Industrial Crops and Products 49 (2013) 188–195

Contents lists available at SciVerse ScienceDirect

Industrial Crops and Products

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

The growth rate modulates time to first bud appearance in *Physaria mendocina*

Liliana B. Windauer[a,*], Edmundo L. Ploschuk[a], Roberto L. Benech-Arnold[a,b]

[a] *Cátedra de Cultivos Industriales, Universidad de Buenos Aires, Facultad de Agronomía, Av. San Martín 4453, C1417DSE, Buenos Aires, Argentina*
[b] *IFEVA, Universidad de Buenos Aires, Facultad de Agronomía, Av. San Martín 4453, C1417DSE, Buenos Aires, Argentina*

ARTICLE INFO

Article history:

Keywords:
Physaria mendocina
Development
Floral induction
Radiation
Water
Nutrients
Growth rate
Gibberellins
Perennials

ABSTRACT

Physaria mendocina is under domestication because its seeds contain significant amounts of hydroxy fatty acids for several industrial uses, but displays a facultative biennial behavior which may represent a drawback in terms of production. Previous work revealed that the time to flower induction in this species is insensitive to temperature, photoperiod and vernalization, but suggested that this length of time could be determined by radiation, water and nutrients and/or the acquisition of a minimum growth rate. We aimed to determine whether the attainment of a threshold plant growth rate (GRt) triggers the initiation of the flowering phase in *P. mendocina*. Nutrient, water and radiation availability were manipulated to modify the timing of acquisition of that rate, expecting a concomitant modification of the time to flowering. We also explored the possibility that the stimulus is mediated by an accumulation of active gibberellins (GAs). Linear regressions were fitted between plant dry weight and time, and slopes of the relationships were considered as the growth rates. Radiation, water and nutrients constraints increased the duration of the phase between emergence and, concomitantly, first bud appearance (FBA). However, plants from all treatments reached FBA, after acquiring a growth rate of around 0.01 g d^{-1} pl $^{-1}$ (GRt).When exogenous GAs was applied under limiting radiation, plants reached FBA despite the fact that they never acquired a GRt; conversely, when GAs biosynthesis was inhibited under high irradiances, the plants required more days to reach FBA than controls, despite the fact that they acquired a GRt. The information obtained allow us to conclude that the time to FBA, which is the first visible manifestation of floral induction in this system, is modulated by factors controlling growth mediated by an accumulation of (GAs) and suggest that the acquisition of GRt is the internal feature that triggers floral induction. This knowledge offers a frame within which cropping systems could be designed in order to avoid or not a biennial behavior.

1. Introduction

Some species of the genus *Physaria* (formerly *Lesquerella* – Al-Shehbaz and O'Kane, 2002; O'Kane and Al-Shehbaz, 2004) are potential alternative crops for commercial oilseed production and are currently under domestication (Ploschuk et al., 2001; Dierig et al., 2006; Adam et al., 2007). For example, *Physaria fendleri* is a domesticated species characterized by an annual cycle; however, its low tolerance to water stress and low temperatures is well documented (González-Paleo and Ravetta, 2011a; Ploschuk et al., 2003; Dierig et al., 2006). This precludes its utilization in semi-arid environments as those that prevails in the central and southern parts of Argentina. In contrast, the perennial *P. mendocina*, native of the Monte Region of Argentina (Correa, 1984) also contains significant amounts of hydroxy fatty acids for several industrial uses (Thompson, 1990), but displays yield stability even under harsh environments, thus making it suitable for cropping areas that are too dry and/or cold for *P. fendleri* (González-Paleo and Ravetta, 2011a,b). It develops a perennial rosette with lateral spicate inflorescences every year with the central meristem remaining at vegetative stage.

Like other herbaceous perennial species, *P. mendocina* can flower during the first year if a favorable growing environment prevails (Hirose and Kachi, 1982); otherwise the plant delays the entrance in the reproductive stage until the second year of life (Kelly, 1985; De Jong et al., 1986; Prins et al., 1990; Klinkhamer et al., 1991; Wesselingh and De Jong, 1995; Burd et al., 2006). This facultative biennial behaviour clearly may represent a drawback in

---

[*] Corresponding author. Tel.: +54 11 4524 8040/8075; fax: +54 11 4514 8737.
E-mail addresses: windauer@agro.uba.ar, windauerliliana@gmail.com (L.B. Windauer).

0926-6690/$ – see front matter. Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.indcrop.2013.04.049

terms of production (Windauer et al., 2004, 2006). Thus, knowing the way in which the environment determines time to flowering is of paramount importance if the species is intended to be domesticated. For this reason, phenological responses to environmental factors have been studied in *P. mendocina* under controlled and field conditions (Windauer et al., 2004, 2006). The results revealed that time to flower initiation in this species is relatively insensitive to temperature, photoperiod and vernalization but, at temperatures higher than 24 °C, *P. mendocina* displayed a qualitative response (i.e. no development progression was observed) (Windauer et al., 2004). Even though, field experiments showed that the rate of development was accelerated as sowing date was delayed although, under late spring sowing dates, a biennial behaviour was observed, possibly due to the prevalence of mean temperatures higher than 24 °C (Windauer et al., 2006). Taken together these results indicate that, while temperatures are lower than 24 °C, there is an unknown factor, other than the above-mentioned, whose inductive capacity increases throughout the growing season. According to these results (i.e. no response to photoperiod and temperature), *P. mendocina* is likely to fall in the category of "autonomous-flowering" plants. Plants falling in this category are usually sensitive to irradiance (Bernier et al., 1993). Hence, the hypothetical factor behind initiation of the flowering phase might have been the incident radiation which, as in the case of photoperiod, is strongly associated to sowing date. Developmental response to radiation has been reported for other crops (Salisbury and Green, 1991, in rapeseed; Rawson, 1993 in wheat; Bertero, 2001 in quinoa). In biennial or perennial species, the influence of incident radiation on time to flower induction can be attributed to its effect on growth and, therefore, plant size, threshold size or physiological minimum size and threshold growth rate (Wesselingh et al., 1997).

