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Gibberellic Acid is Active Only in Orchid Cross-Pollination

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ABSTRACT

The aim of this study is to determine the endogenous hormone activities of Gibberellic acid (GA) in compatible (Intraspecific=ISP) and incompatible pollination (Intergeneric=IGP). It was designed to be *Himantoglossum robertianum* in ISP experiments and *H. robertianum* and *Orchis italica* in IGP experiments. For this reason, some polynariums taken from *O. italica* have been applied with needles to the flower stigmas of *H. robertianum*. Ovaries with stigma have been taken from both types of pollination for 10 days, and quantitative hormone analyses have been performed by LC-MS/MS. As a result, GA was not found in the ISP experiments. Likewise, it did not appear at all in the tests between the 1st and 6th days of IGP; it was found only on the 7th, 8th, 9th, and 10th days of IGP and at increasingly higher values. For the first time, endogenous ovary-stigma GA amounts in the post-pollination process of orchid IGP were determined in this study, and its importance was discussed. According to the statistical analysis, there is a significant difference between almost all values. It has been understood that additional histological and embryological studies are needed to understand the reason for the very high activity, especially on days 9 and 10.

Gibberellik Asit Yalnızca Orkidelerin Çapraz Tozlaşmasında Aktiftir

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ÖZ

Bu çalışmanın amacı Gibberellik asitin (GA) uyumlu (Intraspesifik=ISP) ve uyumsuz tozlaşmada (Intergeneric=IGP) endojen hormon aktivitelerini belirlemektir. ISP deneylerinde *Himantoglossum robertianum* ve IGP deneylerinde *H. robertianum* ve *Orchis italica* olacak şekilde tasarlandı. Bu nedenle, *O. italica*'dan alınan bazı polinariumlar *H. robertianum*'un çiçek stigmalarına iğnelerle uygulanmıştır. Her iki tozlaşma türünden de stigmalı yumurtalıklar 10 gün süreyle alınmış ve LC-MS/MS ile kantitatif hormon analizleri yapılmıştır. Sonuç olarak, ISP deneylerinde GA bulunamadı. Aynı şekilde IGP'nin 1. ve 6. günleri arasında yapılan testlerde de hiç görünmedi; IGP'nin sadece 7, 8, 9 ve 10. günlerinde ve giderek daha yüksek değerlerde bulundu. İlk kez bu çalışmada orkide IGP'nin tozlaşma sonrası süreçteki endojen yumurtalık-stigma GA miktarları belirlenmiş ve önemi tartışılmıştır. İstatistiksel analizlere göre hemen hemen tüm değerler arasında anlamlı bir fark vardır. Özellikle 9. ve 10. günlerde görülen çok yüksek aktivitenin nedeninin anlaşılabilmesi için ilave histolojik ve embriyolojik çalışmalara ihtiyaç duyulduğu anlaşılmıştır.

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1. Introduction

Considered being the largest family of plants, Orchidaceae consists of approximately 31.000 species (Hassler, 1994 - 2024). Orchids have been the focus of attention of many researchers and animals with their labellums, which vary in shape and color, and their patterned flower structures consisting of three petals and three sepals. Orchids are considered unusual among flowering plants. Food-deceptive and rewarding flowers, seen as pollination strategies, or attractive flower structures that secrete sex-deceptive and chemical pheromones attract the attention of many pollinator agents (Lanzino et al., 2023). After such reciprocal pollination events with pollinator insects, the complex events in flower structures and metabolisms are entitled "post-pollination phenomena," and the findings on this subject are outlined below:

The first action that triggers hormonal events post-pollination is the penetration of auxin into the stigma in the pollen (Arditti and Flick, 1976; Strauss and Arditti, 1984). Auxin from pollen diffuses through the columna and stimulates ethylene production, which triggers perianth senescence (Clifford and Owens, 1988). Orchid flowers are very sensitive to ethylene (Dijkman and Burg, 1970). Ethylene is also released in the flower after the polynarium leaves the flower by a pollinator insect (Arditti et al., 1973; Strauss and Arditti, 1984) and with the activity of auxin, the amount of ethylene increases even more in the flower (Strauss and Arditti, 1984). Various studies have attempted to reveal the responses of different flower parts to exogenous hormonal experiments. For instance, Absisic acid (ABA) and Naphtalen acetic acid (NAA), ethylene, and partially Gibberellic acid (GA) in the lateral petals, sepals, and labellum, yellowing and hooding in the dorsal sepal, senescens and anthocyanin synthesis are initiated. Again, in this process, ovule development (Zhang and ONelll, 1993), swelling, development, and coordination of male and female gametophytes (Zhang and ONelll, 1993) are provided in the ovary, while a change in curvature is observed in the pedicel. In addition, stigmatic closure with auxin in the stigma, auxin promotion in the column, and Ethylene production after pollination, RNA synthesis, anthocyanin synthesis, swelling, straightening, and greening are seen. With these, the movement of substrates from the perianth to the ovary and column is observed (Arditti, 1969; Arditti et al., 1971; Arditti, 1979b). This post-pollination process is monitored in all orchid taxa, autogamic or allogamic.

