

Characterization of junglerice: growth habit and morphological plasticity determined by population density

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Abstract: **Background:** Numerous studies have described junglerice (*Echinochloa colona*) competitiveness against crops, but its behavior concerning plant density as an outcome of intraspecific competition has not been well documented. **Objective:** This study aimed to characterize morphology based on population density and determine the degree of density dependence. **Methods:** Junglerice was grown in field conditions in a range of densities from 0.25 to 300 plants m⁻². Plant height and width, tillering, aerial dry weight, seed weight, seed number, and hundred-seed weight were determined and related to growth habits by principal components analysis. The variables were fitted to the growth habits using a general linear model. Aerial dry weight, tiller number, seed number, and seed weight per plant (pl⁻¹) and per area (m⁻²) were

fitted to plant density using non-linear functions. **Results:** Plants exhibited prostrate habit at 0.25 plants m⁻², semi-prostrate habit at 2-4 plants m⁻², and erect habit at 35 plants m⁻². Prostrate plants displayed a width of 196 cm, a height of 40 cm, 158 tillers per plant, and over 32,000 seeds per plant, whereas erect plants had an average width of 13.7 cm, a height of 114.5 cm, 10 tillers per plant, and approximately 1,700 seeds per plant. The aerial dry matter per area adhered to the law of constant final yield. In contrast, tiller number, seed number, and weight per area had a nonlinear dome-shaped relationship.

Conclusions: Junglerice modifies its aerial structures according to population density, showcasing extensive morphological plasticity. This characteristic allows junglerice to adopt different growth habits.

Keywords: Density Dependence; Adaptability; Aerial structures; Monospecific Experiments; Intraspecific Interactions

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1. Introduction

Junglerice (*Echinochloa colona* (L.) Link) is one of the most globally significant weeds due to its various attributes, notably its competitiveness and adaptation to diverse environments (Damalas et al., 2008; Tahir, 2016). However, it has also been described as having low phenotypic plasticity (Awan et al., 2014). Phenotypic plasticity is a characteristic that allows individuals to modify a set of traits in response to environmental changes, thereby serving as a critical adaptive strategy for evolution (Pigliucci et al., 2006; Munier-Jolain et al., 2014).

Damalas et al. (2008) described the ability of junglerice to optimize solar radiation utilization through stem arrangement modifications. In addition, several studies have shown that junglerice plants can exhibit different growth habits through morphological variations, such as height ranging from 10 to 100 cm (Cabrera et al., 1970; Tahir, 2016) or stem arrangements varying from prostrate to erect (Damalas et al., 2008; Awan et al., 2014; Catindig et al., 2019).

In several weed species, plant height is one of the variables most sensitive to intraspecific density changes. However, unlike that observed in broadleaf species, grasses like *Alopecurus myosuroides* may be seriously affected by self-shading (Munier-Jolain et al., 2014). Moreover, increased intraspecific density often leads to lower biomass of stems, roots, and leaves (self-thinning), reducing total biomass and directly impacting seed production (Springer, 2020; Zhao et al., 2021).

Understanding the adaptive strategies used by junglerice individuals in response to variations in population density is crucial to understand the expected response, particularly regarding weed-crop interactions (Swanton et al., 2015). Moreover, identifying variations in the relationships between individuals within a population is relevant to understanding potential changes within a community from an evolutionary ecology perspective (Callaway et al., 2003).

We postulated that when junglerice plants grow under different population densities, they can modify their vegetative and reproductive aerial structures as a density-dependent morphological plasticity response, allowing them to acquire different growth habits. The prediction is based on a wide density-dependent variation in the vegetative and reproductive aerial structures, so a plant acquires a prostrate or erect habit if it grows at a lower or higher density, respectively, with density-dependent adjustment. This adjustment allows for finding critical density values in weed productivity. This study aimed to evaluate the morphology of the vegetative and

reproductive aerial structures of junglerice and characterize the growth habit of individuals based on population density. This may allow for determining both the possible plasticity of individuals and the degree of density dependence.

