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Effects of temperature on pollen viability and *in vivo* pollen tube growth in *Citrus sinensis*

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Summary

Temperature is the major factor in global warming and strongly influences the success of plant sexual reproduction. Therefore, there is an urgent need to assess the vulnerability of species for breeding and planning effective actions. In this study, effects of different temperatures and storage duration on pollen viability and *in vivo* pollen tube growth were analysed in *Citrus sinensis* 'Kozan yerlisi'. The pollens were obtained before anthesis and stored at 10 °C, 20 °C and 30 °C for 1, 2 or 3 days before analysis.

The pollen viability decreased with increasing temperatures and storage duration from 61.3% to 5.8%. *In vivo* pollen germination results showed that for one day storage, the pollen growth rates were similar to the control treatment while storing pollens two or three days differed from the control. Pollen germination after storage at 10 °C was lower and not efficient, while after storage at 30 °C no pollen tube germination at all was seen on the stigma. At the same time, storing pollen in low temperature caused delay in pollen tube germination and pollen tube growth, suggesting that pollen that are stored in low temperatures pass into a dormancy process for three to five days.

In conclusion, this study indicated that pollen storage in 30 °C for a long time causes loss of pollination ability while storage in 10 °C causes dormancy in pollen.

Keywords: *Citrus sinensis*, local variety, temperature, dormancy, pollen tube, progamic phase

Introduction

The cultivated land in several regions of the world has been affected by environmental stresses, which causes a substantial amount of reductions in crop productivity (Mahajan and Tuteja, 2005). It is predicted that environmental stresses will become more intense and frequent with climate change, especially by global warming. The world population is estimated to be 10 billion in 2050, which will require 70% more food. Crop tolerance to heat stress has to be considered for planning effective actions (Aronne et al., 2021) and tolerant crops should be developed (Thomas et al., 2020) for feed the increasing population.

The reproductive phase of plants is much more sensitive than the vegetative phase to the effects of global warming (Hedhly et al., 2008) and must be studied urgently especially for native species. For sexual reproductive success of plants pollen is crucial, which must survive and interact with the environment throughout the period from pollen release until ovule fertilization (Mulcahy, 1979; Aronne et al., 2021). Within this scope, new knowledge is needed about the effects of low and high temperature in the progamic phase to optimise breeding programmes in order to obtain new varieties to adapt climate change scenarios. Researchers should determine the tolerances of plants to extreme temperatures in terms of reproductive biology to provide generation continuity.

The progamic phase, the time from pollination to fertilization, is one of the most critical phases during the sexual reproduction process in plants. In this period, specific interactions occur between the male gametophyte and pistil (Montalt et al., 2019), which include stigmatic receptivity, pollen grain germination, pollen tube growth and ovule degeneration (Hedhly, 2011). These phases depend not only on genotype but also on the environmental conditions during flowering and pollination (Distefano et al., 2012). Although temperature has a clear effect and high temperature accelerates pollen germination *in vitro* and pollen tube growth in the style, it also accelerates the loss of stigmatic receptivity (Hedhly et al., 2005) and pollen germination capacity (Distefano et al., 2012; Akhoundnejad et al., 2020).

Although Citrus is grown in various regions of the world currently, the global climate change is predicted to lead to an increase in average temperatures in the future. This could limit plant cultivation in some areas and affect Citrus growing areas (Montalt et al., (2019). Therefore, determining pollen performance and temperature sensitivity is especially relevant for Citrus (Distefano et al., 2018). In Turkey, average temperatures in the flowering period of Citrus are generally between 15-20 °C, with a gradual increase of up to 30 °C in daytime and decrease to less than 10 °C at night. The cultivation and breeding programmes in Turkey are located in the Mediterranean region in warm conditions; in the Aegean region with moderate temperatures and at the Eastern Black Sea and Western Marmara region characterized by colder temperatures, where both frost and high temperature risks exists to some extent (Çimen and Yeşiloğlu, 2016; Yeşiloğlu et al., 2018). The results of this study may be useful for planning breeding programmes with regard to choosing the most favourable time and location to perform pollination depending on temperature forecasts.

This research aimed to study the effects of pollen storage at different temperatures and duration periods on pollen viability and *in vivo* pollen tube growth in the progamic phase of *Citrus sinensis* 'Kozan yerlisi'.