Pollen has auxin (Arditti 1979a). Although auxin is secreted from pollen, some researchers have emphasized that other post-pollination factors should be examined (Strauss and Arditti, 1982). Therefore, in our first trials, salicylic acid, Abscisic acid, and jasmonic acid hormones were detected in polinia, apart from auxin (unpublished result). Because different studies have also referred to the presence of JA in pollen (Yamane et al., 1982). For this reason, it has been noted that there is a lack of knowledge in the form of whether there are other hormones in flowers after post-pollination and to what extent the activities of the endogenous GA change in pollination between different taxa. Additionally, many studies have attempted to elucidate the post-pollination process by applying exogenous hormones (Arditti et al., 1973; Strauss and Arditti, 1984; Clifford et al., 1988). In *Arabidopsis thaliana* (Swain, 2005), tomato (*Lycopersicon esculentum*) (Proels et al., 2006), *Petunia hybrida* (Kovaleva et al., 2005),

and *Lilium* (Barendse et al., 1970), it has been described GA to support germination and tube growth of pollen. On the other hand, it has been reported that GAs inhibit pollen growth in vitro when not applied at species-specific concentrations (Kovaleva et al., 2005). From this it is understood that GA is active at a very sensitive fine-tuned concentration for pollination and pollen tube performance, and it could affect pollen performance, even ovule development and fertilization, in applications other than this concentration. Also, it has been stated in different studies that the effect of GA is bidirectional and inhibitory, or it is even reduced to zero at increasing doses (Zhou ve Zhang, 2010). Arditti et al. (1971), stated that GA was less effective than NAA in the post-pollination process other than anthocyanin synthesis. It is hypothesized that gibberellic acid (GA), as a bidirectional hormone, may function to inhibit successful fertilization in the context of incompatible pollination (IGP). The delayed synthesis and increased levels of GA observed in the later stages of IGP could indicate that GA serves as a physiological mechanism to prevent fertilization, thereby contributing to reproductive failure in intergeneric pollination. For this reason, the first aim of the study is to investigate the endogenous hormone GA that could not be detected in the ovaries with stigma before or during post pollination, its secondary objective is to determine the activities of this hormone in pollination experiments performed within the same taxon (ISP) or with different taxa (IGP).

2. Materials and Methods

In the study, two different pollination experiments have been conducted: 1. Compatible pollination made with members of the same taxon (Intraspesific=ISP), 2. Incompatible cross-pollination experiments have been carried out with specimens from different genera (Intergeneric=IGP) to prevent fertilization as much as possible. As a material, samples belonging to *Himantoglossum robertianum* (Loisel.) P. Delforge and *Orchis italica* Poir. have been used in the experiments. The samples were collected from Muğla and Çanakkale in the previous year, some were dried and recorded in the herbarium Edirne, Trakya University Herbarium (EDTU 22869, EDTU 10417), and some were kept in pots. Manual pollination experiments were carried out on specimens blooming in March the following year (Pollination was done on the first 1 or 2 days after the flower emerged from the bud). In order to confirm the accuracy of the samples, they were also identified (Deniz, 2022; Güler, 2022).

For this reason, polynariums taken from *H. robertianum* flowers by hand were placed on the stigmas of the flowers of the same taxon with the help of needle and forceps. Additionally, some polynariums from *O. italica* were also applied to another *H. robertianum* flower stigma. Therefore, both in-species pollination and hybridization between different genera were tested. The ovaries with the stigma of the flowers taken from both types of pollination each day separately for 10 days were taken into liquid nitrogen and then kept in depfreeze at -80 °C until hormonal tests.

