturing of proteins, which may cause inactivation of enzymes. If this is the case, the orderly association of proteins into mitochondria or ribosomes may be prevented (Simon *et al.* 1976). These organelles provide the energy for, and formation of newly synthesized mRNAs that are required for commencement of radicle elongation and further development (la Londe and Bewley 1986; Datta *et al.* 1987). Russo and Biles (1996) suggest that low germination rates at suboptimal temperatures are due to: 1) the leakage of minerals, and/or 2) the lack of formation or denaturation of proteins of specific weights. The latter appears to support the importance of proteins in activities affecting germination as proposed by Simon *et al.* (1976). In addition, proteins of specific K_d weights were found, that appear to be important in germination.

In contrast to the seeds of other Cucurbitaceae, cucumber seeds are able to germinate while completely submerged in water. Alhokol dehydrogenase activity of control and submerged cucumber seeds were similar. However, the ethanol content of submerged seeds was substantially higher than that of control seeds. Isocitrate lyase activity of control seeds increased following radical protrusion while no increase in activity was observed in the submerged seeds after radicle protrusion. The oxygen uptake of seeds after 16 h submersion was much lower than that of the control (Rabie *et al.* 1989).

Magnetic field pre-treatments (0.2 and 0.45 T) increased cucumber seed germination rate, seedling growth and development, lipid oxidation and ascorbic acid contents. Also this pre-treatment increased the sensibility of cucumber seedlings to UV-B radiation (Yao *et al.* 2005). Osmo-conditioning also improved the rate of germination of cucumber seeds (cv. 'Telegraph') at 25°C and 15°C in water and NaCl solutions of up to 200 mM. At 15°C the total percentage of germination was also increased. Osmoconditioning promoted the rates of radicle extension, seedling emergence and expansion of the cotyledons and first leaf, but the benefits of treatment did not persist beyond the seedling stage (Passam and Kakouriotis 1994).

Soil-borne pathogen *Pythium ultimum* can cause severe losses to field- and greenhouse-grown cucumber and other cucurbits. Live cells and ethanol extracts of cultures of bacterium *Serratia marcescans* N4-5 provided significant suppression of damping-off of cucumber caused by *P. ultimum* when applied as a seed pre-treatment. Live cells of this bacterium also suppressed damping-off caused by *P. ultimum* on muskmelon and pumpkin (Roberts *et al.* 2007).

Cucumber plants irrigated with effluent mixtures from rubber sheet factories had higher yield than control plants (Chaiprapat and Sdoodee 2007). The effect of different concentrations of distillery effluent (raw spent wash) (from 0 to 100%) on cucumber seed germination, germination rate, peak value was studied by Ramana *et al.* (2002). They show that the distillery effluent did not show any inhibitory effect on seed germination. At highest concentration (75 and 100%) complete failure of germination was observed and a concentration of 25% was critical for cucumber seed germination.

Plants need to be included to develop a comprehensive toxicity profile for nanoparticles. Nanoparticles (multi-walled carbon nanotube, aluminum, alumina, zinc and zinc oxide) not effected on cucumber seed germination but inhibited root growth. The inhibition occurred during the seed incubation processes rather than seed soaking stage (Lin and Xing 2007).

Pre-germination seed treatments and plant growth and development

Temperature pre-germination seed treatment is well known as a pre-sowing hardening method. Russian researchers have actively studied it in the 1950s. Grachev (1875) was

the first who used the method of seed pre-sowing hardening to increase the development of corn plants in the St. Petersburg region. The method was widely used for promoting seed germination, increasing plant resistance to low positive temperatures and short-term freezing and increasing plant productivity, especially in the regions with continental climate (Strekova 1962; Kushnirenko 1961, 1962; Genkel' and Kushnirenko 1966). In seed pre-germination treatment either constant low positive temperature (seed cooling) or negative temperatures (seed freezing) can be used. These treatments have different effects on seed germination and after-effects on subsequent plant growth and development.