2. Material and Methods

2.1 Experimental field and junglerice densities

The experiment was conducted at the National Institute of Agricultural Technology (INTA) in Pergamino (Buenos Aires, Argentina), in a field where soybeans was grown during 2014, 2015, and 2016. Different densities of junglerice were identified and maintained throughout the plant cycle based on the natural infestation levels from each year, categorized as low, medium, and high density. The density values (DENS) were as follows: 2 pl m⁻², 156 pl m⁻², and 300 pl m⁻² in 2014; 4 pl m⁻², 45 pl m⁻², and 250 pl m⁻² in 2015; and 0.25 pl m⁻², 35 pl m⁻², and 250 pl m⁻² in 2016.

Four 2 m x 2 m plots were delimited for each density value (twelve plots per year). Since the seedlings emerged simultaneously, the population maintained an even-aged throughout. Any seedlings that emerged later were manually removed. At plant maturity, one junglerice plant from each plot was randomly selected to be evaluated.

2.2 Measurements

Plant height (PLH, cm), measured from the base to the most distant panicle, and plant width (PLD, cm), measured as the diameter of a cylinder projected from the edges of the plant toward the base, were recorded, and the growth habit was characterized as prostrate, semi-prostrate or erect. Subsequently, the plants were cut from the soil surface and transported to the laboratory. The primaries (PT1), secondaries (PT2), and tertiaries (PT3) tillers per plant were counted, and the total number of tillers per plant (PTT) was determined by summing up the previous three categories, and seeds were extracted and placed in glasses. Then, both plants and seeds were dried in an oven at 52 °C for 48 hours. Seed weight (SEW, g) and seed number (SEN) per plant were measured, the hundred-seed weight (HSW, g) was calculated, and aerial dry matter (PLW, g) was measured.

2.3 Statistical analysis

The data obtained were analyzed by means of principal component analysis (PCA) to group characteristics associated with the growth habit. To examine the relationship between the variables measured and the growth habits, a general linear model (GLM) was applied, and a cluster-based method (DGC) was used to identify groups of nonhomogeneous means (Di Rienzo et al., 2002).

The height-biomass ratio (HBR) index (cm g⁻¹), which represents the proportional relationship between PLH and PLW (Perthame et al., 2022), was calculated. A GLM analysis was conducted on all the variables measured

per plant, including HBR, and a mean comparison was performed using the DGC test. Also, the slopes of the log-log relationships for the variables PLD, PLW, PTT, SEN, and SEW were determined as a function of DENS. Subsequently, these slopes were compared with the -3/2 and -4/3 power law exponents to assess the adaptive responses of plants to changes in density (Radosevich et al., 2007).

Finally, PLW, PTT, SEN, and SEW per unit area (m²) were estimated, and the relationship between variables and population density was fitted using hyperbolic (Eq. 1) or parabolic (Eq. 2) functions. Model selection was based on the Akaike Information Criterion (AIC). All data analyses were performed using InfoStat 2020p (Di Rienzo et al., 2020).

$$Y = a \times (1 - \beta \times e^{-\gamma x}) \quad (\text{Eq. 1})$$

$$Y = -\delta \times x^2 + \rho \times x \quad (\text{Eq. 2})$$

where Y is the estimated PLW, PTT, SEN, or SEW per area, is the maximum of the parameter, is the inflection point, is the slope, , and are proportional parameters of the slope and asymptote, and is the density of junglerice.

3. Results

3.1 Growth habits

The bivariate plot of the first two principal components revealed three distinct groups of individuals (Figure 1).

