Original Article

Phenotypic Plasticity of *Pimenta pseudocaryophyllus* (Gomes) Landrum Under Different Light Conditions

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ABSTRACT

The heterogeneous light pattern in forest environments leads to specific morphological and physiological responses. However, anthropogenic pressures in areas such as Atlantic Forest and Cerrado are modifying the light availability, and consequently the forest community composition. The aim of this study was to investigate the plasticity of forest species *Pimenta pseudocaryophyllus* under full sunlight and shade conditions. *P. pseudocaryophyllus* showed typical shade plant phenotype, with higher net photosynthesis, transpiration, and chlorophyll *a* and *b* contents when cultivated under this condition. The decrease in net photosynthesis under full sunlight conditions is probably related to PSII photoinhibition. In addition, under full sunlight, reduced height, number of leaves, and specific leaf area was observed, while plants in shade increased these characteristics. *P. pseudocaryophyllus* did not show high morphological and physiological plasticity, which may be a maladaptive response. It was concluded that forest disturbances could compromise the occurrence and survival of *P. pseudocaryophyllus*.

Keywords: initial growth, RDPI, full sunlight, shade, pau-cravo.

1. INTRODUCTION

Forest environments have heterogeneous light pattern due to the predominance of trees with continuous canopy (Rossatto et al., 2010; Valladares & Niinemets, 2008). Light conditions can affect plant growth and development, modifying leaf expansion and canopy development (Wu et al., 2018). Thus forest species have some characteristics that help their survival and maximize light interception, such as high growth rate, high specific leaf area, high chlorophyll content, low leaf thickness, in addition to low nitrogen investment per leaf area (Franco et al., 2014; Gotsch et al., 2010; Mathur et al., 2018; Valladares & Niinemets, 2008; Wu et al., 2018).

However, some human actions have abruptly modified the dynamics of forest radiation. Such events could result in alteration of vegetation types, their range shifts, and the crowding of trees (Nicotra et al., 2010), modifying light availability, and consequently plant growth, leaf area production, and the known patterns of community composition (Pinheiro et al., 2016; Silva & Horwath, 2013; Valladares & Niinemets, 2008). Cerrado and Atlantic forest are among the domains most affected by such changes, which puts several species at risk (Franco et al., 2014; Scarano & Ceotto, 2015).

In this context of disturbance in the light availability dynamics, some species are expected to be restricted to either closed or open environments (Rossatto et al., 2009), while others may have strategies that allow their coexistence in different areas (Rossatto & Franco, 2017). It is observed during the seedling phase, once the development of structures is related to plant growth needs (Vieira et al., 2015). Although it varies among species and environments, the phenotypic plasticity, through variations in morphological and physiological traits, seems to be the main attribute for the adjustment of species in different light environments (Chevin et al., 2010; Matesanz et al., 2010; Valladares et al., 2000).

Quantifying the phenotypic plasticity is important to understand how species can adjust or not to environmental modifications (Gratani, 2014; Valladares et al., 2000). *Pimenta pseudocaryophyllus* (Gomes) Landrum (Myrtaceae), an endemic and secondary type species, popularly known as pau-cravo, was chosen due to its wide distribution, occurring in high-altitude areas in Atlantic Forest Domain and Cerrado *lato sensu* (Landrum & Kawasaki, 1997; Lorenzi, 2009; Oliveira-Filho & Fontes, 2000; Sobral et al., 2015). Considering the replacement of forest communities by savanna due to fragmentation, deforestation, or fire for land clearing in Atlantic Forest and Cerrado areas (Franco et al., 2014; Scarano & Ceotto, 2015), the distribution and survival of *P. pseudocaryophyllus* may be threatened.

Considering possible changes in natural light environments, it has been hypothesized that a widely distributed species such as *P. pseudocaryophyllus* may modify morphological structures and physiological responses, and consequently present high phenotypic plasticity in order to survive in different light availability conditions. The aim of this study was to investigate which physiological and morphological traits may confer plasticity to *P. pseudocaryophyllus* plants during their initial establishment under full sunlight and shade conditions.