Seed freezing

Freezing of melon seeds (*Cucumis melo* L., *Melo zard*, cvs. 'Umir-Vaki' and 'Asma') at -4°C for 6 and 24 h had no effect on seed germination under laboratory conditions, but increased germination in the field (Buduryan 1962). Freezing of cucumber seeds (*Cucumis sativus* L., cv. 'Nerosimiyi') at -2 to -5°C for 2 days (Vladimirova 1952), melon seeds (*Melo zard*) at -2.5°C for 2.5 days (Tarbaeva 1957), *Melo zard* (cvs. 'Umir-Vaki' and 'Asma') at -4°C for 6 and 24 h (Buduryan 1962) inhibited growth of the main root at the early stages of ontogenesis, but later increased root development and stimulated growth and formation of lateral roots. Freezing of seeds affected *Cucurbitacea* plant growth and development viz. increased leaf formation, leaf and shoot dry weight, and stimulated the formation of female flowers. For instance, in melon (*Melo zard*, cvs. 'Umir-Vaki' and 'Asma') freezing of seeds at -4°C for 6 h twice promoted increment of leaf formation in compare with control, increased leaf area by 44-67%, induced earlier and intensive flowering, increased flower number from 16% (cv. 'Umir-Vaki') to 69% (cv. 'Asma'), promoted early fructification (for 6-7 days) and increased yield by 37-42% (Buduryan 1962). Edel'shtein (1949) and Tarbaeva (1957) also showed accelerated development, flowering and yield after freezing of melon seeds at -2°C for 2-5 days. According to Lebl (1954) effect of temperature of -2 to -5°C during 1 day on moister seeds of squash promoted increment of leaf blade and yield by 10-20%. In cucumber (cvs. 'Nerosimiyi' and 'Nerosimiyi-Havsky') freezing of seeds at -2 to -5°C induced the intensive flowering, early fructification (for 3-8 days) and increased the yield by 40-70% (Vladimirova 1952). The positive effect of cucumber seeds freezing (cv. 'Nerosimiyi') at -0.5 to -5°C for 12-24 h was also shown in more early experiments (Androsova 1940; Raudsepp 1957). Then, Kandina (1958) increased yield by 25.9% after freezing cucumber seeds (cvs. 'Berlizovsky', 'Nezhinsky-12' and 'Tiraspol'sky-6') at -2°C for 12-24 h. Studies with another cucumber cultivar ('Nerosimiyi') also demonstrated an increment in early yield by 22% after freezing of seeds at -3°C for 3-4 days (Genkel' and Kushnirenko 1966). The effect of freezing temperatures on seeds induces the changes in plant metabolism, such as the increase in ascorbic acid and chlorophyll contents (Buduryan 1962; Kandina 1962) that in turn leads to an increase in plant cold resistance (Androsova 1940; Vladimirova 1952; Lebl 1954).

Some authors showed a negative effect of seed freezing on subsequent growth and development of cucurbit seeds i.e. delayed plant development and decreased yield (Zauralov and Tarhanova 1960).

Seed cooling

Pre-germination treatment of cucumber seeds by low positive ($\geq 0^{\circ}\text{C}$) temperatures is also a very effective tool to increase plant cold resistance and productivity (Voronova 1953; Genkel' and Kushnirenko 1966). Seed proteins and carbohydrate compounds have been implicated in a regulatory role, with higher oligosaccharide (fructose, sucrose, raffinose, stachyose) concentrations lending more cold-tolerance (Jennings 1999; McPhee *et al.* 2002). Germination at cold temperature also appears to be associated with

proteins, possibly proteases. For instance, the increment of proteolytic activity, activity of invertase and amylase, accumulation of soluble sucrose and starch already at the early development stage in seeds and then in seedlings and adult plants have been shown by Kandina (1962) and Buduryan (1962) after cooling of moister cucumber (cv. 'Tiraspol'sky-6') and melon (cvs. 'Umir-Vaki' and 'Asma') seeds at 0°C for 1 day.

Seed cooling promotes subsequent plant growth and development during the acclimatization of warm-sensitive species and cultivars to northern latitudes (Panteleeva 1953; Tarbaeva 1957; Buduryan 1958, 1962). Studying the acclimation of melon (*Cucumis melo* L., convar. *zard* (Pang.) Greb.) from Central Asian to Moldavia Panteleeva (1953) observed that cooling of moister seed at 0°C hastened flowering and ripening to 6-8 day in compare with control. Analyzing the biological mechanisms of development melon of Central Asian in region of Siberia (city Novosibirsk) Tarbaeva (1957) came to the conclusion that seed hardening at 0°C to $+2^{\circ}\text{C}$ for 2-5 days induced early germination and rapid plant growth and development in comparison with control, stimulated growth of main root and increased formation of lateral roots, leaf area, early and intensive flowering and ripening, yield. Buduryan (1962) also suggested that cooling melon seeds (*Melo zard* cvs. 'Umir-Vaki' and 'Asma') at 0°C for 24 h stimulated root growth, abundant root branching and accelerated fruit growth. Cooling of cucumber seeds (cvs. 'Nerosimiyi' and 'Nerosimiyi-Havsky') at 0°C to $+2^{\circ}\text{C}$ for 2 days increased plant cold resistance during the early stage of ontogenesis, induced root development, leaf area, formation of female flowers, hastened ripening to 3-7 days and increased yield by 40-70% (Vladimirova 1952). According to Kandina (1958, 1962) cooling of cucumber moister seeds (cv. 'Tiraspol'sky-6') at 0°C for 12 or 24 h increased contents of soluble sugar, protein nitrogen, chlorophyll and ascorbic acid, caused an increase in respiratory activity of young plant, as well as stimulated formation of female flowers, increment of yield by 17.2% and improvement of fruit quality (more content of dry weight, sugar, vitamin C and total nitrogen).

EFFECTS AND AFTER-EFFECTS OF DAILY ALTERNATING TEMPERATURES

There is much data in the literature proving that seeds germinate better under alternating temperatures than under a constant daily temperature (Genkel' *et al.* 1955; Tarbaeva 1957; Buduryan 1962; Felipe 1980; Shin *et al.* 2006). Alternating temperature regimes are faster and stronger inducers of germination compared to constant low-temperature regimes and are characterized by the following parameters: temperature value, value of temperature DIF (difference between day and night temperatures), duration of temperature treatment per day and total duration of treatment (days) (Markovskaya and Sysoeva 2004).