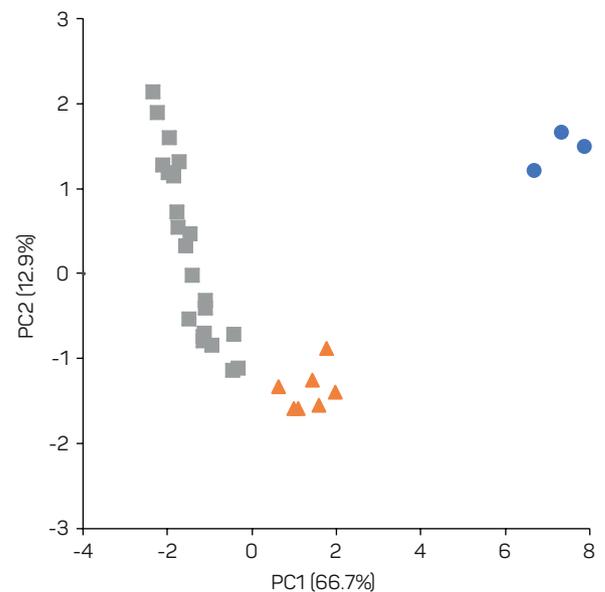


Figure 1 - Principal component analysis (PCA) of the variables measured for each junglerice (*Echinochloa colona*) individual: density (DENS, pl m⁻²), plant height (PLH, cm), plant width (PLD, cm), number of primaries (PT1, pl⁻¹), secondaries (PT2, pl⁻¹), tertiaries (PT3, pl⁻¹) and total (PTT, pl⁻¹) tillers, plant weight (PLW, g pl⁻¹), seed number (SEN, pl⁻¹) and seed weight (SEW, g). Growth habit: prostrate (circles; PC1>0, PC2>0), semi-prostrate (triangles; PC1>0, PC2<0) and erect (squares; PC1<0)

The first group consisted of plants with a prostrate growth habit, which grew at the lowest density (isolated plants). These plants exhibited the highest PLW, PLD, PTT, SEN, and SEW values. The second one comprised plants with a semi-prostrate growth habit that grew at 2 or 4 pl m⁻², and the third one included the tallest plants with an erect habit.

PLD and PLW were significantly different among the three growth habits ($p < 0.001$). Additionally, PLH was statistically significant ($p < 0.001$) for plants with an erect growth habit, while SEW was higher ($p < 0.001$) in the prostrate individuals (Figure 2). Furthermore, PTT showed significant differences among the described

growth habits ($p < 0.001$), and variations in the hierarchy of tillers were observed. Specifically, PT1 did not differ between prostrate and semi-prostrate plants, while PT2 exhibited differences among all three growth habits ($p < 0.001$). It is worth mentioning that PT3 was only observed in prostrate plants (Figure 2).

3.2 Morphological changes as a density-dependent response

Only HSW ($r = 0.92$) and PLH ($r = 0.28$) had a positive relationship with DENS (Table 1, Figure 3). This means that heavier seeds were observed at higher densities ($r = 0.92$)