2.1. Preparation of extracts

Extracts were prepared according to the procedure of Müller and Munné-Bosch (2011) with some modifications. The samples were pulverized using a grinder, as follows: A 1.5 mg sample was dissolved in 10 mL ethanol (95%), followed by ultrasonic-assisted extraction in an ultrasonic cleaning bath for 60 min at 40 °C. This mixture was centrifuged at 5000 rpm for 30 min at +4 °C, and the supernatant was collected into a volumetric flask. The extraction procedure was repeated twice. 5 mL ethanol was added to the sample again, and an ultrasonic bath was performed at 40 °C for 30 min and centrifuged. Finally, the supernatants were combined into a 25 mL volumetric flask, and the volume was made up to the mark with ethanol (95%). 100 µL of sample was mixed with 900 µL extraction solution (water, methanol, formic acid:v:v:v, 79:20:1), and samples were vortexed for 30 s. After that, the mixture was homogenized using a sonicator at 45°C 10 min. Samples were centrifuged at 13500 rpm for 5 min, and the supernatant was injected into the LC-MS/MS system for quantitative analysis.

2.2. Calibration curve and quantification in liquid chromatography-tandem mass spectrometry (LC-MS/MS).

LC was performed using an Agilent 6460 (Agilent Technologies, Waldbronn, Germany) LC system. Data acquisition and processing were accomplished using MassHunter, the Agilent LC-MS software. The concentration of the hormons in each sample was calculated using the calibration curve. Samples were prepared on the same day and analyzed in the same analytical run. All calibration curves were prepared with the following concentrations: Blank (water, methanol, formic acid:v:v:v, 79:20:), 5, 10, 25, 50, 100 ng / mL, and injected all points three times. The linearity of all the hormone was $R^2 \geq 0.995$. Total GA was used, and the standards were prepared from total GA in the amounts given above. It has been obtained from the calibration standards of the commercial company to which the device is affiliated (Agilent 6460=Agilent Technologies, Waldbronn, Germany). These samples were analyzed according to the procedure described for sample preparation.

Hormone analysis was performed using an LC system (Agilent Technologies, Waldbronn, Germany). MS/MS analyses were conducted on an Agilent 6460 triple quadruple LCMS equipped with an electrospray ionization interface. 1 g sample was taken into a falcon, and 10 mL extra-pure water was added. The solution was vortexed for 1 min and sonicated for 15 min at 45 °C. BB and BP samples were centrifuged for 5 min at 13500 rpm. Then, 50 mL clear supernatant was mixed with 50 mL internal standard and 900 mL extraction solution (Mobile phase A, methanol, acetonitrile: v:v:v, 5:15: 5), and the sample was injected into the LC-MSMS system. Both types of 10-day trials were repeated three times and the differences in the hormonal values were compared using ANOVA with means separation by the Duncan's test using the SPSS 26 software at a significance level of $p \leq 0.05$.

3. Results and Discussion

GA was active only on IGP days 7, 8 and 9 in this study and increasing gradually, and has no activity in ISP experiments (Figure 1 and Table 1). According to statistical tests, the differences between the GA activities of the 9th and 10th days and the values on the other days (IGP 7.8) are generally significant (Table 2).