Pre-germination seed treatments and germination

Seed pre-treatment by daily alternating temperature regimes including negative temperatures (seed freezing) had no effect on cucumber seed germination or decreased germination under the optimal temperature of $22-25^{\circ}\text{C}$ (Kushnirenko 1962; Belik *et al.* 1964; Genkel' and Kushnirenko 1966), but significantly increased seed germination under 80% soil humidity (Genkel' and Kushnirenko 1966). Seed pre-treatment by daily alternating temperature regimes including low positive temperatures had either no effect on cucumber seed germination (Buduryan 1962; Genkel' and Kushnirenko 1966) or increased it (Buduryan 1962; Makaro and Kondrat'eva 1953; Genkel' and Kushnirenko 1966), especially under unfavorable conditions (Genkel' and Kushnirenko 1966).

The germination response of cucumber seeds to light is temperature sensitive. Daily alternating temperatures $25/10$ and $25/5^{\circ}\text{C}$ in combination with white light fully counter-

acted the inhibitory effect of light on germination of cucumber seeds (Felippe 1980). The germination is inhibited by both blue light and far red and promoted by red light and darkness. The inhibitory effect of far red light is reversed by red light (Noronha *et al.* 1978). Darkness is very effective in promoting germination of *C. sativus* when the temperature is kept constant at 25°C (Noronha *et al.* 1978). The short exposure to high temperature in darkness had no effect for germination of cucumbers, but low temperature promoted germination. It was suggested the ecological consideration: alternating temperatures often occur during autumn-winter in various regions of Brazil and cucumber seeds should germinate regardless of the light regime. The germination of *C. sativus* occurs when far red is given together with 5°C followed by white light at 25°C (Felippe 1980).

The daily temperature gradient of 15/35°C strongly promoted germination of cucumber seeds (Felippe 1980). Germination percentage estimated as a fraction of germinated seed of the total number of sown seeds changed from 30% at 15°C to 72% at 25°C (Markovskaya 1994). The region of optimum temperatures for maximal germination percentage involved the range from 21 to 31°C for day temperature and from 24 to 35°C for night temperature (Markovskaya 1994). Northern cucumber cultivars had a more pronounced response to pre-germination seed treatments by daily alternating temperatures than southern cultivars (Belik *et al.* 1964).

Pre-germination seed treatments and plant growth and development

In Russia the method of seed hardening by daily alternating temperatures was first introduced by Voronova in the 1950s. She conducted research in Northern Ural, a region with continental climate, where sharp diurnal temperatures fluctuate and where there are frequent morning frosts from April to June and in August create many problems for growing heat-loving plants. Pre-germination seed treatments by daily temperature alternating regimes resulted in enhanced plant development, increased cold and/or frost resistance and improvement of plant productivity. The method proposed by Voronova has been extensively used in the 1950-1960s in Russia for growing resistant seedlings outdoors and studying after-effects of seed pre-hardening on a plant's physiological status (Kushnirenko 1962; Belik 1963; Genkel' and Kushnirenko 1966). The method was based on the use of daily alternating temperatures, which included combinations of optimal and negative temperatures (seed freezing) or optimal and low positive temperatures (seed cooling). As a rule the temperature has been decreased from +18 to +20°C to -3 to +9°C for 12-18 hours during 3-30 days. Seeds were soaked for 12 h at +18-+20°C for swelling before hardening. Duration of soaking and hardening depends on the plant species and even on the cultivar. For instance, Kushnirenko (1962) has recommended to use the daily alternating temperatures for hardening of tomato and maize seeds: temperatures from -3 to -5°C for 18 h and from +15 to +18°C for 6 h; duration of seeds hardening was 7-10 days for tomato and 14 days for maize. A combination of low (-3 to +1°C for 18 h) and optimal temperatures (+15 to +18°C for 6 h) during 3-5 days was used for cucumber (*C. sativus* L., cv. 'Nerosimiyi') (Kushnirenko 1962; Genkel' and Kushnirenko 1966). Duration of seeds soaking before hardening was 2-12 h for cucumber, 12 h for tomato and 24-48 h for maize (Kushnirenko 1962; Genkel' and Kushnirenko 1966). The following combination of optimal (+18 to +20°C for 6 h) and low temperatures (0°C for 18 h) was used for tomato seeds with total duration of hardening of 16 days and duration of soaking - 24 h (Shutov and Belyaev 1955). According to Belik (1963) seeds of southern cucumber cultivars (*C. sativus* L., cvs. 'Azovka-5', 'Astrahansky-136', 'Donskoi-175') should harden at the combination of optimal (+18 to +20°C) and low positive (+2 to +5-9°C) temperatures than seeds of northern cultivars (*C. sativus* L., cvs. 'Muromsky-6', 'Altaysky ranny-166').

Seed freezing

Freezing of cucumber seeds (*C. sativus* L., cvs. 'Nerosimiyi', 'Nerosimiyi-Havsky', 'Nezhensky') at temperatures from -2 to -5°C for 16-18 h during 3-5 days decreased subsequent plant growth and development, but increased the number of leaves, flowers and fruits, the latter by 33% (Genkel' and Kushnirenko 1966), earliness and yield by 18-35% (Alexandrov and Brisov 1954; Voronova 1956; Kushnirenko 1962; Genkel' and Kushnirenko 1966). Seed hardening by alternation of negative temperatures of -3 to -5°C and optimal temperatures of +18 to +20°C increased the protoplasm viscosity at early stages of ontogenesis and decreased it later (Strekova 1960), and increased cold resistance of plants and roots (Strekova 1960; Kushnirenko 1961, 1962; Genkel' and Kushnirenko 1966).