Materials and methods

This study was conducted in the Citrus research fields of Cukurova University, Adana/Turkey in April 2019. In the present work the local orange variety *Citrus sinensis* 'Kozan yerlisi' was used. Kozan yerlisi is a seeded, self-compatible and locally produced cultivar in Turkey with a high manner.

Pollen storage in different temperatures and durations

To obtain fresh pollen, lots of flowers were collected one day before anthesis. Anthers were removed from the flowers and left for dehiscence at room temperature overnight. Obtained fresh pollens were separated into 10 cups. Pollen cups were placed in silica gel cups for 2 hours for removing humidity for 5 hours. One of the cups was left for fresh pollen studies and each 3 pollen cups of remaining 9 cups were placed to different temperature regime at 10 °C, 20 °C and 30 °C. Each stored pollen cup was removed at 1st, 2nd and 3rd day of the storage.

Pollen viability tests

For each storage temperature (10 ºC, 20 ºC and 30 ºC) and storage duration (1, 2 and 3 days), pollens were immediately tested with 1% 2,3,5 triphenyl tetrazolium chloride (TTC) solution according to NORTON (1966). The pollen viability of fresh pollens was determined using the same method.

Pollination studies

Sixty unopened flower buds were carefully emasculated with forceps to avoid any injury of the stigma just prior to their opening. All previously opened flowers and small immature buds were removed from selected branches. The emasculated flowers were covered with cotton bags to avoid free pollination. One day later, at anthesis, the emasculated flowers were pollinated with fresh pollen by hand using a small brush and covered with cotton bags immediately. Then, 180 flowers (60 for each temperature regime) were emasculated and were hand-pollinated one day later with pollen, stored for 1 day at 10 °C, 20 °C and 30 °C. The experiment was repeated with pollen, which was stored for 2 and 3 days, respectively.

The day of pollination was accepted as the beginning of anthesis and day count was started after this day. Pollinated flower samples were collected in 2 days intervals from 1 DAP (days after pollination) to 15 DAP separately for each temperature and pollen storage period. Five pistils were collected for each sampling date and immediately fixed in FPA 70 (STÖSSER et al., 1985; KARABIYIK and ETI, 2020).

***In vivo* pollen tube growth rate**

Pollen tube growth rates on pollinated pistils were evaluated from the samples collected and fixed from pollination studies. Pollen tubes in the stigma and style, as well as ovules were monitored on squash preparations of pistils, previously softened in 8N sodium hydroxide for 5-7 h, stained with 0.1% aniline blue in 0.1 N K_3PO_4 (KHO and BAER, 1970; PREIL, 1970) and observed under a fluorescence microscope (Olympus BX51, Tokyo, Japan) equipped with a U-MWU filter (Olympus, Tokyo, Japan). Pollen tube growth was determined as percentage of the style traversed by the longest pollen tube in each pistil by a digital micrograph system (Olympus DP72 camera, Tokyo, Japan).

Statistical Analysis

The pollen viability studies were conducted in completely randomised design with two factors and three replications. JMP 8.0.1 was used for Anova test and the results were compared with LSD test. Arc-sin transformation was used in percent values before analysis.

Results

Pollen viability level

Effect of storage temperatures and duration days on pollen viability level is expressed as percentage in Tab. 1. The statistical analysis revealed significant differences between different temperatures, storage duration and temperature-duration interaction. The viability rate of fresh pollens derived just after anthesis was 61.3% (not shown in table). In terms of average values of different temperatures, the highest viability was obtained from 10 ºC with an average of 41.9%

Tab. 1: Pollen viability levels of 'Kozan yerlisi' orange stored in different temperatures and different durations (%)

Temperature	Duration			TemperatureAverage
	1	2	3	
10 °C	54.7 a[1]	38.6 b	32.4 c	41.9 **A**
20 °C	51.2 a	34.3 c	13.4 d	33.0 **B**
30 °C	40.9 b	27.6 c	5.8 e	24.8 **C**
DurationAverage	48.9 *A*	33.5 *B*	17.2 *C*	
LSDdurat= 2.785***	LSDtemp= 2.785***		LSDdurat × temp= 4.823***	

[1]Differences between averages showed by different letters are statistically important ***p ≤ 0.001.