2. MATERIALS AND METHODS

2.1. Experimental design and plant material

The experiment was carried out in greenhouse in the municipality of Lavras (21°13'40" S and 44°57'50" W GRW), southern Minas Gerais state, Brazil. *P. pseudocaryophyllus* seeds were harvested in a wooded area in the municipality of Ijaci (21°10'12" S e 44°55'31" W GRW), southern Minas Gerais state. Seeds were cleaned and sown in plastic trays containing non-autoclaved washed sand substrate. They were distributed into two light environments: i) Low-density clear plastic, simulating full sunlight conditions; ii) Shade by undercover with Sombrite® shade net, with 50% interception of short and long wave radiation. Two months after the emergence of seedlings, the most uniform individuals were selected and transplanted into Citropotes® (33.5 × 14 cm) with 4 L of washed sand. Plants were kept in the same environments to acclimate for 30 days. After acclimation period, they were fertilized with one-fourth strength nutritive solution, according to Malavolta (2006). Plants were evaluated for 120 days in a completely randomized design, with five replicates and two light environments. Growth analyses were performed every month. The other variables were assessed at the end of the experimental period using healthy and fully expanded leaves.

2.2. Monitoring of environmental conditions

The quality and amount of light were determined at plant height in the different light environments at midday in a clear-sky day. The quality of light in each wavelength was measured using portable spectroradiometer USB-650 RED TIDE (Ocean Optics), while the photosynthetic active radiation (PAR) was measured using LI-COR Quantum Sensor Q41031 (coupled to IRGA model LI-6400XT). Daily air temperature (T, in °C) and air relative humidity (RH, in %) were measured every 3 h using thermohygrometer model RHT10 (Extect Instruments). Vapor pressure deficit (VPD) was calculated using temperature and relative humidity data, according to Jones (1992). Substrate field capacity was 0.21 $m^3.m^{-3}$ and the amount of water needed to keep constant water availability was estimated using the ML2x TetraProbe. Irrigation was conducted every three days, aiming to keep water volumetric content (θ) between 65% and 70% field capacity. Air temperature, VPD, and water volumetric content were similar for the different treatments throughout the experimental period (Table 1).

Only PAR differed significantly between environments, decreasing 110% from full sunlight to shade, in addition to reduction in the quality in each wavelength (Table 1, Figure 1). This way, any change of morphological or physiological traits was expected to be a result of the different light availability.

2.3. Growth analysis

Growth measurements were performed monthly during the experimental period. Plant height (cm) was measured using graduated ruler, stem diameter (mm) was measured in the same previously marked position, 1 cm from the soil, using digital caliper rule, and the number of leaves was counted. At the end of 120 days, specific leaf area (SLA- $m^2.kg^{-1}$) was determined using 5 leaves per plant, using leaf area meter (CID Bio-Science, CI-203). Leaves were oven-dried and SLA was calculated dividing total leaf area by leaf dry mass. Subsequently, plants were harvested and divided into leaves, stem, and roots and dried in oven at 70 °C for 48 h. The dried weight was used to determine the root to shoot biomass ratio (R:S ratio).

2.4. Gas exchange and content of chloroplast pigments

Gas exchange was evaluated between 09:00 and 11:00 a.m. using infrared gas analyzer (IRGA model LI-6400XT, LI-COR). The photosynthetic photon flux density was provided by a LED light source and set at 600 $\mu mol.m^{-2}.s^{-1}$ and chamber temperature was set at 25 °C. The net photosynthesis ($\mu mol.m^{-2}.s^{-1}$), stomatal conductance ($mol.m^{-2}.s^{-1}$) and transpiration values ($mmol.m^{-2}.s^{-1}$), as well as internal carbon dioxide concentration (ppm) were determined. The concentrations of chloroplast pigments, chlorophyll *a*, *b*, and carotenoids (xanthophylls + carotene) ($\mu g.g^{-1}$) were also determined according to the method of Lichtenthaler & Buschmann (2001).

