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GENETIC AND ENVIRONMENTAL REGULATION OF ISOFLAVONE CONTENT IN SOYBEAN: AN OVERVIEW

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ABSTRACT

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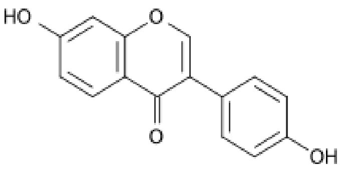
An estrogen-like substance made by some plants, including the soybeans plant. Soybeans are the prime source of isoflavones in human foods. Soy isoflavones are being studied in the prevention of cancer, hot flashes that occur with menopause and osteoporosis (loss of bone density). There are a lot of researches about the genetic and environmental control of isoflavone content in soybean. However, there is a lack of review about concrete information on isoflavone control in soybean. This review aims to make advance the knowledge of genetics and the environmental underlying isoflavone accumulation. The result showed that there is a big variation of isoflavone among the varieties of soybean as well as isoflavone content was genetically regulated and greatly affected by environmental conditions. This review provides updated information on isoflavone which will help to understand the importance of isoflavones and it's genetic and environmental regulation in soybean plant.

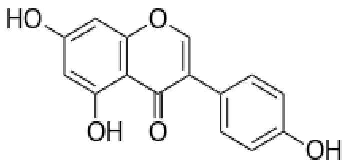
Key words: *maturity group, location, QTL and gene, planting date, UV-C*

INTRODUCTION

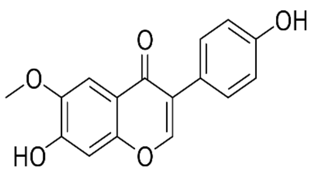
A search of the literature reveals a lot of articles and reviews reporting the effects on human health associated with soy isoflavone. Soy isoflavones have potential health benefits, including cancer, cardiovascular disease, malignancies and osteoporosis (Pingxu *et al.* 2022). Besides, isoflavones fight with fungal pathogens, which cure fungal diseases (Subramanian *et al.* 2004). Adlercreutz *et al.* (1991) reported that soybean reduced the incidence of breast cancer in Asian populations. Isoflavones in the diet may have antioxidant and estrogenic activities and a broad spectrum of pharmacological properties (Messina 1999). Isoflavone prevents bone loss and increases bone formation (Kenneth *et al.* 1996; Pingxu *et al.* 2022). Isoflavone mitigates menopausal symptoms related to acute ovarian estrogen loss in women (Col *et al.* 1997). Thus, soy isoflavones play a vital role in human health. Isoflavones conjugated glucosides forms in soybean are daidzin, genistin, and glycitin, their corresponding aglycones daidzein, genistein, and glycitein. The malonyl glucosides 6"-O-malonyl, 6"-O-malonyl and 6"-O-malonyl for daidzein, genistein and glycitin respectively (Naim *et al.* 1973; Ohta *et al.* 1979, 1980; Xiang *et al.* 2022). The total isoflavone content in the hypocotyl was higher compared with the cotyledons (Kudou *et al.* 1991). The chemical structures of isoflavones are shown in fig. 1.



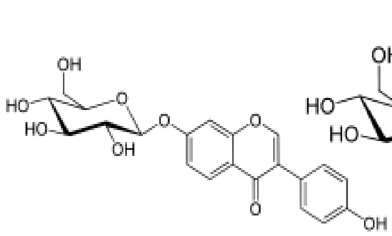
Daidzein



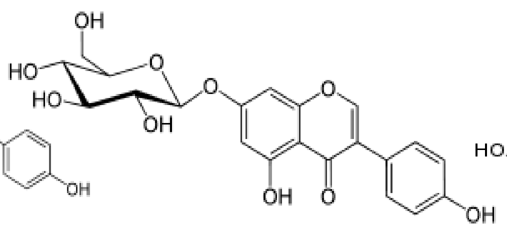
Genistein



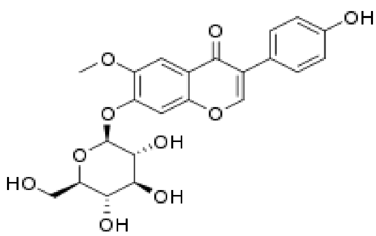
Glycitein



Daidzin



Genistin



Glycitin

Fig. 1. Chemical structures of isoflavones

Isoflavone levels in soybeans vary by both genetic and environmental factors e.g., cultivars, gene, climate, planting location, crop year, planting dates and storage conditions (Hoeck and Fehr, 2000; Lee *et al.* 2003b).