Seed cooling

Pre-germination seed treatments by daily alternating temperatures with low positive values (seed cooling) stimulated subsequent growth and development of cucumber plants, especially under unfavorable conditions. Using the following combination of optimal (+18 to +19°C for 6 h) and low temperatures (around 0°C for 18 h) for seed of melon (*Melozard*, cvs. 'Umir-Vaki', 'Asma', '№ 4464b') Buduryan (1962) showed stimulation of root growth and lateral root branching, increment of top and stem length, increase in number of second-order branches. Furthermore, acceleration of flowering (to 3-10 days in compare with control), doubling the number of female flowers, increase of fruit ripening and enhanced the yield by 35-64% were shown. Early work by Tarbaeva (1957) also indicated positive effect of melon seed cooling by daily alternating temperatures (+18 to +20°C/+2°C, day/night) on enhancement of root growth and acceleration of ripening. To increase the yield of cucumber (*C. sativus* L., cv. 'Leningradsky teplichny') Lugovkin (1957) recommended cooling cucumber moist seeds at daily alternating temperatures (0°C for 18 h and +20 to +25°C for 6 h during 14 days): increment of early yield was 11.8%, of total yield, 16.8%. Cucumber seed cooling also increased stem length (Genkel' and Kushnirenko 1966), enhanced root growth (Tarbaeva 1957; Buduryan 1962), leaf formation (Buduryan 1962; Genkel' and Kushnirenko 1966) and dry matter accumulation (Belik 1963). Seed cooling induced biochemical changes in plants by changing the activity of proteolytic enzymes, invertases and amylases and increasing the content of soluble sugars, starch, chlorophylls and ascorbic acid (Kandina 1958; Buduryan 1962; Kandina 1962), and affected physiological processes by increasing the activity of redox processes, intensifying plant respiration (Shutov *et al.* 1955; Kandina 1962; Buduryan 1962), increasing plant cold resistance (Vladimirova 1952; Tarbaeva 1957; Genkel' and Kushnirenko 1966), vascular wilt plant resistance and anthracnose resistance (Buduryan 1962). Low cucumber germination rates at suboptimal temperatures were related to leakage of minerals and/or the lack of formation or denaturation of proteins associated with germination and radicle elongation (Russo and Biles 1996).

Seed cooling by daily alternating temperatures and enhanced the yield by 18-64% (Buduryan 1962; Makaro and Kondrat'ev 1953; Belik 1963; Genkel' and Kushnirenko 1966).

Temperature drop

Temperature drop is now widely used in the modern technologies of greenhouse production at the seedling stage (Moe and Heins 2000) but not intensively used as a pre-germination seed treatment. Short exposure of cucumber seeds from 25°C to 0°C for 55 min promoted germination in white light (Felippe 1980). Pre-germination treatment of cucumber seeds by a 2 h temperature drop from 23°C to 10°C for 6 days and a long-term pre-germination treatment at 10°C increased plants' resistance to cold by the end of the first

week after sowing, but the level of cold resistance was three times higher after the temperature drop treatment than after the constant low temperature (Sherudilo *et al.* 2006a). Therefore, temperature drop treatment at the seed stage can enhance cold resistance in plants (Sherudilo *et al.* 2006a).

Pre-germination seed treatment by a temperature drop is an effective technique not only for increasing cold resistance but also for promoting plant growth and development (Sherudilo *et al.* 2006b). Pre-germination treatment by a temperature drop of *Tagetes patula* L. and *Petunia* seeds stimulated seed germination by 30%, hastened plant development by a week, increased plant dry weight, and promoted flowering by 33% in both species (Sherudilo *et al.* 2006b).

Pre-germination seed treatments by a temperature drop is an effective tool for improving plant quality and promoting plant growth and development.

TEMPERATURE AND PHYTOCHROME CONTROL

Most seeds germinate when incubated in absolute darkness (Ranjan 2002). This indicates that the phytochrome in far-red form (Pfr) is already present in the seed and/or that germination does not require Pfr. Cresswell and Grime (1981) have shown a negative correlation between germination in darkness and chlorophyll content in extra-embryonic tissues. Those seeds that retain green tissues around the embryo for a prolonged period have most of the phytochrome in the red form. The red/far-red ratio experienced by the mother plant can also be important for the germination of dark-imbibed seeds.