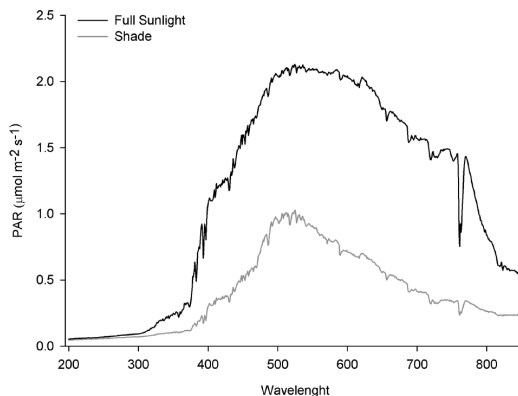**Figure 1.** Incident photosynthetic active radiation at midday under two light environments: Full Sunlight (black line) and Shade (dark gray line).

Table 1. Environmental conditions of full sunlight and shade environments throughout the experimental period.

Environmental Variables	Light Environment	
	Full Sunlight	**Shade**
VPD (kPa)	2.64±0.38[a]	2.25±0.37[a]
PAR ($\mu mol.m^{-2}.s^{-1}$)	592.5±64.7[a]	280.7±24.1[b]
T (°C)	27.8±1.8[a]	25.1±2.6[a]
θ ($m^3.m^{-3}$)	0.138±0.014[a]	0.147±0.022[a]

VPD = Vapor pressure deficit; PAR = Photosynthetic Active Radiation; T = daily average air temperature; θ = water volumetric content. Values followed by same letter do not show significant differences according to t-test (P < 0.05). Values are presented as means ± standard error.

2.5. Relative distance phenotypic index

Morphological (SLA and R:S ratio) and physiological (gas exchange and content of chloroplast pigments) values were used to calculate the Relative Distance Phenotypic Index (RDPI), according to Valladares et al. (2006).

2.6. Statistical analysis

Growth, gas exchange and content of chloroplast pigments data were submitted to t-test (P < 0.05). Morphological and physiological RDPI data were compared using one-way ANOVA and Tukey's test (P < 0.05). Both analyses were performed in Sigma Plot software (version 11.0).

3. RESULTS AND DISCUSSION

P. pseudocaryophyllus plants grown under shade conditions showed 56% higher net photosynthesis in comparison to full sunlight. Under that condition, higher transpiration, chlorophyll *a* and carotenoid content were also observed (Table 2). Higher chlorophyll content was observed in plants grown under shade conditions, which is related to an increase in photosynthetic capacity under low light condition (Díaz-Barradas et al., 2018; Mathur et al., 2018; Valladares & Niinemets, 2008). The same can be observed for carotenoid content, which function in light capture is also related to shade environments (Sánchez-Gómez et al., 2006). The results have demonstrated that *P. pseudocaryophyllus* have light harvesting apparatus adjusted to low light environments. Thus, when the species is adapted to low irradiance, individuals can adjust their photosynthetic apparatus by increasing the photosynthetic pigment content,

transpiration, and stomatal conductance in order to use light and CO_2, optimizing the photosynthetic process (Barros et al., 2012; Catoni et al., 2015; Habermann et al., 2011). In this context, the greater transpiration observed in plants under shade conditions can also contribute to higher net photosynthesis (Table 2).

There was no difference for stomatal conductance; however, in relation to intercellular CO_2, plants grown under full sunlight showed result 51% higher when compared to those grown under shade conditions (Table 2). Even with the highest intercellular concentration, *P. pseudocaryophyllus* reduced photosynthesis when exposed to high light intensity. Additionally, the reduction in chlorophyll *a* and carotenoid contents observed in full sunlight may indicate low acclimatization to intense radiation (Table 2).

A reduction in leaf chlorophyll content together with an increase in carotenoid contents are observed under high irradiance conditions, which are related to a reduction in light harvesting, and consequently to photodamage (Balaguer et al., 2002; Díaz-Barradas et al., 2018). In full sunlight environments, high carotenoid contents are related to energy dissipation by the xantophyll cycle, an important strategy for the reduction of photoinhibition damages (Lichtenthaler et al., 2007; Sánchez-Gómez et al., 2006). However, considering that carotenoids play a fundamental role in non-photochemical quenching mechanisms (Díaz-Barradas et al., 2018), the lower net photosynthesis observed in full sunlight may be related to a limitation of photosystem II (PSII) caused by excess radiation, since there was no stomatal limitation.

