EFFECT OF TEMPERATURE ON ROOTS AND SHOOTS FORMATION IN THREE VANILLA SPECIES (ORCHIDACEAE) UNDER CONTROLLED CONDITIONS †

[EFECTO DE LA TEMPERATURA EN LA FORMACIÓN DE RAÍCES Y BROTES EN TRES ESPECIES DE VAINILLA (ORCHIDACEAE) BAJO CONDICIONES CONTROLADAS]

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SUMMARY

Background. *Vanilla planifolia* is a species of commercial and cultural importance. However, its growth and development could be affected by the increase in temperature caused by climate change. In contrast, *V. pompona* and *V. insignis* are wild species with potential use as aromatic species and they show greater tolerance to prolonged exposure to high temperatures. **Objective.** To determine the effect of temperature on the development of roots and shoots of *V. planifolia*, *V. pompona* and *V. insignis* under controlled conditions. **Methodology.** Cuttings of approximately 20 cm with two nodes were grown at 25, 32, 35 and 38 °C under controlled conditions, with a relative humidity of 100%, for six weeks. To evaluate cutting development, the number of roots produced was recorded, as well their length, their growth rate and their diameter. Likewise, the number of shoots generated, their length, growth rate and diameter were also counted. The experimental design was completely random, and the data were analyzed using Tukey *post hoc* analysis of variance ($P < 0.05$). **Results.** The increase in temperature affected the promotion and root growth in *V. planifolia,* which showed the greatest length at 25 °C (20.64 ± 0.26 cm) and the lowest value at 35 °C (1.22 ± 0.49 cm), contrary to *V. insignis*, where the increase in temperature at 35 °C favored root elongation (4.76 ± 0.07 cm), while the lowest growth was observed at 25 °C (1.74 ± 0.13 cm). *V. pompona* did not present significant differences in root growth at the three temperatures evaluated. Similarly, the increase in temperature showed a distinct influence on the promotion and growth of the shoot. *V. planifolia* only produced shoots at 32 °C (8.4 ± 0.4 cm) and *V. pompona* generated them at 32 and 35 °C, being those of greater length at 35 °C (3.3±0.13 cm) and did not produce at 25 °C; while *V. insignis* showed the highest shoot growth at 25 °C (7.22 ± 0.2 cm) and the lowest at 32 °C (6.56 ± 0.12). At 38 °C, 100% mortality was observed in the three species. **Implications.** The growth of roots and shoots of *V. planifolia* are affected by an increase in temperature above 32 °C, therefore, conservation and genetic improvement programs are needed that could start from the qualities that *V. pompona* and *V. insignis* showed. **Conclusion.** Temperature ranges between 25 and 35 °C have a differential effect on the promotion and growth of roots and shoots for the species *V. planifolia*, *V. insignis* and *V. pompona*.

Key words: Cultivation; tropical crops; climate change; abiotic stress; *Vanilla*

RESUMEN

Antecedentes. *Vanilla planifolia* es una especie de importancia comercial y cultural, la cual podría presentar afectaciones en su crecimiento y desarrollo debido al aumento de temperatura causado por el cambio climático. En contraste, *V. pompona* y *V. insignis* son especies silvestres con potencial uso aromático, las cuales muestran mayor tolerancia a la exposición prolongada a altas temperaturas. **Objetivo.** Determinar el efecto de la temperatura en el desarrollo de raíces y brotes de *V. planifolia*, *V. pompona* y *V. insignis* bajo condiciones controladas. **Metodología.** Se utilizaron esquejes de aproximadamente 20 cm con dos nudos, los cuales fueron cultivados a 25, 32, 35 y 38 °C bajo