Although the attainment of a critical plant size as a trigger for floral induction has been suggested for several species (Wesselingh et al., 1997; Werner, 1975; Gross, 1981; Kachi and Hirose, 1983; Klinkhamer et al., 1987; Kagaya et al., 2009), recent studies in other facultative biennial crop revealed that the rate of development towards flowering under inductive photoperiods is strongly affected by rosette's growth rate and not by a critical size (Gimenez et al., 2013). Moreover, previous information in *P. mendocina* showed a great variation in plant size at the onset of flowering (Windauer, 2002), suggesting that the initiation of this stage might be related to the acquisition of a threshold growth rate rather than to the acquisition of a certain plant size. This "threshold growth rate, GRt" would trigger floral initiation. Since growth rate is strongly modulated by the availability of resources such as nutrients, radiation and water (Taiz and Zeiger, 2006), it seems reasonable to predict that any limitation in the availability of these resources (and not only incident radiation) would delay the onset of flowering in *P. mendocina*.

Genetic and physiological studies indicate that gibberellins (GAs) modulate the autonomous flowering pathway (Jacobsen and Olszewski, 1993). Moreover, there is genetic evidence for crosstalk between the autonomous and gibberellin-dependent flowering pathways (Mier et al., 2001). Hence, if in the end floral induction is indeed elicited once a threshold plant growth rate is attained, it might be expected that the stimuli is mediated by an accumulation of active GAs.

In this paper we tested the hypothesis according to which the attainment of a threshold plant growth rate triggers the initiation of the flowering phase in *P. mendocina*. To do this we experimentally manipulated variables as nutrient, water and radiation availability to modify the timing of acquisition of that rate, expecting a concomitant modification of the time to flowering. We also explored the possibility that the stimulus is mediated by an accumulation of active GAs.

2. Materials and methods

2.1. Plant material and management

Seeds of *P. mendocina* were collected from a native stand at Lihuel Calel, La Pampa, Argentina (37° 57′S, 65° 33′W). The seeds used for the experiments were reproduced and selected for morphological traits (i.e. plant size and seed size) under the same environmental conditions during five generations in our experimental field (Facultad de Agronomía, UBA; 34° 37′S, 58° 20′W). All experiments were carried out at the Facultad de Agronomía with seeds of the year (i.e. less than 1 year storage), and plants were grown under adequate water conditions and kept free from weeds, diseases and insects.

2.2. Experiment 1: radiation availability

A field experiment was carried out during 2007 on a salty clay loam soil (Vertic Argiudoll) with the aim to explore the possibility that radiation intensity (a factor strongly associated to sowing date) is behind the initiation of the flowering phase. Flower induction suggests an early event during which meristems commit to reproduction. It was beyond our possibilities to determine and to identify the first meristem changing to a reproductive stage. In addition, due to the architecture of this plant, the moment of floral initiation is not easily related to the number of leaves initiated. Therefore, first bud appearance (FBA, floral buds within the same inflorescence joined, still covered by the terminal leaves) was regarded as the first visible signal of floral induction, and time to FBA was recorded in calendar days; indeed, due to the absence of a relationship between developmental rate and temperature, thermal time for the phase emergence (EM)-FBA is meaningless for *P. mendocina* (Windauer et al., 2004). Plots were considered to be at a given phase when 50% of the plants reached that stage.

The experiment was hand sown on 5 June 2007 and urea (170 kg ha^{-1}) was applied before sowing. Treatments were arranged in three randomized complete blocks with three replicates (plots). Each plot consisted of eight rows, 0.2 m apart and 1 m long for a total density of 50 plants m^{-2}. Treatments consisted of a control (TC, 100% of incident radiation) and four treatments with low radiation (shaded treatment) imposed two weeks after EM for all plots over a period of increasing duration depending on the treatment: R1: 21 days, R2: 42 days, R3: 64 days and R4: maintained at low radiation until FBA. These treatments allowed for the accumulation of different amount of radiation. Low irradiance plots were shaded with black shade netting placed 0.20 m above the canopy. The shade netting intercepted 67% of incident radiation (i.e. 33% of incident radiation reaching the canopy) but did not modify light quality (i.e. R/FR ratio). Air temperature sensors, connected to a Data Logger (LI-COR model 1000, Lincoln, NE, USA) were placed into the canopy to test the impact of shading on canopy temperature. The nets used to reduce incident radiation (shaded treatment) reduced the canopy average daily temperature by only 0.7 °C.

2.3. Experiment 2: water availability

A field experiment was hand sown on 18 June 2011 in rectangular boxes (1.2 m × 1.00 m × 0.12 m deep), containing a mixture of soil (80%) and sand (20%). Treatments were arranged in a completely randomized design with four replicates (microplots) per treatment and consisted of a control (W+, the microplots were maintained at field capacity) and one treatment of water stress; the microplots were restricted in the irrigation in order to generate water stress (water stress treatment, W-). This treatment was imposed two weeks after emergence and it was applied during 40 days approximately when the supply water was re-established