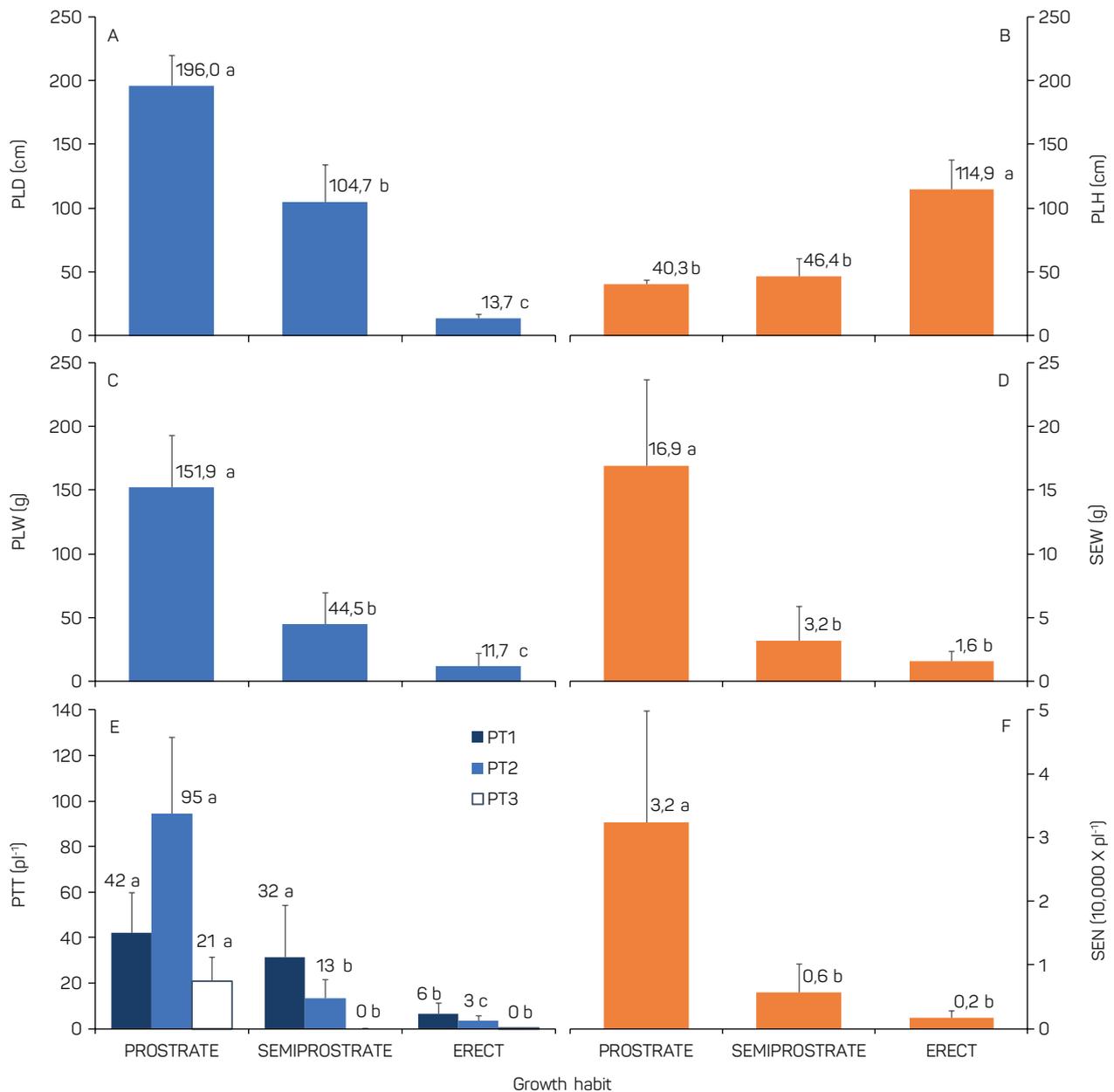


Figure 2 - Functional traits of junglerice (*Echinochloa colona*) plants expressed according to growth habit (prostrate, semi-prostrate, and erect): (A) plant width (PLD) and (B) height (PLH), in cm. (C) Plant weight (PLW) and (D) seed weight (SEW), in g.pl⁻¹. (E) Number of primaries (PT1), secondaries (PT2), and tertiaries (PT3) tillers and (F) number of seeds per plant (SEN). Different letters indicate significant differences between growth habits according to the DGC exclusionary group formation test ($p \leq 0.05$)

and, to a lesser extent, in taller plants ($r=0.40$). This can be attributed to the fact that PLH reached its maximum exponentially at 45 pl m^{-2} ($147.3 \pm 7.9 \text{ cm}$) and gradually decreased to $96.5 \pm 10.6 \text{ cm}$ at 300 pl m^{-2} .

PLD exhibited the strongest inverse relationship with DENS ($r=-0.57$). An isolated plant (without neighboring plants around it) reached a width of 220 cm, while at the maximum density evaluated (300 pl m^{-2}), the plants did not exceed 13 cm in width (Figure 3). Additionally, the increase in density influenced PLD, PLW, PTT, SEN, and SEW, as indicated by the negative slopes in the log/log relationships (Table 2).

The HBR index and DENS were positively related (Figure 3). Although the height of individuals increased up to a density of 45 plants m^{-2} and then decreased, along with the drastic reduction in PLW across the density gradient evaluated, this behavior contributed to the dynamics of the HBR index.

Between 0.25 and 2 pl m^{-2} , PLH values and HSW did not differ significantly ($p<0.001$), while PLW decreased by approximately half (from 151.9 to 62.8 g pl^{-1}). Subsequently, at densities of 4, 35, and 45 pl m^{-2} , PLH exhibited a statistically significant increase (60.7 cm, 103.8 cm, and 147.3 cm, respectively), while PLW and HSW remained similar. This change in PLH, accompanied by similar PLW, resulted in a significant reduction in PTT per plant (73, 18, and 11 tillers pl^{-1}). From 45 pl m^{-2} onwards, a significant reduction in individual PLH was observed as DENS increased to 300 pl m^{-2} . This reduction may be associated with the earlier description of the HBR index, where plants might allocate fewer photoassimilates to aerial structures.

