



## Longevity and temperature response of pollen as affected by elevated growth temperature and carbon dioxide in peanut and grain sorghum

P.V.V. Prasad<sup>a,\*</sup>, K.J. Boote<sup>b</sup>, L.H. Allen Jr.<sup>c</sup>

<sup>a</sup> Department of Agronomy, Kansas State University, Manhattan, KS 66506, USA

<sup>b</sup> Department of Agronomy, University of Florida, Gainesville, FL, USA

<sup>c</sup> United States Department of Agriculture – Agricultural Research Service, Center for Medical, Agricultural, and Veterinary Entomology, Chemistry Research Unit, Gainesville, FL, USA

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### ABSTRACT

It is important to understand the effects of environmental conditions during plant growth on longevity and temperature response of pollen. Objectives of this study were to determine the influence of growth temperature and/or carbon dioxide (CO<sub>2</sub>) concentration on pollen longevity and temperature response of peanut and grain sorghum pollen. Plants were grown at daytime maximum/nighttime minimum temperatures of 32/22, 36/26, 40/30 and 44/34 °C at ambient (350 μmol mol<sup>-1</sup>) and at elevated (700 μmol mol<sup>-1</sup>) CO<sub>2</sub> from emergence to maturity. At flowering, pollen longevity was estimated by measuring *in vitro* pollen germination at different time intervals after anther dehiscence. Temperature response of pollen was measured by germinating pollen on artificial growth medium at temperatures ranging from 12 to 48 °C in incubators at 4 °C intervals. Elevated growth temperature decreased pollen germination percentage in both crop species. Sorghum pollen had shorter longevity than peanut pollen. There was no influence of CO<sub>2</sub> on pollen longevity. Pollen longevity of sorghum at 36/26 °C was about 2 h shorter than at 32/22 °C. There was no effect of growth temperature or CO<sub>2</sub> on cardinal temperatures ( $T_{min}$ ,  $T_{opt}$ , and  $T_{max}$ ) of pollen in both crop species. The  $T_{min}$ ,  $T_{opt}$ , and  $T_{max}$  identified at different growth temperatures and CO<sub>2</sub> levels were similar at 14.9, 30.1, and 45.6 °C, respectively for peanut pollen. The corresponding values for sorghum pollen were 17.2, 29.4, and 41.7 °C. In conclusion, pollen longevity and pollen germination percentage was decreased by growth at elevated temperature, and pollen developed at elevated temperature and/or elevated CO<sub>2</sub> did not have greater temperature tolerance.

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### 1. Introduction

In recent years, crops across the world have experienced more variable and extreme weather events, including episodes of high temperatures during crop growing seasons. These weather events will become more aggravated because of global climate change associated with increases in concentration of greenhouse gases, deforestation, and consumption of fossil fuels (IPCC, 2007). It is estimated that by the end of this century, carbon dioxide (CO<sub>2</sub>) concentration will be in the range from 540 to 970 μmol CO<sub>2</sub> mol<sup>-1</sup> (IPCC, 2007). Increases in CO<sub>2</sub> and other greenhouse gasses will be associated with increases in global surface temperatures in the range of 1.4–5.8 °C (Schneider, 2001; IPCC, 2007). These climate changes will have a significant effect on crop production.

Seed set percentage which determines seed numbers is one of the most important components of crop yield. Seed set pri-

marily depends on the functionality of male and female gametes (pollen and ovule, respectively), which are highly sensitive to environmental factors. Environmental conditions during growth and development of reproductive organs and during and after anthesis can influence performance of gametes and seed set (Stephenson et al., 1994; Saini, 1997; Prasad et al., 2003, 2006). In general, pollen is more sensitive to environmental stress relative to the ovule. Pollen performance can be hindered by the duration for which pollen is viable and can germinate after anther dehiscence (pollen longevity) and its ability to reach and fertilize the ovule. Pollen longevity is defined as the duration for which pollen grains has the ability to germinate after dehiscence from anther. Pollen performance influences transmission of genes from one generation to the next. Thus, understanding the factors affecting performance of gametes is important (Stephenson et al., 1994).