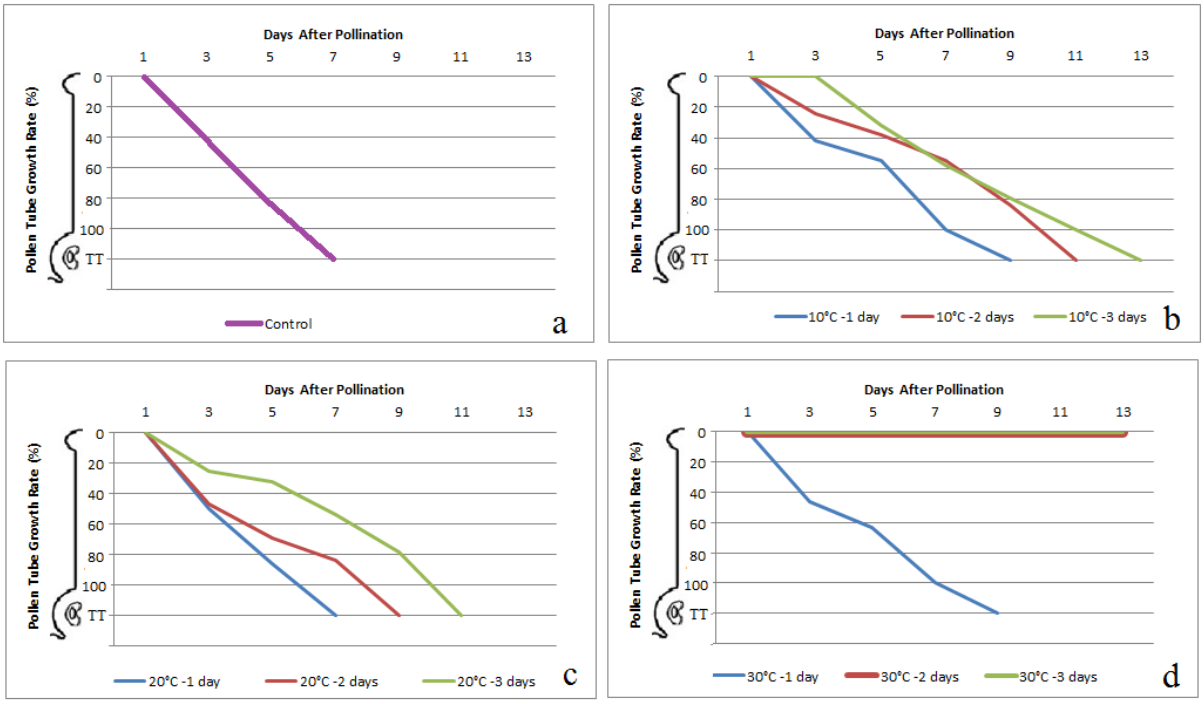

Fig. 1: Pollen tube growth rate in control and different temperatures during 1-3 days. **a.** Pollen tube growth rate of control treatment. **b.** Pollen tube growth rate in 10 ºC. **c.** Pollen tube growth rate in 20 ºC. **d.** Pollen tube growth rate in 30 ºC. (TT: Ovule)

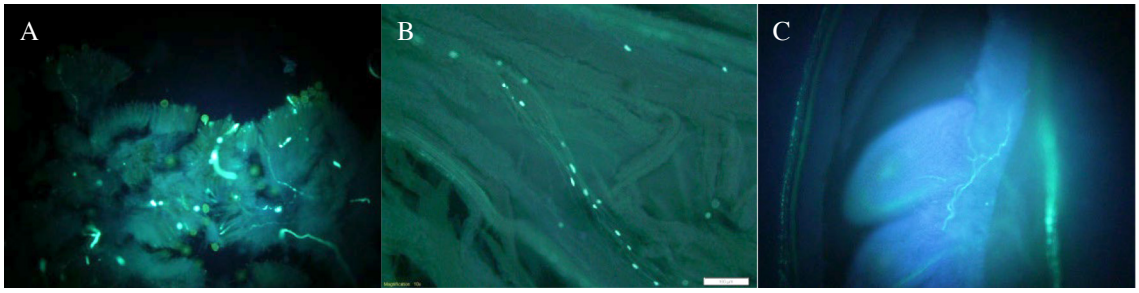

Fig. 2: Pollen tube growth in 'Kozan yerlisi' orange cultivar. A. Normally germinated and dormant pollens on stigma. B. Pollen tube elongation inside the stylar canals. Scale bar = 100 µm. C. Pollen tube penetration to the ovule.

and is followed by 20 ºC (33.0%) and 30 ºC (24.8%). The pollen viability level decreased with longer storage periods.