3.3 Population adjustment with density-dependent relationship

The estimates of PLW ($p=0.0003$), PTT ($p<0.0001$), SEN ($p=0.0005$), and SEW ($p=0.0002$) per unit area (m^2) exhibited

significant changes depending on DENS. These findings and the modifications observed in each individual confirmed the density-dependent behavior of junglerice.

The best fit for PLW per m^2 was achieved using the monomolecular model, with an estimated asymptote of $999.2 \pm 94.6 \text{ g m}^{-2}$ ($p<0.0001$). At a DENS equal to or greater than 35 pl m^{-2} , PLW showed no significant differences (Figure 4). Additionally, PTT, SEN, and SEW per m^2 showed a better fit with the polynomial function. In the density gradient evaluated, these variables did not reach a constant final yield but reached a maximum value and began to decrease (Figure 4).

Based on the estimates from the polynomial functions, a maximum production of 243,419 seeds m^{-2} , 1571 tillers m^{-2} , and 268 g m^{-2} of seeds can be achieved at population densities of approximately 193, 222, and 259 pl m^{-2} , respectively.

4. Discussion

4.1 Plasticity in growth habit

As observed in the results obtained, junglerice plants showed a variation in their growth habit (prostrate, semi-prostrate, or erect) depending on the population density in which they grew. Therefore, the type of growth habit and aerial morphology could be considered attributes from an intra-specific competitive perspective as a strategy to achieve a better capture of aerial resources (Bannett et al., 2016; Thiel et al., 2018), which does not agree with that proposed by Liu et al. (2022), who associated this species with a defined and less plastic growth habit.

Although it has been considered that junglerice have low phenotypic plasticity (Awan et al., 2014) and that, within the *Echinochloa* genus, this species exhibits

Table 1 - Correlation index (R), mean, standard deviation (Dev), and coefficient of variation (CV) of the variables measured in the experiment for each junglerice (*Echinochloa colona*), plant (pl^{-1}) density (DENS): plant height (PLH, cm), plant width (PLD, cm), plant weight (PLW, g), number primaries, secondaries, tertiaries, and total tiller (PT1, PT2, PT3, and PTT, respectively) hundred-seed weight (HSW, g), seed number (SEN, n°), and seed weight (SEW, g)

	SEW	SEN	HSW	PTT	PT3	PT2	PT1	PLW	PLD	PLH	DENS
DENS	-0.40	-0.39	0.92	-0.47	-0.27	-0.38	-0.56	-0.53	-0.57	0.28	1
PLH	-0.50	-0.51	0.40	-0.55	-0.41	-0.48	-0.57	-0.59	-0.80	1	-
PLD	0.82	0.79	-0.62	0.81	0.67	0.79	0.67	0.90	1	-	-
PLW	0.83	0.76	-0.57	0.85	0.79	0.90	0.58	1	-	-	-
PT1	0.42	0.37	-0.49	0.84	0.46	0.69	1	-	-	-	-
PT2	0.76	0.69	-0.38	0.97	0.91	1	-	-	-	-	-
PT3	0.70	0.69	-0.33	0.84	1	-	-	-	-	-	-
PTT	0.70	0.64	-0.45	1	-	-	-	-	-	-	-
HSW	-0.40	-0.48	1	-	-	-	-	-	-	-	-
SEN	0.98	1	-	-	-	-	-	-	-	-	-
SEW	1	-	-	-	-	-	-	-	-	-	-
Mean	3.35	5452	0.89	31	2	14	15	31.99	50.7	92.9	-
Dev	4.99	10238	0.32	48	7	28	18	44.92	62.3	38.6	-
CV	1.49	1.88	0.36	1.53	3.38	1.99	1.17	1.4	1.23	0.42	-