The duration for which pollen is viable and can germinate after anther dehiscence under natural conditions is crucial for successful pollination and fertilization. Similarly, response of pollen grains to temperature is also important to understanding the physiological basis of decreased seed set under stress environments. Some studies have documented the influence of instantaneous temperature,

\* Corresponding author. Tel.: +1 785 532 3746; fax: +1 785 532 6094.

E-mail address: [vara@ksu.edu](mailto:vara@ksu.edu) (P.V.V. Prasad).

humidity, and solar radiation on pollen longevity (Luna et al., 2001; Aylor, 2004). Cardinal temperatures ( $T_{\min}$ ,  $T_{\text{opt}}$ , and  $T_{\max}$ ) for pollen germination for some cultivars of crops such as peanut (*Arachis hypogaea* L. Kakani et al., 2002), common bean (*Phaseolus vulgaris* L.; Farlow et al., 1979), tomato (*Lycopersicon esculentum* Mill; Weaver and Timm, 1989) and cotton (*Gossypium hirsutum* L. and *Gossypium barbadense* L.; Burke et al., 2004) were reported at a particular growth temperature. A few studies have investigated the influence of growth conditions such as mineral nutrition (Lau and Stephenson, 1993; Poulton et al., 2002), temperature, and CO<sub>2</sub> (Aloni et al., 2001; Prasad et al., 2002, 2003, 2006) on pollen performance, the influence of growth temperature and/or CO<sub>2</sub> on pollen longevity or cardinal temperatures for pollen germination has received far less attention.

It has been established that processes such as photosynthesis, stomata conductance, seed number, seed size and composition of seeds, and enzyme activities in leaves and seeds are influenced by growth temperature and CO<sub>2</sub> concentration (Reddy and Hodges, 2000; Thomas et al., 2003; Prasad et al., 2003, 2004, 2009). Studies have shown that photosynthesis and photosynthetic capacity acclimates under elevated growth temperatures and CO<sub>2</sub> conditions (Vu et al., 1997; Bunce, 2000). However, acclimation responses of pollen grains to season-long higher growth temperatures are not well understood.

The present research was conducted on peanut and grain sorghum (*Sorghum bicolor* L. Moench.) due to their importance in semi-arid regions. The productivity of these two crops is limited by occurrences of environmental stresses during reproductive stages of crop development. The most sensitive stages to high temperature stress occur just before flowering and during flowering in peanut (Prasad et al., 1999a) and sorghum (Prasad et al., 2008). These two stages coincide with microsporogenesis and anthesis, respectively. High temperature stress during microsporogenesis causes poor pollen viability, fewer numbers of pollen grains, resulting in lower seed set. Similarly, high temperature stress during flowering causes poor anther dehiscence, poor pollen germination, slower pollen tube growth and hampers fertilization, resulting in lower seed set. Analyses of weather data suggests that both peanut (Prasad et al., 2003) and sorghum (Prasad et al., 2006) crops in the semi-arid regions are already being grown at optimum or above optimum temperature for their yield. Thus, any further increases in mean temperature or occurrences of short episodes of high temperatures during reproductive stages of crop development will decrease yields. Understanding physiological and biochemical basis of sensitivity of pollen to high temperature stress and exploring differences among crop species and cultivars within species can help determine new avenues for genetic improvement for stress tolerance.

Objectives of the present study were to (a) determine pollen longevity of grain sorghum under different growth temperatures and/or CO<sub>2</sub> conditions, (b) determine whether temperature response of sorghum and peanut (representative of monocot C<sub>4</sub> and dicot C<sub>3</sub> crops of tropical region) in terms of cardinal temperatures,  $T_{\min}$  (minimum temperature at which pollen germinates),  $T_{\text{opt}}$  (optimum temperature at which pollen germination in maximum) and  $T_{\max}$  (maximum temperature beyond which pollen does not germinate) for pollen germination was influenced by temperature and/or CO<sub>2</sub> conditions during the formation and development of pollen grains, and (c) compare pollen longevity and cardinal temperatures (i.e.  $T_{\min}$ ,  $T_{\text{opt}}$  and  $T_{\max}$ ) of two crops species (peanut and sorghum). The hypothesis tested was that growth at elevated temperature and/or CO<sub>2</sub> does not improve tolerance of pollen performance in terms of pollen germination, pollen longevity, or cardinal temperatures for pollen germination.

