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

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; Felippe 1980; Mayer and Poljakoff-Mayber 1989) and also have an after-effect on subsequent plant growth and development (Kandina 1958; Buduryan 1962; Genkel’ and Kushmirenko 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 environmental 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. (1974), Simon (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 Shariples (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 cold germination 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 (Mancinelli and Tolkowsky 1968; Eisenstadt and Mancinelli 1974). Simon et al. (1974), Simon (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 Shariples (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 cold germination 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 (Mancinelli and Tolkowsky 1968; Eisenstadt and Mancinelli 1974). Simon et al. (1974), Simon (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 Shariples (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 cold germination 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 (Mancinelli and Tolkowsky 1968; Eisenstadt and Mancinelli 1974). Simon et al. (1974), Simon (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 Shariples (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 cold germination 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 (Mancinelli and Tolkowsky 1968; Eisenstadt and Mancinelli 1974). Simon et al. (1974), Simon (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 Shariples (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 cold germination 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.

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 sensitivity of cucumber seedlings to UV-B radiation (Yao et al. 2005). Osmoconditioning 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 marcescens 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 (Strekov 1962; Kushnirenko 1961, 1962; Genkel' and Kushnirenko 1966). In seed pre-germination treatment either through 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. ‘Nerosimyi’) 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 increased later 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. ‘Nerosimyi’ and ‘Nerosimyi-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. ‘Nerosimyi’) 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 25-30% after freezing cucumber seeds (cvs. ‘Berlizovskiy’, ‘Nehzinsky-12’, and ‘Tiraspol’-sky-6’) at -2°C for 12-24 h. Studies with another cucumber cultivar (‘Nerosimyi’) 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 1958). Increased 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; Felippe 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°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°C in combination with white light fully counter-
acted the inhibitory effect of light on germination of cucumber seeds (Felipe 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 30% of cucumber cultivars had a 2-4°C drop of cucumbers, but low temperature promotes germination. It was suggested the ecological consideration: alternating temperatures often occur during autumn-winter in various regions of Brazil and cucumber seeds should germination 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 (Felipe 1980).

The daily temperature gradient of 15-35°C strongly promoted germination of cucumber seeds (Felipe 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). North cultivars had a 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 Urals, 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 freezing) or optimal and low positive temperatures (seed hardening temperatures was first introduced by Voronova in the 1950s.

Seed freezing

Freezing of cucumber seeds (*C. sativus* L., cvs. ‘Nerosimyi’, ‘Nerosimyi-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 1954; Voronova 1955; 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 (Strekoeva 1960), and increased cold resistance of plants and roots (Strekoeva 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 temperature (around 0°C for 18 h) for seed of *Melazur*, cvs. ‘Umir-Vaki’, ‘Asma’, ‘N 4464b’) Budryan (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’) Lu-govkin (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; Budryan 1962), leaf formation (Budryan 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; Budryan 1962; Kandina 1962), and affected physiological processes by increasing the activity of redox processes, intensifying plant respiration (Shutov et al. 1955; Kandina 1962; Budryan 1962), increasing plant cold resistance (Vladimirova 1952; Tarbaeva 1957; Genkel’ and Kushnirenko 1966), vascular wilt plant resistance and anthracnose resistance (Budryan 1962). Low cucumber germination rates at suboptimal temperatures were related to leakage of minerals and the lack of formation or maturation 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% (Budryan 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 (Felipe 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 and Chandler 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 (Ranjjan 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-imbeded 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°C/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 the 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 recovery is faster than at low temperature and may thus override the effects 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 temperatures as well as negative temperatures. The mechanism of cold-tolerant germination is complex and only partially understood. It is Nelya 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 changes 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.

**ACKNOWLEDGMENTS**

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

**REFERENCES**

*In Russian*

Alekseev SB, Brison NS (1954) Priemny poluchenija vysokih ustoichivosti i vysshih urozhaj ovogorov. Sad i Ogorod 4, 28*.


Androsova MP (1940) O vlijanii oshlаждения семян i вшодов на урожай огурцов. Vestnik Sel'skokhozajstvennyi Nauki, Oroschi i Kartoflo 3, 98*.

Barton L (1964) Hranenie Semjan i ih Dolgovechnost', Izdatel'stvo "Kolos", Moskva, SSRN, 204 pp*.

Belik VF (1963) Vlijanie zakalki semen reymennymi temperaturami na fiziologicheskie osobennosti i holodostoyost' ovogorov. Fiziologija rastenij 10, 51-57*.


Edel'shtein VI (1949) Proizvodzenie bahchevych kul'tur v serevyje raznye strany. Doklady TES 10, 21-28*.


Felippe GM (1980) Germination of the light-sensitive seeds of *Cucumis anguria* and *Rutaceae* produced on economic crops in southern Thailand. Izdatel'stvo "Shtiinca".

Genkel' PA, Sarycheva AP, Stinikova OA (1955) Vlijanie obrabotki semjan peremennoj temperaturoj na razvite i sozrevanie kukuryz. Fiziologija Rastenij 7, 447-453

Grachev EA (1875) O razvedenii kukuzy pod Peterburgom. Trudy Vsesojuznogo Temeparaturnogo Obchestva 1, 165 pp

Jennings PH (1999) Increasing chilling tolerance of seeds during imbibition and effects of imbibition conditions. Seed Science Technology 27, 56-71


Cucumber seeds germination and temperature. Markovskaya et al.

van Steveninck J, Ledeboer 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


Vladimirova AE (1952) Vlijanie termicheskoy obrabotki semjan na plodono-
shenie ogurcov. Referaty dokladov TSHA 16, 272*

Voronova AE (1956) Zakalka semjan i rassady teploljubivyh kul'tur. Sad i Ogro-
md 12, 19*


Zauralov OA, Tarhanova RM (1960) Izuchenie holodostojkosti tykvennyh v Sibiri. Pervaja konferencija fiziologov i biohimikov rastenij Sibiri, Irkutsk, pp 24-25*