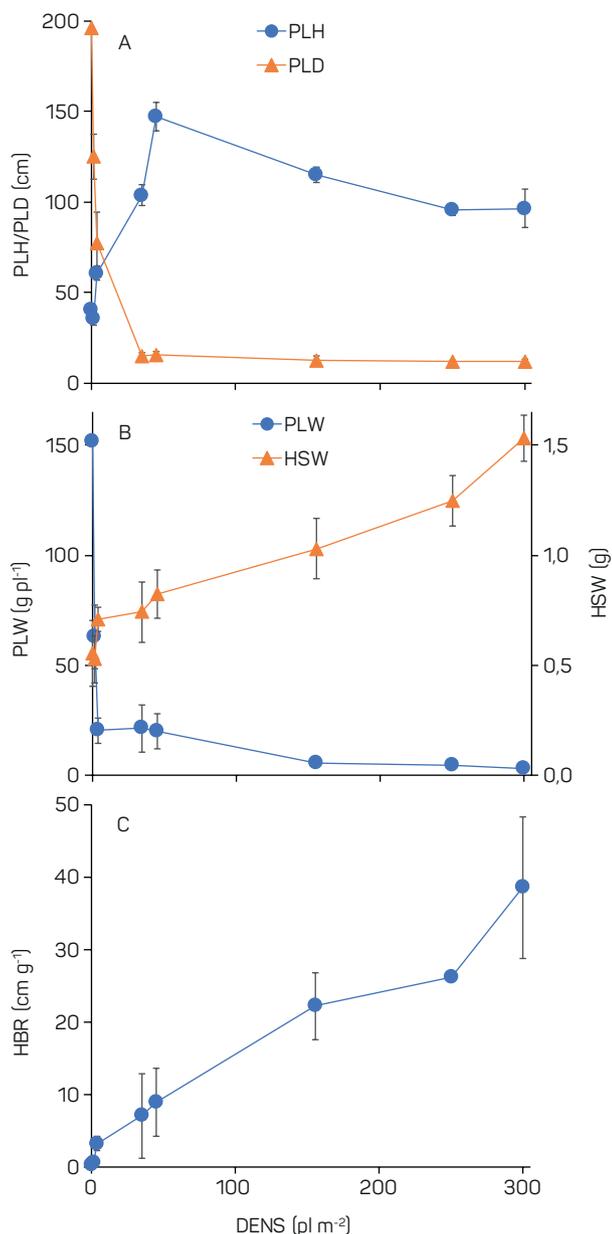


Figure 3 - Effect of junglerice (*Echinochloa colona*) plant density (DENS) on (A) size, represented by the plant height (PLH, circles) and plant width (PLD, triangles); (B) productivity, indicated by the plant dry weight (PLW, circles) and the hundred-seed weight (HSW, triangles); and (C) the height-biomass ratio (HBR (cm g⁻¹), circles). Means of individual plants with their respective standard deviations