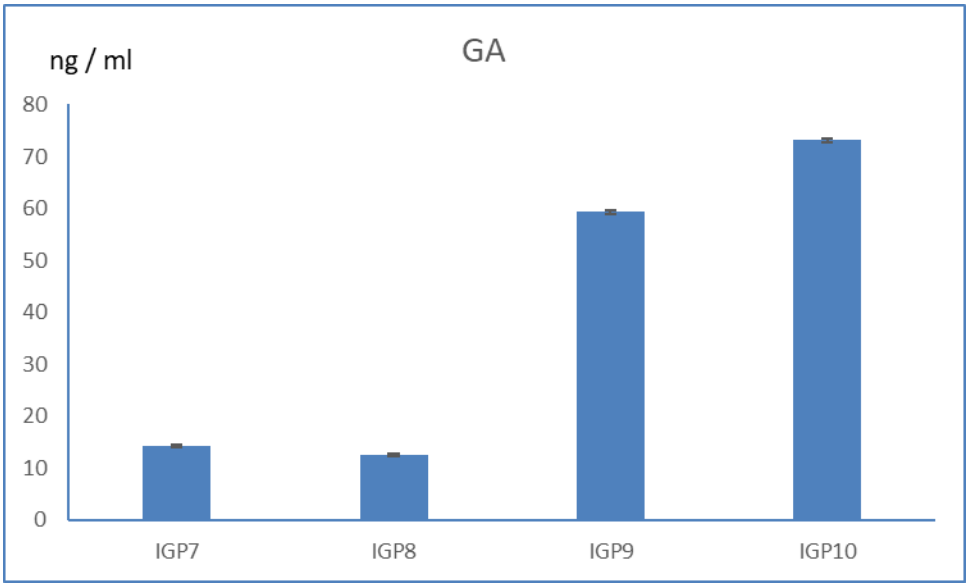

Figure 1. GA hormone mean values in IGP trials. The numbers (IGP 7, 8, etc.) show which day the trial belongs to. Standard error values are above the columns. The values, expressed in ng/ml, were 14.21 (±0.29) for IGP7, 12.47 (±0.29) for IGP8, 59.26 (±0.29) for IGP9, and 73.10 (±0.29) for IGP10. As observed, these values show a gradual increase from IGP7 to IGP10.

It has been reported that some gibberellins in orchids have different effects on flowering depending on the plant species or variety, and flowering in *Phalaenopsis* Blume hybrids is promoted by GA application under high-temperature conditions (Chen et al., 1997). It has also been stated that GA plays a role in microsporogenesis (Cid, 2000). Additionally, GA is also effective in the pollination process. For instance, while GA increased gradually after compatible pollination, it increased until the day 8 in incompatible pollination and did not increase afterward (Kojima, 1996). However, in another study, the application of GA to antesis negatively affected and ceased pollen performance and elongation of pollen tubes (Mesejo et al., 2008). It was even concluded that applying GA3 in cross-pollinated Clementine mandarin cultivars impairs fertilization by increasing ovule abortions or reducing pollen tube growth (Mesejo et al., 2008). In fact, it is known that the high parthenocarpy feature in tangerine varieties is due to the high gibberellins in the plant (Talo et al., 1992).

Table 1. Basic descriptives and Anova test results belonging to GA hormone activities in the groups (The values for ISP 1-10 and IGP 1-6 are not available due to the absence of the hormone).

		95% Confidence Interval for Mean							
Groups	**N**	**SD[1]**	**LB[2]**	**UB[3]**	**Min[4]**	**Max[4]**	**F[5]**	**df[6]**	**Sig[7]**
IGP7	3	0.21099	13.6886	14.7369	14.00	14.42	70.660	3	0.000
IGP8	3	1.87577	7.8169	17.1362	10.60	14.35	70.660	3	0.000
IGP9	3	9.68893	35.1958	83.3331	49.58	68.95	70.660	3	0.000
IGP10	3	8.13232	52.9058	93.3094	64.98	81.24	70.660	3	0.000

[1]**SD**: Std. deviation, [2]**LB**: Lower Bound, [3]**UB**: Upper Bound, [4]: minimum (Min) and maximum (Max) values, [5]: F-value (Anova), [6]**: df** (degrees of freedom), [7]: Sig (significance)

In *Arabidopsis thaliana* (L.) Heynh (Swain, 2005), tomato (*Solanum lycopersicum* L.) (Proels et al., 2006), *Petunia hybrida* (Hook.) Regel (Kovaleva et al., 2005), and *Lilium* L. (Barendse et al., 1970), it has been described GA to support germination and tube growth of pollen. On the other hand, it has been reported that GAs inhibit pollen growth in vitro when not applied at species-specific concentrations (Kovaleva et al., 2005). From this, it is understood that GA is active at a very sensitive fine-tuned concentration for pollination and pollen tube performance, and it could affect pollen performance, even ovule development and fertilization, in applications other than this concentration.

Table 2. Mean comparison of GA activities in IGP experiments based on Duncan's test.

Group	**IGP7**	**IGP8**	**IGP9**	**IGP10**
IGP7		1.73621	-45.0517*	-58.89485*
IGP8			-46.7879*	-60.63106*
IGP9				-13.84316
IGP10				

*: significant at $p \leq 0.05$. As a result, there is statistical significance in the differences between IGP7 and IGP and IGP10 as well as between IGP8 and IGP10. Similarly, there is a considerable difference between IGP9 and IGP10 and all other groups (IGP7 and IGP8).