## 2. Materials and methods

This research was conducted in controlled environment facilities of the University of Florida and United States Department of Agriculture at the Plant and Soil Science Field Teaching Laboratory in Gainesville, FL (latitude 29.64°, longitude 82.34°, and altitude 30 m). Details of the controlled environments and quality of environmental controls, experimental conditions, and plant husbandry from these experiments are available elsewhere (peanut, Prasad et al., 2003; and sorghum, Prasad et al., 2006), along with growth and yield data. A brief summary of growth conditions and plant husbandry is described in the following section.

### 2.1. Experimental conditions

Peanut and grain sorghum plants were grown in outdoor, sunlit Soil–Plant–Atmosphere Research (SPAR) growth chambers during 2002 and 2003, respectively. These growth chambers have unique computer controlled programs, equipment and structure to control air temperature, dew-point temperature and CO<sub>2</sub> at pre-determined set points. Each chamber is airtight and has an upper aluminum frame measuring 1 m wide, 2 m long and 1.5 m high covered with a polyethylene terephthalate “six light” film (Taiyo Kogyo Co., Tokyo, Japan) walls which enclose the crop canopy. The bottom rooting-chamber (aluminum lysimeter) has the same cross-section as the upper frame and is 0.6 m deep. All chambers contain the same natural topsoil of Kendrick sand (loamy, siliceous, Arenic Paleudult) obtained from a nearby field (90.7% sand, 5.6% silt and 3.7% clay).

Carbon dioxide was controlled and maintained at 350  $\mu\text{mol mol}^{-1}$  in all eight chambers from sowing to appearance of first leaf; thereafter, CO<sub>2</sub> concentration in half (four) of the chambers was increased to 700  $\mu\text{mol mol}^{-1}$ . From sowing to full emergence (7 days after sowing, DAS), the air temperature was set at 36/26 °C (daytime maximum/nighttime minimum) in all chambers; thereafter, four temperature treatments of 32/22, 36/26, 40/30, and 44/34 °C were randomly allocated to eight chambers in paired sets (one each at 350 and 700  $\mu\text{mol mol}^{-1}$ ). The CO<sub>2</sub> and temperature control continued until final harvest at maturity. Temperature was controlled in a sinusoidal wave function and data on all environmental variables were measured at 20 min interval through the experiment.

Quality of the temperature and CO<sub>2</sub> control and chamber performance is presented elsewhere (sorghum, Prasad et al., 2006; peanut, Prasad et al., 2003). In brief, the chamber performance was tested from the measured data on growth and dry matter production of crops in each chamber when controlled at similar environments (either temperature or CO<sub>2</sub>) in two different experiments (Prasad et al., 2006). Overall, the data clearly demonstrated that all chambers performed similarly and produce similar results in terms of plant development, growth and dry matter production when grown under similar environmental and crop management conditions (Supplemental Table 1). In addition the quality of the environmental controls in all chambers was similar when set at similar air temperature and/or CO<sub>2</sub> levels (Prasad et al., 2006). Together, these data provide assurance on uniformity of the chambers (no chamber effects), chamber-conditions and reliability of data collected from experiments in SPAR growth chambers without true replications.

The set point temperature regimes for current study were chosen based on optimal temperature for growth and development of each crop. Our previous studies on peanut has shown that exposure to daytime temperatures >34 °C significantly decreased pollen viability, pollen production and resulted in decreased seed set and fewer number of seeds (Prasad et al., 1999b, 2001). Similarly, studies on grain sorghum have shown that daytime temperature >33 °C

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