Cucumber seeds are dark-germination, light-inhibited seeds. Inhibition of germination requires prolonged exposure to light (Mancinelli *et al.* 1967; Yaniv *et al.* 1967; Mancinelli *et al.* 1975; Noronha *et al.* 1978) and can be brought about by blue, FR, various combinations of R and FR, and white light from incandescent lamps (Eisenstadt 1973; Mancinelli *et al.* 1975; Noronha *et al.* 1978). Phytochrome control of cucumber seed germination is temperature-dependent. In experiments in which the daily alternating temperature 25/5°C was combined with FR cucumber seeds germination was promoted when FR was given during the 5°C period followed by light or darkness at 25°C, but when FR was given at 25°C followed by white light or darkness during the 5°C period germination was not promoted (Felippe 1980). It has been shown that the germination of cucumber seeds for 4 or more days at an inhibitory light treatment is not promoted by a short R at temperatures below 20°C, but at 25°C the germination is promoted without exposure to R (Mancinelli *et al.* 1967; Eisenstadt 1973). It has been concluded that these results seem to show that phytochrome is no longer the factor responsible for the activation of germination and that at high temperatures there is an escape from phytochrome control. Later Eisenstadt and Mancinelli (1974) concluded that if higher temperatures are used for short periods only, from 2 to 6 hours, in combination with short R, one can demonstrate that activation of germination of cucumber (*C. sativus* L., cv. 'Pixie') at high temperatures is still dependent on phytochrome. Phytochrome is probably destroyed during prolonged exposure to FR. Thus, the subsequent short R establishes levels of Pfr, which may not be sufficient to promote germination at low temperatures but are probably adequate at high temperatures. The authors believe that the apparent escape of cucumber seed germination from phytochrome control is not real. At high temperatures the rate of the Pfr-dependent reactions is faster than at low temperatures and probably overrides the effect of phytochrome destruction. Thus, high germination rates occur even at low concentrations of Pfr.

FUTURE PERSPECTIVES

An analysis of the literature showed that temperature treatments affect cucumber seed germination and have long after-effects on subsequent plant growth and development. Pre-germination treatments could include low positive tem-

peratures as well as negative temperatures. The mechanism of cold-tolerant germination is complex and only partially understood. It is Nleya *et al.*'s (2005) opinion that an alternating temperature signal around the base temperature can achieve equivalent results to exposure constant temperature and, possibly, an alternating temperature signal for less time may achieve the same response as a more lengthy exposure to a constant but higher temperature. Seed appears to respond to several degrees above the base temperature for several days, or a larger jump in temperature for less time. It is very important that temperature pre-germination treatments of cucumber seeds by constant low temperatures and daily temperature gradients can enhance plant development, increase plant productivity and plant resistance. Recently, it has been shown that seedlings can remember the temperatures and photoperiod prevailing during zygotic embryogenesis and seed maturation (Johnsen *et al.* 2007). An epigenetic memory of plants from embryo development should be the focus of future studies.

ACKNOWLEDGEMENTS

Study was supported by Russian Foundation for Basic Researches, projects № 05-04-97515, № 07-04-48029.

REFERENCES

*In Russian

- Aleksandrov SB, Brisov NS** (1954) Priemy poluchenija vysokih ustojchivyh i rannih urozhaev ogurcov. *Sad i Ogorod* **2**, 28*
- Amritphale D, Sreenivasulu Y, Singh B** (2000) Changes in membrane fluidity and protein composition during release of cucumber seeds from dormancy by a higher temperature shift. *Annals of Botany* **85**, 13-18
- Androsova MP** (1940) O vlijanii ohlazhdenija semjan i vshodov na urozhaj ogurcov. *Vestnik Sel'skhozajstvennoj Nauki. Ovoschi i Kartofel'* **3**, 98*
- Barton L** (1964) *Hranenie Semjan i ih Dolgovechnost'*, Izdatel'stvo "Kolos", Moskva, SSSR, 204 pp*
- Belik VF** (1963) Vlijanie zakalki semjan peremennymi temperaturami na fiziologicheskie osobennosti i holodostojkost' ogurcov. *Fiziologija rastenij* **10**, 351-357*
- Belik VF, Solomina IP, Plahova SM, Koziner Eh** (1964) Nekotorye fiziologicheskie osobennosti prarastanija semjan ogurcov i bahchevyh kul'tur pri razlichnom temperaturnom rezhime. In: Belik VF (Ed) *Biologicheskie Osnovy Povyshenija Kachestva Semjan Sel'skhozajstvennyh Rastenij*, Izdatel'stvo Nauka, Moskva, SSSR, pp 17-31*
- Betty M, Finch-Savage WE** (1998) Stress protein content of mature Brassica seeds and their germination performance. *Seed Science Research* **8**, 347-355
- Buduryan NN** (1958) Vlijanie predpovednoj obrabotki semjan dyn' na process vydelenija pasoki. *Izvestija Moldavskogo filiala AN SSSR* **5**, 87-93*
- Buduryan NN** (1962) Vlijanie predpovednogo ohlazhdenija semjan na fiziologicheskie i biohimicheskie processy dyni vida Melo zard. In: Dorohov LM, Ivanov SM, Biblina BI (Eds) *Voprosy Fiziologii i Biohimii Kul'turnyh Rastenij* (Vol 1), Izdatel'stvo "Shtiinca" Akademii nauk Moldavskoj SSR, Kishinev, SSSR, pp 52-70*
- Chaiprapat S, Sdoodee S** (2007) Effects of wastewater recycling from natural rubber smoked sheet production on economic crops in southern Thailand. *Resources, Conservation and Recycling* **51**, 577-590
- Cressel EG, Grime JP** (1981) Induction of a light requirement during seed development and its ecological consequences. *Nature* **291**, 583-585
- Datta K, Parker H, Averyhart-Fullard V, Schmidt A, Marcus A** (1987) Gene expression in the soybean seed axis during germination and early seedling growth. *Planta* **170**, 209-216
- Edwards MD, Lower RL, Staub JE** (1986) Influence of seed harvesting and handling procedures on germination of cucumber seeds. *Journal of the American Society of Horticultural Science* **111**, 507-512
- Edel'shtein VI** (1949) Prodvizhenie bahchevyh kul'tur v severnyje rajony strany. *Doklady TSHA* **10**, 21-28*
- Eisenstadt FA** (1973) Diverse aspects of phytochrome controlled seed germination. PhD Thesis, Columbia University, New York, 50 pp
- Eisenstadt FA, Mancinelli L** (1974) Phytochrome and seed germination. VI. Phytochrome and temperature interaction in the control of cucumber seed germination. *Plant Physiology* **53**, 114-117
- Felippe GM** (1980) Germination of the light-sensitive seeds of *Cucumis anguria* and *Rumex obtusifolius*: effects of temperature. *New Phytologist* **84**, 439-448
- Genève RL** (1998) Seed dormancy in commercial vegetable and flower seeds. *Seed Technology* **20**, 236-249
- Genkel' PA, Kushnirenko SV** (1966) *Holodostojkost' Rastenij i Termicheskie Sposoby ee Povyshenija*, Izdatel'stvo "Nauka", Moskva, SSSR, 223 pp*