It has been stated in different studies that the effect of GA is bidirectional and inhibitory, or it is even reduced to zero at increasing doses (Zhou ve Zhang, 2010). Our findings suggest that endogenous GA only appeared between 7-10 days in IGP pollination, inhibiting and completely ceasing pollen performance by showing increasing doses with each passing day. As a result of the experiment, it was seen that empty seeds without embryo were poured from the fruits. From this, it is understood that GA is inactive in ISP and more in IGP. Arditti et al. (1971) stated that GA was less effective than NAA in the post-pollination process other than anthocyanin synthesis. However, our results show endogenous GA, especially in IGP and especially in the last days (7-10 days) and in increasing doses, indicating that

this hormone is also very effective in incompatible pollination. It is thought that why GA did not appear in the first days of the trials and reached such a rapid peak in the last days could only be better understood with additional embryological studies. Thus, additional histological and embryological studies must be conducted concurrently, focusing on stigma, stylus anatomy, and female gametophyte development.

According to Arditti et al. (1971), GA is active after pollination; However, the status of the hormone in compatible and incompatible pollination is not specified. Additionally, in this study of Arditti et al. (1971), the trials were conducted with exogenous hormone application; in our findings, endogenous hormone levels were examined, and intergeneric cross-pollination conditions were also carefully followed in the trials, and the endogenous and natural activities of this hormone were determined. During our literature analysis, no cross-pollination experiments such as IGP were encountered in post-pollination studies in orchids. Therefore, our findings represent a novelty as they aim to detect endogenous hormone levels and GA activity for the first time in both pollination experiments.

While the importance of gibberellic acid (GA) in guiding plant developmental processes has long been understood, its role in the context of incompatible pollination has come to occupy considerable research attention in recent years. Below is a summary of the literature concerning GA's function in incompatible pollination and how these understandings could potentially be integrated into biotechnological and agricultural applications:

Biotechnological and Agricultural Applications Cross-Species Hybridization: GA has the ability to promote pollentube growth between genetically incompatible plants providing opportunities for alternative routes in hybridbreeding. These applications could be useful to generate new plant species or varieties (Nair et al., 2020). Breaking of Self-Incompatibility: In commercial agriculture, application of GA may improve fertilization rates in plants characterized by self-incompatible system. Meng et al. (2021) showed that GA applications can enhance fertilization and seed set of self-incompatible plants as well Enhancing Seed and Fruit Development during Adverse Conditions: In high stress environmental or low pollinator activity agricultural regions, GA application could improve the seed and fruit yield of plants in such conditions. In such conditions the use of GA can increase plant biomass which in turn, leads to higher agricultural yield (Aloni et al., 2019). Studies reviewed with this literature further indicate that GA is vital for plant growth and development but also functions as a strategic intervention to break genetic limitations and improve agricultural performance. The study results of the endogenous gibberellic acid content are a promising discovery at identification of parent plants which will enable to obtain in combination new hybrids (strains) according human needs with cultivation and work out tuber bearing orchids and species having medicinal value. This appears to be the first study addressing this issue.

The study's findings suggested that gibberellic acid (GA) acts as a physiological mechanism to prevent fertilization because of its delayed synthesis and the higher amounts of GA seen in the latter stages of interspecific germination processes (IGP). This result validates our hypothesis, which statistical analysis

have verified. Furthermore, this event serves as an important safeguard for the ongoing spread of the species.

4. Conclusion

GA hormone was seen only in IGP experiments and only on the 7^{th}, 8^{th}, 9^{th}, and 10^{th} days during the orchid post-pollination process. In ISP experiments, no activity of the GA hormone was detected. In IGP experiments, GA activity was detected at close values on the 7^{th} and 8^{th} days but at very high levels on the 9^{th} and 10^{th} days. According to the statistical tests, the increase in activity, especially on the 9^{th} and 10^{th} days, is significant. Additionally, performing orchid post-pollination studies with endogenous hormone activity detection produces more efficient results. In addition, the findings are made for the first time in ovaries with stigma and endogenous GA activity. In addition, it has been revealed that simultaneous histological and embryological studies should be carried out to understand the excessive GA activity on the 9^{th} and 10^{th} days with the events in the ovary and stigma.

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Conflict of Interest

The author of the article declares that he has no conflict of interest.

Researchers' Contribution

The author declares that he has contributed 100% to the article.

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