Perspectives in Plant Ecology, Evolution and Systematics 24 (2017) 48–60

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

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

Reproductive efficiency and photosynthetic pathway in seed plants

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ARTICLE INFO

Article history:
Received 7 December 2015
Received in revised form 10 October 2016
Accepted 8 December 2016
Available online 10 December 2016

Keywords:
C_3
C_4
CAM
Life form
Reproductive efficiency
Self-compatibility

ABSTRACT

We aimed at determining whether C_4 and CAM species had a higher reproductive efficiency than C_3 species because of their higher water- and nitrogen-use efficiency. The resource-limitation hypothesis was also examined in the context of photosynthetic pathway. Reproductive efficiency was evaluated by measuring fruit set (fruit/flower ratio), seed set (seed/ovule ratio), and relative fecundity (the proportion of well-developed seed formed per ovule per infrutescence), along with seed abortion, and flower, fruit and seed biomass were evaluated. Photosynthetic pathway was determined according to literature, taxonomy, leaf anatomy and carbon isotopic composition ($\delta^{13}C$). Additionally, carbon and nitrogen content and nitrogen isotopic composition ($\delta^{15}N$) were determined. Plant life form and breeding system were considered. The traits of $\delta^{13}C$ and $\delta^{15}N$ were found to be positively correlated to fruit set, seed set and relative fecundity. The C_4 species exhibited the highest values of fruit and seed set associated to the lowest biomass of flower, fruit, seed, and seed/fruit. The CAM species exhibited the highest values of flower and seed/fruit biomass and C_3 species had the highest values of fruit and seed biomass. Reproductive efficiency was negatively related to the cost of reproductive structures in C_3 species. The highest values of maximum relative fecundity were reached in CAM and C_4 species under contrasting costs of reproductive structures: high values of fruits and seeds biomass in CAM species and low values of fruit and seed biomass in C_4 species, suggesting that CAM species may reach high values of maximum fecundity irrespectively of fruit and seed cost. Patterns found in reproductive efficiency may be slightly modified according to life form and breeding system: fruit set was higher for annual than perennial herbs, which may be initially associated to the self-compatibility and autogamy of annual herbs. Fruit set increased from C_3 to CAM species for annual herbs and decreased from C_3 to CAM species for perennial herbs, indicating that C_4 and CAM photosynthetic pathways could be associated with the increment of reproductive efficiency in annual species. Besides the traditionally acknowledged relationship with resistance to stressful environments, reproductive strategies of C_4 and CAM plants could be also related to an increment in plant reproduction.

1. Introduction

Flowering plants often produce more flowers than fruits (Stephenson, 1981; Sutherland, 1986, 1987; Ramírez, 1992, 1993). Such disparity between fruit and flower production is also frequently found between the number of ovule/flower and the number of seed/fruit (Stephenson, 1981; Ramírez, 1992) and is generally affected by the same factors. Several hypotheses and some specific factors have been proposed to explain the selective advantages of surplus flowers and ovules. The main factors affecting fruit and seed production are: self-incompatibility, genetic load, plant life form, male function of hermaphrodite flower, selective abortion, sexual system, pollinator limitation, bet hedging, latitude, fruit cost, resource limitation, pollination system (Sutherland, 1986, 1987), morphological fruit type and dispersal syndromes (Ramírez and Berry, 1993), inflorescence attributes (Ramírez and Berry, 1995), fruit and seed costs (Ramírez, 1992), herbivory, seed predation, and physiological conditions (Stephenson, 1981).

In spite of the large number of factors accounting for fruit and seed set, fruit and seed production need to be examined further in order to continue recognizing the multifactorial character of reproductive efficiency (reproductive efficiency is defined here as any of the output reproductive levels: fruit set, seed set and relative fecundity measured under natural conditions). A few investigations have examined the integration of physiology and reproduction in plants: studies addressing mineral nutrition and plant reproduction (Stephenson, 1981; Mattila and Kuitunen, 2000; Groeneveld et al., 2010), resource distribution (Watson, 1986), the contribu-

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http://dx.doi.org/10.1016/j.ppees.2016.12.004
1433-8319/

tion of photosynthesis of green fruit to fruit and seed development (Cipollini and Levey, 1991; Aschan and Pfanz, 2003) and the effect of the operation of CAM on fecundity (Herrera, 1999), among others. However, the effects of physiological plant traits on reproductive efficiency have not been extensively evaluated. In this context, the main physiological attribute to be examined in the context of reproductive efficiency should be photosynthetic pathway. The relation between photosynthetic pathways and reproductive efficiency may contribute to understand additional functions of the different carbon metabolism types associated to reproduction, besides the traditional correlation between carbon metabolism and environment where the occurrence of C_4 and CAM species has been related to selective pressures imposed by water limitation (Sage, 2004; Borland et al., 2011).

In the context of the evolutionary significance, plant fitness has to increase with the increment of reproductive output, which may be enhancing, among other factors, by means of physiological advantages. In fact, C_4 and CAM species may increase fitness throughout reproductive efficiency (Herrera, 2009). Indirect evidence suggests that C_4 and CAM may have a higher reproductive efficiency than C_3 species: 1) C_4 and CAM species have higher water-use efficiency (Long, 1999; Pierce et al., 2002b) and may have higher nitrogen-use efficiency (Brown, 1978; Griffiths, 1989; Ehleringer and Monson, 1993; Taylor et al., 2010; but see Lüttge, 2004). 2) Photorespiration in C_3 plants can release some of the CO_2 fixed and also has an energetic cost, whereas photorespiration is much lower in C_4 and CAM plants; therefore, CAM and C_4 plants can perform net CO_2 fixation more efficiently (Nobel, 1991). 3) The high potential productivity of certain CAM species under optimal environmental conditions using annual above-ground dry-mass productivity may exceed that of most C_3 plant species (Nobel, 1991). However, there are contrasting results: the biomass productivity of CAM has been found low compared with that of C_3 and C_4 plants (Lüttge, 2004), and cultivated CAM crops may reach productivity values comparable with those of C3 plants under agricultural management (Nobel, 1996). According to reproductive efficiency, CAM induction has been interpreted as a strategy to extend resource allocation to reproductive biomass and maximize reproductive output (Sayed and Hegazy, 1994; Taisma and Herrera, 1998, 2003; Herrera, 2009).