Duration of storage also affected the pollen viability levels (Tab. 1). In terms of duration × temperature values, the highest viability levels were obtained from 1 day-10 ºC (54.7%) and 1 day-20 ºC (51.2%) within the same statistical group. These values were followed by 1 day-30 ºC (40.9%) and 2 days-10 ºC (38.6%). The lowest results were obtained from third day as 5.8%, 13.4% and 32.4%, from 30 ºC, 20 ºC and 10 ºC, respectively.

In vivo pollen germination

The effect of temperature on pollen tube growth in *Citrus sinensis* 'Kozan yerlisi' was evaluated with the pistil squash method. The results of Control and different storage temperature regimes are shown in Fig. 1 as line graphs. Fig. 1a shows that in Control treatments, pollen tubes germinated between the parenchyma cells of the stigmoid tissue reaching the stylar canals in 1 DAP (day after pollination). Then, the pollen tubes expeditiously preceded inside the stylar canals and first pollen tubes were reached to the ovules at 7 DAP.

Pollens which were stored at 10 °C for 1 day had slightly slower pollen tube growth than control treatment until 5 DAP and hereupon they started to elongate normally penetrating to the ovule at 9 DAP (Fig. 1b). The 2 days and 3 days storage in 10 °C were slower than both control and 1 day- 10 °C conditions. At the same time, pollen tubes did not germinate efficiently on the stigma in both treatments and the 3 days storage in 10 °C treatment caused delay in pollen germination on stigma (Fig. 1b). In 2 and 3 days storage, pollen tubes penetrated to the ovules at 11 and 13 DAP, respectively. The pollen tubes reached to the ovule were not as plenty as Control treatments in none of the pollens which were stored in 10 °C.

Pollen germination and tube elongation after storage at 20 °C for 1 day was similar to the Control treatment. However, storing pollens 2 days and 3 days at 20 ºC caused retardation of pollen tubes in penetration to the ovules (Fig. 1c). Moreover, after 3 days storage, the pollen tubes slowed down especially after 3 DAP. This retardation and late reaching to the ovules may be due to low pollen viability capacity.

After 30 °C storage, pollens which were stored for 1 day germinated on the stigma and reached the style until 3DAP. In this treatment, pollen tubes inside the stylar canals were not as much as in 20 °C and 10 °C treatments. However, no pollen germination was detected after 2 and 3 days storage showing that the pollens lost their germination capacity in long storage at 30 °C (Fig. 1d).

Discussion

Various abiotic stresses including global warming are negatively affecting the plant productivity worldwide. Therefore, it is necessary to know the response of plants, especially the local cultivars, in order to cope with this upcoming problem. Citrus is grown in many regions in the world (Montalt et al., 2019). However, temperature limits the geographical distribution of plant species (Hedhly et al., 2005) especially for subtropical fruit trees like Citrus. It has been proven before that reproductive phases such as male and female formation (Distefano et al., 2018), pollen properties (Hedhly et al., 2004; Hedhly et al., 2005; Distefano et al., 2012; Distefano et al., 2018), progamic phase (Distefano et al., 2018; Montalt et al., 2019) and embryo formation (Sanzol and Herrero, 2001) are the most temperate-vulnerable stages. This study aimed to analyse temperature effects on pollens, which were stored in different temperatures and different duration span, on pollen viability level and *in vivo* pollen tube growth rates in local cultivar *Citrus sinensis* 'Kozan yerlisi'.

The results demonstrate that extreme temperatures and prolonged duration of pollen storage in high temperatures can cause loss of pollen viability and hence fruit or seed set ratio. In a previous study, pollen viability level of different Citrus species differed between 12% and 98.6% while viability of *C. sinensis* 'Hamlin' pollens was 85.3% (Yamamoto et al., 2006). In another study conducted in *Citrus reticulata* 'Shogua', researchers reported that pollen storage for 0, 3, 6, 9, 24 and 48 hours at 20 °C decreased the pollen viability level from 96.47% to 17.13% (Chelong and Sdbodee, 2012). Distefano et al. (2018), who have studied the effects of temperature on *in vitro* pollen germination, detected the highest pollen germination level in 25 °C (96%), while it was lower in 15 °C (11%), 20 °C (40%) and 30 °C (25%). Researchers also reported that the incubation temperature affected the germination capacity of the pollen. Bennici et al. (2019) reported parallel results in Clementine as 25 °C gave better germination results than 30 °C.

