Environmental and Experimental Botany 138 (2017) 193–202

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Phenological and ecophysiological responses of *Capsicum annuum* var. *glabriusculum* to native arbuscular mycorrhizal fungi and phosphorus availability

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ARTICLE INFO

Article history:
Received 8 December 2016
Received in revised form 13 March 2017
Accepted 13 March 2017
Available online 16 March 2017

Keywords:
Arbuscular mycorrhiza
Capsicum annuum var. *glabriusculum*
Degrees days
Ecophysiology
Phenology
Sonoran Desert

ABSTRACT

Due to climate change, the assessment of environmental variations associated to phenology and ecophysiology of iconic Sonoran Desert plants such as *Capsicum annuum* var. *glabriusculum* (*Cag*), during their interaction with the native arbuscular mycorrhizal fungi (AMF) and soil nutrients availability, is the keystone to understand its biological significance in the extreme conditions of semiarid environments. Seasonal patterns of high solar radiation regimes and extreme daily air temperatures thresholds were reflected in a high accumulation of heat from physiological maturity (2699 °D) until the end of reproduction season (4002 °D). In treatments without chemical fertilization, low and intermediate P availability, the native AMF*Cag* inoculum significantly increased *Cag*'s relative growth rates and changed the biomass allometric allocation patterns causing a lower partition to the roots and a higher partition to the growth of shoots and photosynthetic assimilation surface. Depending on the phenological stage, the levels of P availability and the levels of native AMF propagules in the soil, significantly modified the content of C, H, S, P, N, Ca, Fe, Mn or Ni in the shoots. The native AMF*Cag* inoculum significantly increased the functional colonization (Arum-Paris type) of roots except with higher P availability. However, when AMF propagules in the soil are low, P increase and presence of other mineral nutrients is detrimental to symbiotic establishment. Conversely, when AMF propagules in the soil are high, symbiotic traits indicate that the native AMF taxa tested, have different tolerance capabilities to colonize functionally the roots to obtain the carbon for their development even under a high P and other mineral nutrients availability in the soil. In extreme conditions of sunlight and air temperatures, *Cag*'s phenological and ecophysiological traits were enhanced by the native AMF*Cag* inoculum in different P availability levels, however, the mycorrhizal growth response decreased significantly as the availability of P increases, and the highest level of native AMF propagules in soil was the factor that promoted the increase of reproductive yield of *Cag* plants, not the increase of nutrients availability. This study provides novel information on AMF-*Cag* symbiotic interactions during plant development and phenological stages, as well as proposes different insights and hypothesis of research about *Cag*-AMF ecophysiology.

1. Introduction

Capsicum annuum var. *glabriusculum* Dunal, Heiser (Cag) is a wild species growing as woody perennials-deciduous shrubs, reproduced by seeds. Cag is an important resource for forests and sustainable agriculture in present and future times for three main reasons: It represents the wild genetic ancestor of all domesticated genotypes of peppers Capsicum annuum L., is a global priority species for ex situ and in situ conservation programs, and represents a potential and valuable genetic resource for breeding programs (Kraft et al., 2013aKraft et al., 2013a,b; Qin et al., 2014; Pickersgill, 2016).

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http://dx.doi.org/10.1016/j.envexpbot.2017.03.008
0098-8472/

The reasons above support a growing interest in *Cag*'s cultivation, genetic characterization, ecology and biogeography (Kraft et al., 2013a,b; Qin et al., 2014). Unfortunately, survival and genetic variability of wild *Cag* population reservoirs are threatened by human encroachment, continuous inappropriate harvesting practices, overgrazing and habitat loss by environmental degradation (González et al., 2011; Pickersgill, 2016). Therefore, in the face of climate change, in order to reduce anthropogenic and environmental pressures on wild *Cag* populations, development of environmentally friendly protocols for its cultivation becomes a priority through the use of native arbuscular mycorrhiza (AMF) as biofertilizers and plant growth promoters (Berruti et al., 2016).

Under natural environmental or field conditions, crops are subjected to multiple stresses; therefore, instead of using specific inoculations with a single AMF morphotypes, a more diverse native AMF communities is required for growth stimulation and increasing performance may be found when AMF are obtained from native plants (Berruti et al., 2016), the former applies for ecological restoration as well (Berruti et al., 2014). In order to achieve such wide objectives in the long term, it would be necessary to perform studies on the phenological and ecophysiological performance of *Cag* in response to the climatic change patterns and soil traits (Richardson et al., 2013). The interaction of *Cag* plants with specific native AMF inoculum must also be evaluated from the genetic, biochemical and physiological standpoints, including the dynamics of the functional, successional and seasonal assemblages of AMF communities associated to wild or cultivated *Cag* (Bennett et al., 2013; Berruti et al., 2016). Lekberg and Koide, (2014), proposed that to gain a full understanding of the role of AMF symbiosis in nature, we need to better integrate physiological processes of Plants-AMF with their naturally occurring temporal and spatial patterns.