In view of the above observations, we may expect CAM and C_4 species to exhibit higher values of reproductive efficiency than C_3 species. In addition, reproductive efficiency in seed plants is largely influenced by life form and breeding system (Sutherland and Delph, 1986; Sutherland, 1986; Ramírez, 1993): life-form is intimately related to photosynthetic pathway (Medina, 1995; Ehleringer, 1995; Wang, 2005) and succulence is closely related to CAM species (McWilliams, 1970; Kluge and Ting, 1978; Batanouny et al., 1991). In this context, cross-results of reproductive biology and photosynthetic pathway from comparative studies ought to include information on plant life form and self-compatibility, since herbaceous species are more efficient than woody species, and self-compatible species may be more efficient in reproduction than self-incompatible species (Sutherland, 1986; Ramírez, 1993). Besides, plant life form is not equally distributed across the different photosynthetic pathways. The C_4 pathway is essentially found in only three life-forms: graminoid, evergreen shrub and annual species, and CAM is found mostly in perennial and annual herbs (Ehleringer, 1995), and with lower frequency in shrubs, lianas and arborescent plants (Medina, 1995).

Reproductive efficiency may be also influenced by nutritional status of plant species. The higher nitrogen-use efficiency found in C_4 and CAM species (Brown, 1978; Griffiths, 1989; Ehleringer and Monson, 1993; Taylor et al., 2010; but see Lüttge, 2004; Hietz et al., 1999) could be linked to higher reproductive efficiency. The effect of leaf nitrogen content and nitrogen sources on plant nitrogen uptake in the field, assessed through the relative isotopic N composition ($\delta^{15}N$), has been also evaluated in the context of reproductive efficiency, because of the positive effects of nutrient application on reproductive success in perennial plants (Mattila and Kuitunen, 2000). Some applications using $\delta^{15}N$ in plant tissues include assessing contributions of various N sources to plant N uptake in the field, including symbiotic nitrogen fixation and atmospheric deposition, the role of mycorrhizal infection, uptake of dissolved N, and the interpretation of $\delta^{15}N$ profiles in soils (Marshall et al., 2008). In this context, we aimed at finding out whether a relationship existed between $\delta^{15}N$ and the different levels of reproductive efficiency because of the relationship between the values of $\delta^{15}N$ and N availability (Medina et al., 2008; Marshall et al., 2008).

Resource limitation hypothesis propose that fruit set is limited by the cost of the fruit and seed, where plants with expensive fruits would have a lower efficiency than species with inexpensive fruit (Sutherland, 1986; Ramírez, 1993). Bearing this in mind, the relation among biomass allocation to reproductive structures, reproductive efficiency and seed abortion was also examined in the context of the photosynthetic pathway. Species with expensive fruits and seeds (high biomass values) would have lower reproductive efficiency than those with cheap fruits and seeds (Stephenson, 1981; Sutherland, 1986; Ramírez, 1992, 1993; Ramírez and Berry, 1993), which is related to resource limitation when the energy allocated to fruit maturation is fixed (Sutherland, 1986). Low levels of fruit set are associated to high energetic cost of fruits (Ramírez, 1992). In this context, physiological traits of the photosynthetic apparatus may be linked to the production of costly fruits and flowers and high values of reproductive efficiency.

In the light of the CAM/C_4 high reproductive efficiency hypothesis, the following predictions were tested: 1) In the absence of factors limiting fruit and seed set, C_4 and CAM species would exhibit higher reproductive efficiency than C_3 species, because C_4 and CAM species have higher water-use efficiency, and 2) the comparatively higher reproductive efficiency expected in C_4 and/or CAM species could be related to cheaper fruits and seeds than in C_3 species, or could occur through the physiological benefits of such photosynthetic pathways.

2. Methods

2.1. Localities

Plant species were selected in such a way to maximize number of plant families and taxa included. Species grew in 15 Venezuelan communities which included a great variety of vegetation types according to Huber and Alarcón (1988), and comprised areas from sea level to close to 4000 m (Appendix S1). Overall, photosynthetic pathway was evaluated in 1258 species of 135 families from Venezuela.

2.2. Reproductive efficiency

In most of the species included in this study, reproductive efficiency was determined experimentally; however, some information on reproductive efficiency was completely or partially available from previous studies (Sobrevila et al., 1983; Enrech et al., 1988; Ramírez, 1993, Ramírez and Brito, 1990; Ramírez and Seres, 1994; Madriz and Ramírez, 1997; Nassar et al., 1997; Grases and Ramírez, 1998; Raimúndez and Ramírez, 1998; Raimúndez, 2000; Castro-Laporte and Ruiz-Zapata, 2000; Valerio and Ramírez, 2003; Nassar and Ramírez, 2004; Hokche and Ramírez, 2006, 2008; Nassar et al., 2007; Ramírez, 2007; Barrios and Ramírez, 2008; Ramírez et al., 2008; Hokche and Ramírez, 2008; Herrera and Nassar, 2009; Villalobos and Ramírez, 2010). Three levels of repro-