For *in vivo* pollen germination and pollen tube growth rate studies, the pistil squash method was used herein, which enables analysing the daily progression of pollen tubes inside the stigma, style and ovary by fixing the samples 2 days intervals from pollination until 15 days after pollination. This way, the effect of temperature and duration could be investigated more effectively. *In vivo* pollen germination after 1 day storage in all temperatures had quite similar pollen tube growth rates and ovule penetration periods compared to the control treatment. This indicates that there was a decrease in pollen viability level and pollen could conserve germination ability for 1 day without any important effects on germination in field conditions. At the same time, *in vivo* pollen germination capacity, which is expressed as intensity of germinated pollen on the stigma and inside the style (Distefano et al., 2012), was decreased by storing pollens during 2 or 3 days in these temperatures.

This study is the first to show the differences in pollination capacity of pollens stored for 1, 2 or 3 days at different temperatures. In recent studies, only effects of temperature on *in vivo* pollen germination were studied in Citrus and reported that high temperatures were accelerated while low temperatures were decelerated the pollen tube growth in stylar canals (Distefano et al., 2012; Montalt et al., 2019). Hedhly et al. (2004) in sweet cherry and Hedhly et al. (2005) obtained the same results in peaches. Sanzol and Herrero

(2001) also indicated that the temperature has an important effect on pollen tube elongation influencing effective pollination period of species. In this study, storing pollens in 10 °C caused a delay in pollen germination suggesting that pollen storage in low temperature during 2 or 3 days caused dormancy in pollen germination and tube elongation for *Citrus sinensis* "Kozan yerlisi". This was reported by HEDHLY et al. (2005) as peaches grown in 10 °C have been showed a delay in pollen germination compared with 20 °C and 30 °C. These results also suggested that, in order to take more actual results for pollen storage studies, the researchers should store their pollens in normal conditions for a while before testing or using it for pollination, instead of using pollens immediately after storage. On the other hand, ALOISI et al (2020) reported the pollens stored in 15 °C broke down self-incompatibility by inhibiting T-Gase activity resulting with pollen tube growth. By this opinion, pollination in cold stress in self-incompatible cultivars was studied by MONTALT et al. (2022) for breaking down self-incompatibility and the researchers were obtained a few viable seeds. The recent studies and this study showed that this procedure might be useful in breeding studies for alleviating incompatibility effects.

Although other researchers used *in vitro* germination tests to show viability of pollens, in this study pollen viability test was used and pollen germination was examined as *in vivo*. When both viability and *in vivo* germination studies were taken into account, it can be seen that the results give parallel results which shows this test was also usable. In general, pollen viability, *in vitro* pollen germination and *in vivo* pollen tube growth tests show parallel results (KARABIYIK and ETI, 2016; KARABIYIK et al., 2016; KARABIYIK and ETI, 2020). Moreover, since *in vitro* pollen germination can be influenced by the media and environmental conditions, pollen viability and *in vivo* pollen tube growth is not. This situation is originated from pollen viability tests like TTC reflects the activity of dehydrogenase enzymes involved in the respiratory activity of living tissues which is also associated with its germination capacity (DERIN and ETI, 2001). At the same time, by TTC test if there will be any dormancy for pollen tube formation like in this study, pollens would show their actual viability on the stigma without detecting the accurate germination time and germination medium for *in vitro* studies. Similarly, the *in vivo* pollen germination and *in vivo* pollen tube growth studies give optimal results for pollen germination because it shows the real germination performance of pollen on the plant.

Conclusion

In conclusion, this study showed that the temperature influences the pollen viability and pollen tube growth rate in *Citrus sinensis* 'Kozan yerlisi'. Pollens storing at 30 °C for a long time lost their pollination ability while storage at 10 °C caused a slower pollen tube growth but also slower pollen aging. As a result, pollen stored in low temperature conditions showed dormancy which could be broken in field conditions in 3 days. Moreover, pollen incubation in 30 °C caused a strict decrease in pollen viability and no pollen tube growth in stigma and style.

In future researches, it would be relevant to investigate the effect of temperature to male and female organ development and *in vivo* pollen germination rate and intensity by simulating low and high temperatures in laboratory conditions.

Conflict of interest

No potential conflict of interest was reported by the author.

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