AMF (Glomeromycota) are obligated biotrophs that obtain photosynthetically fixed carbohydrates in exchange for mineral nutrients. Also, these fungi are a key biological component for soils fertility conservation and ecosystems productivity (Smith and Smith, 2011a,b, 2012; Berruti et al., 2014, 2016). However, potential benefits of AMF on plants may vary depending on seasonal environmental conditions (e.g. temperature, solar radiation, soil nutrients and water availability), which can consequently change the cost-benefit balance of this symbiotic interaction (Smith et al., 2010).

Moreover, modern crop management systems and agricultural practices (e.g. crop rotation, tillage, soil solarization, use of fungicides, pesticides and chemical fertilizers) can cause a negative impact in AMF consortia growth and composition, spore abundance, colonization ability and functional structures (arbuscules, coils and vesicles) formation. Besides, these common agricultural practices can change AMF functional diversity, as well as soil biological quality and crops productivity (Oehl et al., 2009; Berruti et al., 2014; Schneider et al., 2015).

We focused on the evaluation of *Cag*'s phenological and ecophysiological behavior in response to native AMF and the increase of phosphorus availability. We postulated that during *Cag* phenological development, its ecophysiological performance improves under different phosphorus availability due to the higher levels of native AMF propagules in the soil, exhibiting different patterns in biomass allocation, nutrients content, AMF functional colonization and spore's abundance in the mycorrhizosphere throughout the growing season. Our hypothesis was tested under natural environmental conditions in a shaded-house. Seasonal solar radiation regimes and air temperatures were recorded and *Cag*'s phenological transitions were evaluated in a physiological timeline, expressed in degree's days (°D), physiological growth variables were measured, as well as the AMF dynamics in the mycorrhizosphere.

2. Materials and methods

2.1. Location and source of the native AMFCag inoculum

Ten soil cores (0–30 cm depth) from the mycorrhizosphere of wild *Cag* plants were collected in a Sonoran Desert location ("La Cieneguita", altitude 980 masl, 29.32361 LN, -110.00922 LW, municipality of Baviácora, Sonora, México). To increase the AMF infective potential, all soil cores sampled were mixed and sieved (0.5 cm mesh). They were placed in plastic pots (24 cm width × 35.5 cm height, capacity of 9 kg) and *Cag* plants were grown as hosts for eight months (summer–winter 2013–2014) in shaded-house conditions. Subsequently, all soil in the pots along with all roots were mixed, homogenized and sieved again (0.5 cm mesh) to finally obtain an AMF inoculum, which is referred from now on as the native AMF*Cag* inoculum. Details of the characteristics of this AMF*Cag* inoculum, as well as experimental station and germination protocol are shown in Appendix A.

2.2. Soil type and treatments

Cag plants were cultivated in a substrate with biological and physicochemical characteristics analogous to those in which wild *Cag* plants grow. Therefore, a mixture of solarized river sand with the indigenous AMF*Cag* inoculum (2:1 v/v) was used as the experimental soil described below. Details of sand solarization, soil group taxonomy and soil physical and chemical characteristics are shown in Appendix A.

The soil mixture was placed in plastic pots (24 cm width × 35.5 cm height, and 9 kg capacity). Four fertilization treatments were established: 1. A control without chemical fertilizers (WCF), 2. A low P controlled release fertilization [6%P, one application of 7.93 g kg^{-1} of Osmocote Classic™, 12–14 months of longevity and a composition of 19% N, 6% P, 12% K and other micronutrients], 3. Controlled release fertilization with intermediate P [9%P, one application of 8.20 g kg^{-1} of Osmocote Plus™, 8–9 months of longevity and a composition of 15% N, 9% P, 12% K and other micronutrients] and 4. Liquid fertilization with high P content [LF30%P, which consisted of 500 mL of a 0.1% solution of soluble universal fertilizer Miracle Gro™ with a composition of 15% N, 30% P, 15% K and other micronutrients]. Additional details on liquid fertilization treatment are shown in Appendix A.

In each of the four fertilization treatments designated as WCF, 6%P, 9%P and LF30%P, a high and a low AMF mycorrhization treatments were tested. The high AMF mycorrhization treatment was established with the mixture (2:1 v/v) of the solarized sand with the AMF*Cag* inoculum, which had an initial concentration of 127 ± 20 spores per 100 g of soil of *Glomus* spp. and *Gigaspora* sp., and it's later labeled as AMF*Cag*+. The low AMF mycorrhization treatment was established with the mixture (2:1 v/v) of the solarized sand with the AMF*Cag* inoculum sterilized (121 °C/2 h). This treatment had a low initial concentration of AMF spores (21 ± 3 per 100 g of soil of *Glomus* spp.), and it's later labeled as AMF*Cag*−.

Details of the microbial population replacement of AMF*Cag*− treatment are shown in Appendix A. Forty days after sowing (see Appendix A for details of the germination protocol), plants of uniform size (9.98 ± 0.68 cm height) and without AMF colonization were transplanted, placing a single plant per pot and seven replicates (pots) per treatment. The experimental units (the plants in the pots of all treatments) were arranged in a completely randomized experimental design. Details of growth conditions, as well as of air temperatures and solar radiation regimes are shown in Appendix A.