Plants from shade environments when exposed to full sunlight conditions can experience photoinhibition,

Table 2. Gas exchange characteristics and content of chloroplast pigments of *Pimenta pseudocaryophyllus* plants grown under full sunlight and under shade conditions.

	Light Environments	
	Full Sunlight	**Shade**
Net photosynthesis (μmol.m^{-2}.s^{-1})	5.85±0.44[b]	9.12±0.68[a]
Stomatal conductance (mol.m^{-2}.s^{-1})	0.05±0.013[a]	0.06±0.004[a]
Transpiration (mmol.m^{-2}.s^{-1})	1.19±0.28[b]	1.96±0.15[a]
Internal carbon concentration (ppm)	237.80±3.75[b]	157.66±23.13[a]
Chlorophyll *a* (μg.g^{-1})	786.31±131.45[b]	1605.15±196.02[a]
Chlorophyll *b* (μg.g^{-1})	585.40±126.50[a]	792.70±135.18[a]
Carotenoids (μg.g^{-1})	260.66±98.03[b]	382.25±30.58[a]

Values followed by same letter do not show significant differences according to t-test (P < 0.05). Values are presented as means ± standard error.

which indicates PSII damage and, consequently, reduction in photosynthesis rate (Azevedo & Marenco, 2012; Valladares et al., 2002). It appears that this species has low adjustment capacity of the photosynthetic apparatus to high irradiance, at least during the initial growth, which is worrying in the context of environmental changes.

P. pseudocaryophyllus cultivated in the environment with lower PAR showed 51% higher increment in height and twice the number of leaves, when compared to full sunlight conditions (Figure 2). However, stem diameter remained unchanged, regardless of light environment (Figure 2). An increase of 110% in SLA of plants grown under shade conditions was also observed, while the R:S ratio of plants cultivated in full sunlight was 20% higher (Table 3).

A reduction in SLA and preferential investment in roots indicate adjustment of *P. pseudocaryophyllus* under full sunlight conditions, as it allows plants to reduce their transpiration area, avoiding water loss (Catoni et al., 2015; Hoffmann et al., 2005). In addition, in open and sunny environments, plants usually show preferential biomass allocation to roots as an adjustment

to reach water in deeper soil layers (Gignoux et al., 2016; Ronquim et al., 2003). However, the likely PSII photoinhibition and reduction in net photosynthesis could have caused a phenotype modification, since plants grown under full sunlight conditions showed reduction in height and number of leaves (Figure 2). High net photosynthesis rate is associated to increase in carbon gain, biomass accumulation and consequently structural growth (Oguchi et al., 2008). On the other hand, when grown in shade, *P. pseudocaryophyllus* showed preferential investment in shoots as expected for forest species (Figure 2 and Table 3). In forest environments, individuals with higher height and specific leaf area are more competitive, once they can optimize radiation absorption by increasing the possibility of light interception (Gignoux et al., 2016; Sanches et al., 2017).

The environmental conditions caused different responses in *P. pseudocaryophyllus* plants, allowing the quantification of phenotypic plasticity for some traits. It was observed that the R:S ratio was the least plastic trait, while transpiration was the most plastic trait (Table 4).

In the phenotypic plasticity scale (0 to 1), values below 0.5 are considered low. It was observed that *P. pseudocaryophyllus* can be described as a species with low plasticity. According to Valladares & Niinemets (2008), species that are shade tolerant tend to exhibit lower phenotypic plasticity, not adapting to the light pattern of open environments. Even when characteristics of higher plasticity, such for stomatal conductance, intercellular CO_2, and chlorophyll *a* and *b* are observed, better fit of the species in the full sunlight environment was not observed, once these

Table 3. Specific leaf area (SLA) and root to shoot biomass ratio (R:S ratio) of *Pimenta pseudocaryophyllus* plants grown under full sunlight and under shade conditions.