- Genkel' PA, Sarycheva AP, Sitnikova OA** (1955) Vlijanie obrabotki semjan peremenoj temperaturoj na razvitie i sozrevanie kukuruzy. *Fiziologija Rastenij* 7, 447-453*
- Grachev EA** (1875) O razvedenii kukuruzy pod Peterburgom. *Trudy Vol'nogo Ekonomicheskogo Obschestva* 1, 165*
- Herrera T, Peterson WH, Cooper EJ, Peppler HJ** (1956) Loss of cell constituents on reconstitution of active dry yeast. *Archives of Biochemistry and Biophysics* 63, 131-143
- Jennings PH** (1999) Increasing chilling tolerance of seeds during imbibition and early stages of germination. *Seed Technology* 21, 66-71
- Johnsen Ø** (2007) An epigenetic memory from embryo development affects bud phenology and cold acclimation in Norway spruce plants. *8th International Plant Cold Hardening Seminar*, Saskatoon, Canada, p 14 (Abstract)
- Kandina GV** (1958) O reakcii ogurcov na predposevnuju obrabotku proras-tajuschih semjan holodom. *Izvestija Moldavskogo filiala AN SSSR* 5, 85*
- Kandina GV** (1962) Vlijanie predposevnogo ohlazhdenija proras-tajuschih semjan ogurcov na fiziologo-biohimicheskie processys. In: Dorohov LM, Ivanov SM, Biblina BI (Eds) *Voprosy Fiziologii i Biohimii Kul'turnyh Rastenij* (Vol 1), Izdatel'stvo "Shtiinca" Akademii nauk Moldavskoj SSR, Kishinev, SSSR, pp 71-79*
- Kushnirenko SV** (1961) Neproduktivnoe dyhanie list'ev i ustojchivost' teploljubivyh rastenij k ohlazhdeniju kornevnyh sistem. *Fiziologija Rastenij* 7, 345-354*
- Kushnirenko SV** (1962) Posledestvie preryvistogo ohlazhdenija semjan (zakalivaniya k holodu) na nekotorye fiziologicheskie osobennosti rastenij. PhD Thesis, Institut fiziologii rastenij im. KA Timirjazeva Akademii nauk, Moskva, SSSR, 20 pp*
- LaLonde L, Bewley D** (1986) Patterns of protein synthesis during the germination of pea axes, and the effects of an interrupting desiccation period. *Planta* 167, 504-510
- Lebl D** (1954) Poluchenie rannego vysokogo urozhaja kabachkov putem predposevnoj obrabotki semjan holodom i sposobom rassady v uslovijah Moskovskoj oblasti. PhD Thesis, TSHA, Moskva, SSSR, 24 pp*
- Lewak S, Rudnicki RM** (1977) After-ripening in cold requiring seeds. In: Khan AA (Ed) *The Physiology and Biochemistry of Seed Dormancy and Germination*, North Holland Publ Co, New York, pp 193-217
- Lin D, Xing B** (2007) Phytotoxicity of nanoparticles: inhibition of seed germination and root growth. *Environmental Pollution* 150, 243-250
- Lower RL** (1974) Measurement and selection for cold tolerance in cucumber. *Pickle Pack Science* 4, 8-11
- Lugovkin VD** (1957) Ovoschevodstvo. Moskva: Gosudarstvennoe izdatel'stvo sel'skhozajstvennoj literatury, SSSR, 218 pp*
- Makaro IL, Kondrat'eva AV** (1953) Predposevnaja obrabotka semjan i ovoschnyh kul'tur. *Sad i Ogorod* 2, 9-12*
- Mancinelli AL, Lindquist P, Anderson OR, Eisenstadt FA** (1975) Photocontrol of seed germination. VII. Preliminary observation on the development of the photosynthetic apparatus in light-inhibited seeds of Cucumber (*Cucumis sativus*). *Bulletin of the Torrey Botanical Club* 102, 93-99
- Mancinelli AL, Tolokowsky A** (1968) Phytochrome and seed germination. V. Changes of phytochrome content during the germination of cucumber seeds. *Plant Physiology* 43, 489-494
- Mancinelli AL, Yaniv Z, Smith P** (1967) Phytochrome and seed germination. I. Temperature dependence and relative Pfr levels in the germination of dark-germinating tomato seeds. *Plant Physiology* 42, 333-337
- Markovskaya EF** (1994) Adaptation of cucumber plants to temperature: the ontogenetic aspect. *Russian Journal of Plant Physiology* 41, 517-521
- Markovskaya EF, Sysoeva MI** (2004) Rol' sutochnogo temperaturnogo gradienta v ontogenese rastenii. Nauka, Moscow, 199 pp*
- Mayer AM, Poljakoff-Mayer A** (1989) *The Germination of Seeds*, Pergamon Press, Oxford, NY, 270 pp
- McPhee KE, Zemetra RS, Brown J, Myers JR** (2002) Genetic analysis of the raffinose family of oligosaccharides in common bean. *Journal of the American Society of Horticultural Science* 127, 376-382
- Moe R, Heins RD** (2000) Thermo- and photomorphogenesis in plants. Advances in Floriculture research. *Agriculture University of Norway*, Report № 6, 52-64
- Nelson JM, Sharples GC** (1980) Effect of growth regulators on germination of cucumber and other cucurbit seeds at suboptimal temperatures. *HortScience* 15, 253-254
- Nienhuis J, Lower RL** (1979) The effects of fermentation and storage time on germination of cucumber seeds at optimal and suboptimal temperatures. *Cucurbit Genetics Cooperative Report* 4, 13-16
- Nienhuis J, Lower RL, Staub J** (1983) Selection for improved low temperature germination in cucumber (*Cucumis sativus* L.). *Journal of the American Society of Horticultural Science* 108, 1040-1043
- Nikolaeva MG** (1967) Fiziologija Glubokogo Pokoja Semjan, Izdatel'stvo "Nauka", Leningrad, SSSR, 206 pp*
- Nikolaeva MG** (1979) Uskorennoe Proraschivanie Pokojaschihsja Semjan Drevnyh Rastenij, Izdatel'stvo "Nauka", Leningrad, SSSR, 80 pp*
- Nikolaeva MG** (1982) Pokoj semjan i faktory, ego kontrolirujuschie. In: *Fiziologija i Biohimija Pokoja i Prorastaniya Semjan, Izdatel'stvo "Kolos"*, Moskva, SSSR, pp 72-96*