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condiciones controladas, con humedad relativa del 100%, durante seis semanas. Para evaluar el desarrollo se contabilizó el número de raíces producidas, su longitud, la tasa de crecimiento y el diámetro; así mismo, se contó el número de brotes generados, su longitud, tasa de crecimiento y diámetro. El diseño experimental fue completamente al azar, y los datos fueron analizados mediante análisis de varianza *post hoc* Tukey (P < 0.05). **Resultados.** El incremento de temperatura afectó la promoción y el crecimiento de raíz en *V. planifolia* que alcanzó la mayor longitud a 25 °C (20.64±0.26 cm) y el menor valor a 35 °C (1.22±0.49 cm), contrariamente, para *V. insignis* el incremento de temperatura a 35 °C favoreció la elongación radicular (4.76±0.07 cm) en tanto que, el menor crecimiento se observó a 25 °C (1.74±0.13 cm). *V. pompona* no presentó diferencias significativas en el crecimiento de raíz en las tres temperaturas evaluadas. De igual manera, el incremento de temperatura influyó distintamente en la promoción y crecimiento del brote, *V. planifolia* solo produjo brotes a 32 °C (8.4±0.4 cm) y *V. pompona* los generó a 32 y 35 °C, siendo los de mayor longitud a 35 °C (3.3±0.13 cm), y no produjo a 25 °C; mientras que, *V. insignis* presentó el mayor crecimiento del brote a 25 °C (7.22±0.2 cm) y el más bajo a 32 °C (6.56±0.12). A 38 °C se observó una mortalidad del 100% en las tres especies. **Implicaciones.** El crecimiento de raíces y de los brotes de *V. planifolia* se ven afectados al ocurrir un incremento de la temperatura por arriba de los 32 °C, por lo cual se necesitan programas de conservación y de mejora genética que pudieran partir de las cualidades que mostraron *V. insignis* y *V. pompona*. **Conclusión.** Rangos de temperatura entre 25 y 35 °C tienen un efecto diferencial en la promoción y el crecimiento de raíces y brotes para las especies *V. planifolia*, *V. insignis* y *V. pompona.*

Palabras clave: Cultivo; cultivos tropicales; cambio climático; estrés abiótico; *Vanilla*

INTRODUCTION

Temperature is one of the most important factors for the growth and development of plants because they require specific values to function optimally (Gray and Brady, 2016, Hatfield and Prueger, 2015). Alterations in global temperature are expected due to climate change, but a greater impact on temperature is expected in the tropics (Armenta-Montero *et al*., 2022). An increase in temperature between 3 and 5 °C is expected (Hatfield and Prueger, 2015, Luo *et al*., 2020), but some forecasts anticipate an increase of up to 11 °C (Faget *et al.*, 2013, Reddy *et al.*, 2017). This may cause severe thermal and water stress that could affect plant organ production and strengthening (Hatfield and Prueger, 2015).

Plants respond intraspecifically to increments in temperature. An increment between 1-6 °C above the optimal range can reduce root production and length, as observed in *Solanum lycopersicum,* L., *Pisum sativum* L., and *Oryza sativa* L. (Faget *et al.*, 2013, Fahad *et al.,* 2019); while the same interval favors *Lactuca sativa* L., *Zea mays* L., *Brassica napus* L. and *Helianthus annuus* L. (Faget *et al*., 2013, Gray and Brady, 2016). Similarly, the stem may be favored by an increase in temperature, as in *O. sativa* and *Triticum aestivum* L. (Fahad *et al*., 2019), or it may reduce its size, as occurs in *Gossypium hirsutum* L. (Reddy *et al.*, 2017). Regarding orchids, temperatures upper than the optimum range may have a negative effect on growth and development (Zhang *et al.,* 2018). A little increase in temperature might favor plant growth, as it has been seen in *Phalaenopsis spp.* (Zhang *et al.,* 2018); however, higher temperatures (5 °C above the optimal range) reduce leaf development, and photosynthetic activity, as well to cause a high percentage of the inflorescences abort, as reported in *Cymbidium sazanami*, *Cypripedium flavum*, *Phalaenopsis spp.*, or *Odontioda spp.* (Zhang *et al.,* 2005, 2018); whereas an increase in temperature may cause an increase in root length, as in *C. tracyanum*, or a decrease, as in *C. sinense* (Li *et al.,* 2018).

Vanilla (*Vanilla planifolia* Andrews) is a species of global commercial interest due to the use of its fruit in the food and aromatic industries (Ranadive, 2018). Despite its economic importance, in Mexico *V. planifolia* is in the category "subject to special protection" within NOM-059 (SEMARNAT, 2010). It has been exclusively propagated asexually, which has generated genetic erosion (Menchaca-García, 2018), which has made vanilla susceptible to several factors including higher temperatures (Hernández-Hernández, 2018). Its optimal cultivation temperature ranges between 21 and 27 °C (Hernández-Ruíz *et al.*, 2016; Hernández-Ruíz *et al.,* 2020). Values outside of this range can cause alterations in physiology such as difficulty rooting, reduction in stem growth and decreased fruit production (Hernández-Hernández, 2018).