	Light Environments	
	Full Sunlight	**Shade**
SLA (m^2.kg^{-1})	2.72±0.08[b]	4.45±0.21[a]
R:S ratio	0.36±0.01[a]	0.30±0.01[b]

Values followed by same letter do not show significant differences according to t-test (P < 0.05). Values are presented as means ± standard error.
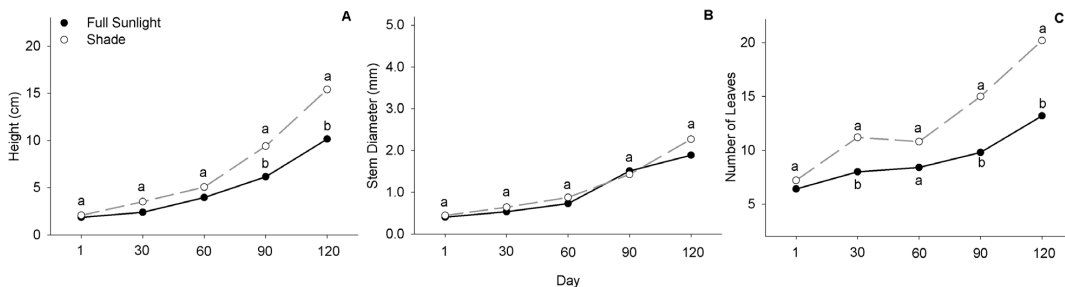

Figure 2. Shoot height (A), stem diameter (B), and number of leaves (C) of *Pimenta pseudocaryophyllus* plants grown under full sunlight and shade conditions. Values followed by same letter, in each evaluation day, do not show significant differences according to t-test (P < 0.05).

Table 4. Relative Distance Phenotypic Index (RDPI) of morphological (SLA and R:S ratio) and physiological (gas exchange and content of chloroplast pigments) traits of *Pimenta pseudocaryophyllus* plants grown under full sunlight and under shade conditions.

Traits	RDPI
Net photosynthesis	0.28 ± 0.03^b
Stomatal conductance	0.47 ± 0.03^{ab}
Transpiration	0.52 ± 0.03^a
Internal carbon concentration	0.45 ± 0.06^{ab}
Chlorophyll *a*	0.43 ± 0.07^{ab}
Chlorophyll *b*	0.45 ± 0.05^{ab}
Carotenoids	0.14 ± 0.03^b
SLA	0.21 ± 0.02^b
R:S ratio	0.05 ± 0.02^c

Values followed by same letter do not show significant differences according to one-way ANOVA and Tukey's test ($P < 0.05$). Values are presented as means ± standard error.

plants showed lower photosynthesis in relation to shade species. It occurs because phenotypic plasticity may be a response to resource limitation, called passive reduction, which may represent a maladaptive response (Nicotra et al., 2010; van Kleunen & Fischer, 2005). In this case, plasticity is not an anticipatory response to environmental threats and, consequently, it is not an adaptation strategy, but a consequence of abiotic modifications (Forsman, 2015).

Considering that phenotypic plasticity is higher for pioneer species due to the heterogeneous environments where they occur (Yuan et al., 2016), it is possible that *P. pseudocaryophyllus*, a secondary type species, may not present high plasticity. In fact, the increase in light availability is responsible for changing plant functional spaces in secondary formations (Chua & Potts, 2018). Thus, even though *P. pseudocaryophyllus* has wide distribution, its low phenotypic plasticity observed in our experimental conditions may indicate low ability to occupy different environments, especially full sunlight areas. Our findings reinforce the fragility of this species and possible developmental and consequently establishment damages caused by the ongoing fragmentation events in Atlantic Forest and Cerrado areas.

4. CONCLUSION

Our results indicate that the adaptation of *P. pseudocaryophyllus* in open and sunny environments is low, which may compromise plant growth and development under these conditions. In this way, the fragmentation process in areas where *P. pseudocaryophyllus* occurs is extremely dangerous for the occurrence and survival of the species.

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