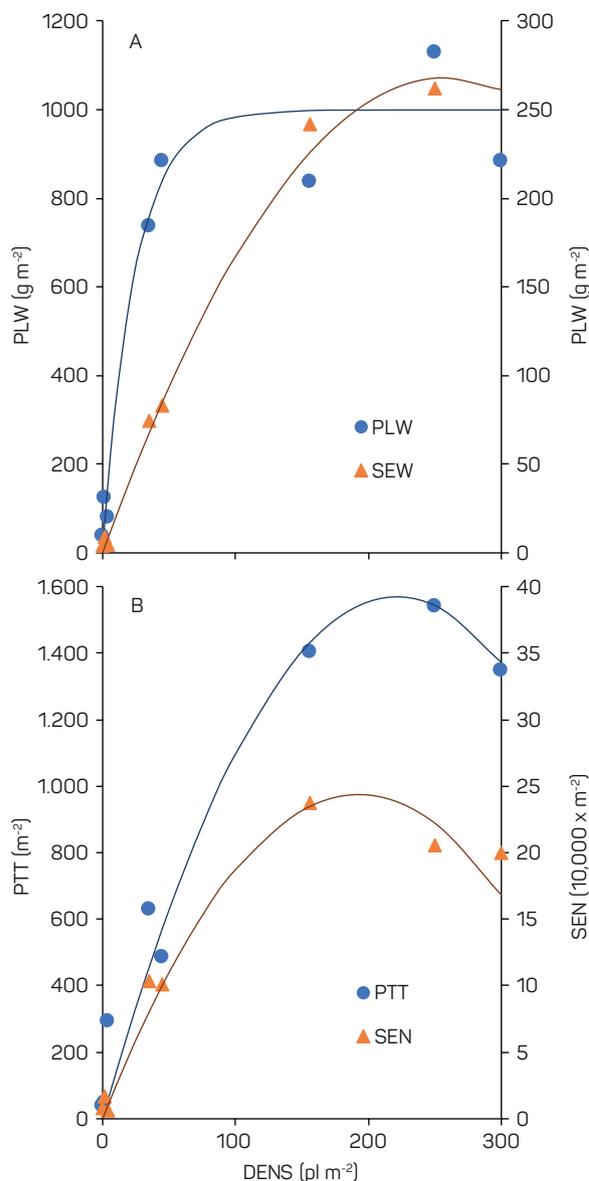


Figure 4 - Junglerice (*Echinochloa colona*) production per area as a function of density (DENS). (A) Plant weight (PLW (g m⁻²), circles) and seed weight (SEW (g m⁻²), triangles), and (B) the total number of tillers (PTT (m⁻²), circles) and the number of seeds (SEN (m⁻²), triangles). The nonlinear functions fitted are as follows: (a) PLW (g m⁻²) = 999.2 × (1 - 0.991 × e^(-0.041 × DENS)) (solid line), SEW (g m⁻²) = -0.004 × DENS² + 2.07 × DENS (dotted line), (b) PTT (g m⁻²) = -0.032 × DENS² + 14,18 × DENS (solid line) and SEN (N° m⁻²) = -6.552 × DENS² + 2525,77 × DENS (dotted line)

Table 2 - Double logarithmic reciprocal relationships among junglerice (*Echinochloa colona*) plant width (PLD), plant weight (PLW), the total number of tillers (PTT), seed number (SEN), and seed weight (SEW) as a function of plant density. Results of the linear regression model include slope (b), experimental error (EE), lower limit (LL), and upper limit (UL) for the 95% confidence interval, t-statistic (T), p-value, and regression coefficient (r²) for each variable

	b	EE	LL (95%)	UL (95%)	T	p-value	r ²
PLD	-0.456	0.026	-0.508	-0.403	-17.668	<0.0001	0.91
PLW	-0.508	0.044	-0.599	-0.417	-11.439	<0.0001	0.81
PTT	-0.436	0.041	-0.519	-0.353	-10.759	<0.0001	0.79
SEN	-0.460	0.057	-0.576	-0.345	-8.135	<0.0001	0.69
SEW	-0.325	0.056	-0.439	-0.211	-5.829	<0.0001	0.53

the least morphological variation (Tahir, 2016), the results here observed demonstrate that all the variables evaluated presented considerable variability (CV between 0.36 and 3.38) (Table 1). In other words, the present results confirm that junglerice exhibits substantial morphological variability. Still, under the conditions of the experiment, it is not possible to ascertain whether this is due to phenotypic plasticity or interpopulation variation (Mortimer, 1997).

4.2 Individual plasticity and density dependence

Regarding the behavior of HSW as affected by DENS, results showed that the plant strategy is to produce heavier seeds as the population density increases, which would allow it to prioritize the allocation of photoassimilates for grain filling, resulting in heavier seeds with potentially higher germination viability (Massimi, 2018).

The behavior of PLH in the plants evaluated expressed an increase followed by a decrease along the density gradient, indicating non-constant growth. This observation partially agrees with the findings of Awan et al. (2014), who recorded taller plants at higher densities but did not detail the increase in PLH at low densities.

Although PLW, PTT, SEN, and SEW were negatively affected by higher DENS, the theories of individual productivity adjustment through logarithmic transformation did not correspond to slope values like $-3/2$ or $-4/3$, as proposed by the reciprocal log/log law (Radosevich et al., 2007). Instead, the slopes of these relationships were equal to or greater than $-1/2$ (Table 2).

Since root biomass was not determined, the fact that the HBR index was positively related to DENS could indicate an increase in photoassimilates allocated to the roots, as suggested by other authors based on functional balance (Foxy, Fort, 2019). However, the increase in the HBR index as affected by DENS indicates a response to potential shading caused by neighboring plants (Perthame et al., 2022).