Wild species within the genus *Vanilla* may be more resistant to possible increments in temperature. This is the case of *V. pompona* Schiede and *V. insignis* Ames (Cameron, 2018). *V. pompona* is the second most utilized species of vanilla because its fruit can be mainly used for perfume (Maruenda *et al.,* 2013). On the other hand, *V. insignis* has not been used in the industry due to its low concentration of vanillin, but it has other metabolites that confer it an aromatic potential (Cameron, 2018, de Oliveira *et al.,* 2022). Both species are able to grow in arid environments with periods of prolonged drought and temperatures between 30.9 and 34.5 °C (Flores-Jiménez *et al.*, 2016, Soto-Arenas and Dressler, 2009). Thus, they may be able to tolerate thermal increments. Therefore, the objective of this study was to determine the effect of temperature on the development of roots and shoots of *V. planifolia, V. pompona* and *V. insignis* under controlled conditions.

MATERIALS AND METHODS

We used cuttings of *V. planifolia* (PL), *V. pompona* (PO) and *V. insignis* (IN), the cuttings of the three species came from the environmental management unit "vainillales Tlali Nantli" (SEMARNAT-UMA-IN-VIV-0281-VER/19), located in Mesa de Guadalupe, Veracruz. The climate is warm sub-humid, with a temperature range of 14-26 °C, and a precipitation range of 1100-1600 mm. The biological material was donated to the germplasm bank of the Universidad Veracruzana orchidarium (SEMARNAT-UMA-IN-VIV-0129-VER/11), where this research was carried out. The three species were identified using the dichotomous key for the genus *Vanilla* proposed by Soto-Arenas and Dressler (2009). Cuttings were washed with water and detergent for 10 minutes; they were then immersed in household bleach solution (0.5 mL/L) for five minutes and were rinsed twice with plenty of sterilized distilled water. We used the method proposed by Adame-García *et al.* (2015), where short cuttings of approximately 20 cm in length with two knots and at least one leaf are placed on Styrofoam trays with absorbent paper moistened with 20 mL of sterilized distilled water, inside transparent plastic bags. These wet chambers were hydrated weekly with 20 mL of sterilized distilled water, to maintain a relative humidity of 100%. To evaluate the effect of temperature on rooting and shoot production, cuttings were placed in incubation stoves under controlled conditions at 25, 32, 35 and 38 °C, in darkness, for six weeks. Five cuttings of each species were used for each of the four temperatures evaluated. We used 20 cuttings in total per species (n = 60). In order to homogenize the biological material, in each species the cuttings were obtained from a single mother plant (approximately five meters in length). At the end of the exposure period, the survival percentage of the cuttings was assessed, as well as the number of roots produced, the length and diameter of the primary root, the number of shoots produces and the length and diameter of the shoots. The growth rate of the primary root and the vegetative shoot was evaluated using the value of weekly measurements with the formula:

$$Growth\ rate = \frac{M_2 - M_1}{\Delta t}$$

Where M_1 corresponds to the value of the initial measurement and M_2 corresponds to the value of the following measurement. Positive values of this variable indicate growth, while values close to zero indicate a decrease in size (Paine *et al.,* 2012). For each variable, we determined the differences between groups using a two-way analysis of variance (ANOVA) and a Tukey *post hoc* test ($p \leq 0.05$) in R (R Core Team, 2020). We additionally counted the number of cuttings that lost their leaf throughout the duration of the experiment.

RESULTS

We obtained a 100% survival rate of cuttings for the three vanilla species subjected to 25, 32 and 35 °C, throughout the duration of the experiment. In contrast, mortality was 100% at 38 °C after one week of thermal exposure. Increased temperature had an effect on the time it took for roots to appear in the different treatments (Table 1). In the case of PL, roots took more days to appear with increasing temperature. In the case of PO an increase in temperature favored the appearance of roots in fewer days compared to the 25 °C treatment. For IN no change was observed. In PL the number of roots ($F_{(3.56)} = 91.2$, $P < 0.001$) decreased as the temperature increased, while in PO and IN the highest number of roots was obtained at 32 °C. Similarly, in PL root length ($F_{(3.56)} = 517.9$, $P < 0.001$) was affected by the increase in temperature. In contrast, IN developed the longest roots at 35 ºC. In PO no differences were observed between the three temperatures. The root growth rate ($F_{(3.56)} = 271.3$, $P < 0.001$) presented the same pattern for length as mentioned above. An increase in temperature also modified root diameter in the three species ($F_{(3.56)} = 100.\ 39$, $P < 0.001$). Roots increased in diameter in PO and IN with increasing temperature, while the opposite was observed in PL.