- Nikolaeva MG, Ljanguzova IV, Pozdova LM** (1999) *Biologija Semjan*, Ros-
- sijskaja Akademiya Nauk, Botanicheskij Institut im. V.A. Komarova, Sankt-Peterburg, Rossija, 232 pp*
- Nleya T, Balkl RA, van den Berg A** (2005) Germination of common bean under constant and alternating cool temperatures. *Canadian Journal of Plant Science* 85, 577-585
- Noronha A, Vicente M, Felipe GM** (1978) Photocontrol of germination of *Cucumis anguria*. *Biologia Plantarum* 20, 281-286
- Panteleeva NI** (1953) Zimmie sredneaziatskie dyni zard v uslovijah Moldavskoj SSR. PhD Thesis, VIR, Leningrad, SSSR, 20 pp*
- Passam HC, Kakouriotis D** (1994) The effects of osmoconditioning on the germination, emergence and early plant growth of cucumber under saline conditions. *Scientia Horticulturae* 57, 233-240
- Pollok BM, Toole VK** (1966) Imbibition period as the critical temperature sensitive stage in germination of lima bean seeds. *Plant Physiology* 41, 221-229
- Rabie AG, Small JGC, Botha FC** (1989) The effect of submergence on germination and some aspects of the respiratory metabolism of *Cucumis sativus* L. seeds. *Plant Science* 63, 7-13
- Rakowski KJ, Behzadipour M, Ratajczak R, Kluge M** (1998) Effect of seed freezing and storage conditions on plasma membrane properties of Norway spruce (*Picea abies* Karst.) seedlings. *Botanica Acta* 111, 236-240
- Ramana S, Biswas AK, Kundu S, Saha JK, Yadava RBR** (2002) Effect of distillery effluent on seed germination in some vegetable crops. *Bioresource Technology* 82, 273-275
- Ranjan R** (2002) *Molecular Biology of Phytochrome*, Jodhpur, Agrobios, India, 120 pp
- Raudsepp AM** (1957) *Opyt Ovoschevodov Zakrytogo Grunta*, Sel'hozgiz, Moskva, SSSR, X pp*
- Roberts DP, McKenna LF, Lakshman DK, Meyer SLF, Kong H, de Souza JT, Lydon J, Baker CJ, Buyer JS, Chung S** (2007) Suppression of damping-off of cucumber caused by *Pythium ultimum* with live cells and extracts of *Serratia marcescens* N4-6. *Soil Biology and Biochemistry* 39, 2275-2288
- Røeggen O** (1987) Variation in minimum germination temperature for cultivars of bean (*Phaseolus vulgaris* L.), cucumber (*Cucumis sativus* L.) and tomato (*Lycopersicon esculentum* Mill.) *Scientia Horticulturae* 33, 57-85
- Russo VM, Biles CL** (1996) Incubation temperature affects changes in cucumber seed proteins and mineral content. *Seed Science and Technology* 24, 339-346
- Sherudilo EG, Markovskaya EF, Sysoeva MI** (2006b) Posledestvie kratkovremennoj nizkotemperaturnoj obrabotki semjan dekorativnyh rastenij na ih rost, razvitie i ustojchivost'. Severnaja Evropa v XXI veke: priroda, kul'tura, ekonomika. Materialy Mezhdunar. konf., posvjashchennoj 60-letiju Karnc RAN (24-27 oktjabrja 2006 g., g. Petrozavodsk). Sekcija "Biologicheskie nauki". Sekcija "Nauki o Zemle". Petrozavodsk: Izdatel'stvo Karnc RAN, pp 239-241*
- Sherudilo EG, Markovskaya EF, Sysoeva MI** (2006a) Temperature drop on moist cucumber seeds affects plant cold resistance. *XXVIIth International Horticultural Congress "Global Horticulture: Diversity and Harmony"*, Seoul, Korea, 13-19th August 2006, pp 414-415 (Abstract)
- Shin JS, Raymer P, Kim W** (2006) Environmental factors influencing germination in seeded seashore paspalum. *HortScience* 41, 1330-1331
- Shinomura T, Nagatani A, Hanzawa H, Kubota M, Watanabe M, Furuya M** (1996) Action spectra for phytochrome A- and phytochrome B-specific photoinduction of seed germination in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences USA* 93, 8129-8133
- Shutov DA, Belyaev NV** (1955) Reakcija tomatov na predposevnoe ohlazhdenie. *Izvestija Moldavskogo filiala AN SSSR* 6, 26*
- Shutov DA, Belyaev NV, Kandina GV** (1955) O reakcii prorstokov teploljubivyh rastenij na predposevnoe vozdejstvie holodom. *Izvestija Moldavskogo filiala AN SSSR* 2, 31*
- Simon EW** (1974) Phospholipids and plant membrane permeability. *New Phytologist* 73, 377-420
- Simon EW, Minchin A, McMenamin M, Smith JM** (1976) The low temperature limit for seed germination. *New Phytologist* 77, 301-311
- Spears JF, Tekrony DM, Egli DB** (1997) Temperature during seed filling and soybean seed germination and vigour. *Seed Science and Technology* 25, 233-244
- Staub JE, Wehner TC** (1987) Effect of treatment of cucumber seeds with growth regulators on emergence and yield of plants in the field. *Acta Horticulturae* 198, 43-49
- Staub JE, Wehner TC, Tolla GE** (1989) The effects of chemical seed treatments on horticultural characteristics in cucumber (*Cucumis sativus* L.). *Scientia Horticulturae* 38, 1-10
- Strekova VJ** (1960) Vjazkost' protoplazmy list'ev nekotoryh teploljubivyh rastenij, zakalennyh k holodu peremennymi temperaturami. *Fiziologija Rastenij* 7, 428-434*
- Strekova VJ** (1962) Izuchenie nekotoryh fiziologicheskikh osobennostej teploljubivyh rastenij, zakalennyh k holodu peremennymi temperaturami. PhD Thesis, Leningradskij Gosudarstvennyj Pedagogicheskij Institut im. AI Gercena, Leningrad, SSSR, 16 pp*
- Tarbaeva LP** (1957) Predposevnaja zakalka semjan dyn' ponizhennymi temperaturami. *Trudy botanicheskogo sada Zapadno-Sibirskij filial Akademii nauk SSSR* 2, 31-36*
- Thomas TH** (1981) Seed treatments and techniques to improve germination.