The variation in population density led to a reduction in PTT, with greater height observed as a photomorphogenic response to favor increased interception of photosynthetically active radiation (PAR) in response to density change (Lecarpentier et al., 2019). These results do not align with those obtained by Mutti et al. (2019), who observed that junglerice could not adjust PLH to achieve greater interception of PAR with increasing plant density, as observed in *E. phyllopogon*. Furthermore, this finding is consistent with descriptions by several authors regarding the behavior of junglerice, where increased density of neighboring plants results in reduced PLH and where the addition of nitrogen to the soil reverses this situation, significantly increasing height (Awan et al., 2014; Mutti et al., 2019).

4.3 Population plasticity and density dependence

PLW per unit area (m^2) fitted the “law of constant final yield” (Harper, Gajic, 1961). This means that, despite the decrease observed in individual plant weight (with increasing density), the accumulation of population-level aboveground dry matter continues to increase until it reaches a maximum asymptote, as stated by this law. Given that aerial biomass of weeds serves as a precise estimator for competition with crops but also demands time for quantification (Gerhards et al., 2017), it is important to consider that, at values equal to or greater than 35 pl m^{-2} under the experimental conditions evaluated, the accumulation of aerial dry matter per plant decreases, and the accumulation of aerial dry matter per unit area tends to remain constant. This response is like the observations of Al Mamun (2014), who explained this population adjustment in *E. crus-galli* due to increased intraspecific competition among plants.

Unlike PLW, the variables PTT, SEN, and SEW did not fit the hyperbolic function but quadratic polynomial functions. While these functions are not recommended for studying additive models (Oliveira et al., 2018), the results of this experiment are consistent with those of Weiner et al. (2001), who observed that the total number of stems and seed production decrease with the progressive increase in the number of individuals, and consequently, the potential increase in intraspecific competition leads to reduced productivity. Additionally, these findings align with the description of density-dependent relationships defined by a parabolic curve (Begon et al., 2006).

Maximum production of SEN, PTT, and SEW per unit area is achieved at approximately 5.5 to 7.5 times the density required to reach maximum PLW per unit area. Furthermore, results showed that SEN per unit area was the first variable to be negatively affected (more sensitive) as density increased, unlike SEW per unit area. This may be associated with the harvest index (HI) and HSW because HSW increased with the increase in DENS and led to fewer but heavier seeds, thus allowing SEW per unit area to continue increasing. Regarding HI, a higher SEW/PLW ratio was obtained with increasing density ($r^2=0.55$). This relationship indicates that, even at 45 pl m^{-2} , the HI did not exceed 12%, while at a density of 300 pl m^{-2} , it reached a value of 38%.

The morphological plasticity of vegetative and reproductive aerial structures measured in junglerice plants would give the weed the capacity to adapt to a wide range of densities. Thus, an isolated individual has the potential to maximize productivity and achieve PLW and SEN values equivalent to those produced by 50 plants at the maximum density evaluated (300 pl m^{-2}). However, the maximum SEN per unit area would occur at a population density rarely reached in production fields, which means that the SEN per unit area observed in this study was higher than that reported in cultivated fields (De Marco et al., 2018).

This behavior could indicate a competitive advantage since each junglerice plant can modify its vegetative and reproductive aerial structures. Thus, in the event of weed control failure within a crop, a population can maintain constant aerial dry matter and optimize propagule production by adjusting the number and weight of seeds to ensure offspring survival.

5. Conclusion

Junglerice exhibits a wide morphological plasticity that is density dependent. In the present study, while the production of aerial dry weight followed the law of constant final yield, the number of tillers and the number and weight of seeds per unit area showed a nonlinear dome-shaped relationship. Critical DENS were identified by fitting these nonlinear functions to significantly maximize productivity. This indicates an intraspecific interaction between vegetative and reproductive structures in a population density gradient.

Considering the plastic nature observed in individuals, monitoring this weed in the field is important. If, after applying a control method, the aerial dry matter is not significantly affected, the number of seeds per unit area becomes a variable highly sensitive to changes in density. Consequently, reducing the re-entry of propagules into the

soil seed bank could be achieved by targeting the decrease in seed production.

Author's contributions

All authors read and agreed to the published version of the manuscript. GP and HA: Conceptualization of the manuscript and development of the methodology. GP: data collection and curation. GP: data analysis. GP and HA: data interpretation. HA: funding acquisition and resources. GP and HA: project administration. HA: supervision. GP: writing the original draft of the manuscript. HA: writing, review, and editing.

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