The increase in temperature promoted shoot formation in PO, shoots were observed at 35 °C a week earlier than at 32 °C. In IN shoot formation at 32 °C occurred a week later compared to 25 °C. The three species studied produced shoots at 32 °C, both PL and PO did not produce shoots at 25 °C, and IN did not produce shoots at 35 °C (Table 2). The average number of shoots was 1 per cutting ($F_{(3.56)} = 311.96$, $P < 0.001$). The length of shoots produced by PO and IN was influenced by the increase in temperature ($F_{(3.56)} = 398.7$, $P < 0.001$). In PO the greatest length was observed at 35 °C, while for IN the greatest length was achieved at 25 °C. Growth rate ($F_{(3.56)} = 179.3$, $P < 0.001$) presented the same pattern as shoot length. Regarding shoot diameter, again the highest value in PO was observed at 35 °C, while in IN the diameter was similar at both 25 and 32 °C ($F_{(3,56)} = 221.9$, $P < 0.001$). Upon prolonged exposure to 32 °C, both PL and PO cuttings lost their leaves. In IN this occurred in 80% of cuttings. The cuttings of the three species under prolonged exposure to 35 °C lost their leaves.

Table 1. Effect of the exposure of different temperatures on promotion and root growth of *Vanilla planifolia* (PL), *V. pompona* (PO) y *V. insignis* (IN).

Temperature	Vanilla	Days until root formation*	Number of roots	Root length (cm)	Root growth rate (cm/Δt)	Root diameter (mm)
25 °C	PL	7	2.2±0.2a	20.64±0.26[a]	2.92±0.26a	7.8±0.2a
	PO	21	1±0c	2.28±0.42de	0.57±0.11de	3.2±0.2d
	IN	14	1±0c	1.74±0.13de	0.29±0.03de	1.8±0.2e
32 °C	PL	14	1.8±0.2ab	10.68±0.36b	1.92±0.28b	7.2±0.2a
	PO	14	1.6±0.24ab	2.14±0.24de	0.52±0.06de	4.4±0.24c
	IN	14	1.4±0.24b	2.92±0.11d	0.45±0.03d	4.4±0.24c
35 °C	PL	28	1±0c	1.22±0.49e	0.2±0.08e	1.8±0.37e
	PO	14	1±0c	2.7±0.03d	0.58±0.09d	6±0.32b
	IN	14	1±0c	4.76±0.07c	0.79±0.05c	4.4±0.24c

The mean value ± standard error is shown. Values with different letters differ significantly from each other ($P < 0.01$), according to ANOVA, *post hoc* Tukey. *Not included in the statistical analysis.

Table 2. *Vanilla planifolia* (PL), *V. pompona* (PO) y *V. insignis* (IN) promotion and shoot growth under the different temperature.

Temperature	Vanilla	Days until shoot formation*	Number of shoots	Shoot length (cm)	Shoot growth rate (cm/Δt)	Shoot diameter (mm)
25 °C	PL	---	---	---	---	---
	PO	---	---	---	---	---
	IN	14	1±0a	7.22±0.2b	1.21±0.03b	3.2±0.2c
32 °C	PL	28	1±0a	8.4±0.4a	1.33±0.05a	4.8±0.2b
	PO	21	1±0a	3±0.14e	0.49±0.04e	5±0b
	IN	21	1±0a	6.56±0.12c	1.09±0.03c	3.2±0.37c
35 °C	PL	---	---	---	---	---
	PO	14	1.2±0.2a	3.3±0.13d	0.55±0.04d	6.2±0.2a
	IN	---	---	---	---	---

The mean value ± standard error is shown. Values with different letters differ significantly from each other ($P < 0.01$), according to ANOVA, *post hoc* Tukey. *Not included in the statistical analysis. "---": Did not produce shoots.