- Scientia Horticulturae* **32**, 47-59
- van Steveninck J, Ledebor FM** (1974) Phase transitions in the yeast cell membrane, the influence of temperature on the reconstitution of active dry yeast. *Biochimica et Biophysica Acta* **352**, 64-70
- van der Woude WJ, Toole VK** (1980) Studies of the mechanism of enhancement of phytochrome-dependent lettuce seed germination by prechilling. *Plant Physiology* **66**, 220-224
- Vladimirova AE** (1952) Vlijanie termicheskoj obrabotki semjan na plodonoshenie ogurcov. *Referaty dokladov TSHA* **16**, 272*
- Voronova AE** (1953) *Zakalka Semjan i Rassady Teploljubivyh Ovosche-bahchevyh Kul'tur*, Izdatel'stvo Ministerstva sel'skogo hozjajstva, Moskva, SSSR, 20 pp*
- Voronova AE** (1956) Zakalka semjan i rassady teploljubivyh kul'tur. *Sad i Ogorod* **12**, 19*
- Wehner TC** (1984) Estimates of heritabilities and variance components for low-temperature germination ability in cucumber. *Journal of the American Society of Horticultural Science* **109**, 664-667
- Yaniv Z, Mancinelli AL, Smith P** (1967) Phytochrom and seed germination. III. Action of prolonged far red irradiation on the germination of tomato and cucumber seeds. *Plant Physiology* **42**, 1479-1482
- Yao Y, Li Y, Yang Y, Li C** (2005) Effect of seed pretreatment by magnetic field on the sensitivity of cucumber (*Cucumis sativus*) seedlings to ultraviolet-B radiation. *Environmental and Experimental Botany* **54**, 286-294
- Zauralov OA, Tarhanova RM** (1960) Izuchenie holodostojkosti tykvennyh v Sibiri. Pervaja konferencija fiziologov i biohimikov rastenij Sibiri, Irkutsk, pp 24-25*