DISCUSSION

In other crops, studies have found that roots can be affected at the cellular level by exceeding their optimum temperature (Faget *et al*., 2013, Zhao *et al*., 2021). The optimum temperature of PL is between 21-27 °C (Hernández-Ruíz *et al.*, 2016). Thus, the increase in temperature in PL interferes with the development of roots. In contrast, in PO and IN the appearance of new roots was favored by the increase in temperature. Both species showed the highest production at 32 °C. Additionally, IN showed the greatest root length at 35 °C, and PO the largest diameter at the same temperature, because they are species with a greater tolerance to high temperatures (Cameron, 2018). Moreover, plants with larger roots and rapid expansion achieve greater adaptation to areas with warmer climates in the face of higher temperatures (until 5 °C above the optimum) (Luo *et al.*, 2020).

Similarly to root production, new vegetative shoots presented an intraspecific response to the increase in temperature. In the case of PL, the highest shoot production at 32 °C indicates that the optimal point for superior development in the species is at this temperature. (Hatfield and Prueger, 2015). However, higher temperatures can inhibit shoot formation (Hasanuzzaman *et al.*, 2013, Zhao *et al.*, 2021). Furthermore, the optimal temperature for the root is usually lower (Gaveliené *et al.*, 2022), as observed in this species. Shoot production in PO was favored by the increment in temperature. In contrast, species in which their roots were favored by the increase in temperature usually exhibit the reverse behavior in stem development (Fahad *et al.* , 2019; Hatfield and Prueger, 2015) and this was the case of IN. The decrease in stem growth and development is associated with effects on photosynthesis: higher than optimal temperatures affect enzymatic activity within chloroplasts as well as denaturation of thylakoidal membranes, reducing the photosynthetic rate (Zhao *et al.*, 2021), in addition to causing dehydration and stomatal closure (Hasanuzzaman *et al.*, 2013). At 32 and 35 °C the cuttings of the three species lost their original leaves (those from the vine from which they were obtained). This happened because the leaves of these species are water and nutrient reserves, due to they are CAM plants, and therefore are able to use these resources to survive until they produce new roots and shoots (Edwards, 2019).

In general, the maximum temperature for the development of both roots and shoots, under the conditions of this experiment, was 32 °C. This is 5 °C higher than the optimal temperature previously reported for PL, and within the optimal range for both PO and IN (Flores-Jiménez *et al.*, 2016; Hernández-Ruíz *et al.*, 2016; Hernández-Ruíz *et al.*, 2020). However, temperature higher than 32 °C would be detrimental to both PL and IN. PO would continue to show optimal responses, as long as prolonged periods at 38 °C do not occur, since all of the species in this study died at a temperature beyond what was tolerated. In future climate change scenarios, PL could be negatively affected if average temperatures exceed 32 °C, so it is necessary to implement conservation plans to avoid crop losses. Such measures may include the use of 50 to 80% shade meshes with a sprinkler irrigation system which may help mitigate insolation, but may also increase costs (Hernández-Hernández, 2018).Vanilla is currently grown at higher altitudes that can exceed 1000 meters above sea level. Displacement of this crop given the current climate change trend has been observed (Menchaca-García *et al.*, 2019), so it is necessary to implement studies that determine the geographical areas in which vanilla plants can develop with adequate growth, flowering and fruiting based on environmental tolerance ranges. PO was able to develop in higher temperature ranges compared to the other species in this study. Thus, we proposed that, to promote its cultivation, vanilla fields exclusive to this species or in association with PL must be establish. In turn, cultivating PO jointly with PL could contribute to the development of genetic improvement programs through species hybridization (Barreda-Castillo *et al.*, 2022) where tolerant plants to these and other scenarios of interest may be obtained.

CONCLUSIONS

The root and shoot production of the three species studied were affected by temperature. The increase in temperature reduced root growth in *V. planifolia* and promoted it in *V. insignis*. Prolonged exposure to 25 °C only stimulated the production of shoots in *V. insignis.* Prolonged exposure to 32 °C was optimal for all three species, as both shoots and roots were produced. *V. pompona* had greater tolerance to increments in temperature by managing to maintain root and shoot production even at 35 °C. Prolonged exposure to average temperatures greater than or equal to 38 °C was harmful to all three vanilla species.

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Compliance with ethical standards. The nature of this work does not require approval by a bioethical committee.

Data availability. All data is presented in the present paper.

Authors contribution statement (CRediT). J. M. Barreda Castillo: Methodology, Data curation, Formal analysis, Software, Validation, Writing. **R. A. Menchaca-García:** Conceptualization, Methodology, Funding adquisition, Resources, Supervision, Writing. **M. A. Lozano-Rodríguez:** Conceptualization, Investigation, Supervision, Visualization, Writing.

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