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It is known that genetic variability is associated with seed isoflavone of soybean cultivars. Key genes linked with isoflavone have been reported in soybean seeds and maternal tissues such as seed coats or pods and other soybean plant parts (Dhaubhadel *et al.* 2003; Ralston *et al.* 2005). Chen *et al.* (2011) reported that 14 key genes and gene homologs were involved in isoflavone synthesis using all plant parts. Chen *et al.* (2009) reported that gene expression differed with cultivar. Furthermore, it is also demonstrated that isoflavone contents in soybean seeds are inherited as complex quantitative traits and over fifty QTLs are responsible for individual or total soybean isoflavone content (Meksem *et al.* 2001; Kassem *et al.* 2006; Zeng *et al.* 2009; Gutierrez *et al.* 2011). Juan *et al.* (2010a) reported that isoflavone accumulation is controlled by a complex environmental adaptable network in soybean seeds. Supanimit *et al.* (2013) documented that isoflavone levels in soybeans varied considerably based on variety. It is also documented that soy isoflavone may differ by high or low temperatures, humidity, light intensity, rainfall, duration and number of rainy days and physical damage (Tsukamoto *et al.* 1995; Carrao-Panizzi *et al.* 1998; Dayde *et al.* 2004). Zhang *et al.* (2014) stated that isoflavone concentrations were significantly affected by the maturity group. Isoflavone assimilation decreased with the increases in storage time and temperature (Jong *et al.* 2005). Although much research has been studied about genetic and environmental control of isoflavone content, there is a lack of review reports that have concrete information. It is important to know all the information about isoflavone content belongs to different factors in a report. This review will gather enough information underlying isoflavone content in soybean in a solid form.

Variation of isoflavone among the varieties in soybean

There are a lot of soybean varieties and their characteristics are different. Therefore, isoflavone may differ from variety to variety. Tsukamoto *et al.* (1995) reported that the average isoflavone content of about 150, 200, 450 and 550 mg per 100 g seed for Brazilian, American, Japanese and Canadian soybean cultivars. Mercedes *et al.* (2009) tested isoflavone with 233 cultivars using the same conditions and reported that the range of isoflavone was 12- 461 mg 100 g^{-1} soybean seed. Genetic variability in isoflavone level is observed while different soybean cultivars are grown in the same conditions. Of 12 different cultivars grown in Conquista and reported that there is a big variation among the cultivars (Carrao-Panizzi *et al.* 2003). Yang and Chung, 2001 tested 60 Korean varieties using the same conditions and reported that isoflavone values ranged from 1.62 to 2.52 mg/g. Similarly, Wang *et al.* (2000) conducted an experiment using 210 soybean varieties grown in South Dakota, United States and found variations of isoflavone were 1.16 to 2.74. Another study of 7 American soybean varieties showed isoflavone range from 2.05 to 4.22 mg/g. Supanimit *et al.* (2013) used 14 soybean varieties grown in Thailand using the same conditions and stated that the isoflavone range varied widely from 0.65 mg/g to 2.75 mg/g. Total isoflavone of soybean seeds from different cultivars were shown in Table 1. Therefore, it can be concluded that there is a big variation of isoflavone among the varieties and some varieties have low isoflavone, some varieties have medium isoflavone and some varieties have high isoflavone.

Table 1. Total isoflavones (mg 100 g^{-1}) in samples of soybean seeds from different cultivars

Cultivars	Total Isoflavone (mg 100 g^{-1})	References
BRS 133	172.49	Mercedes *et al.* 2009
BRS 212	218.68	
BRS 230	66.79	
BRS 258	47.39	
Embrapa 48	103.11	
BRS 215	120.27	
RS 10	153.1	Carrao Panizzi *et al.* 2003
BR 36	105.9	
Mustang M-1000	216	Wang *et al.* 2000
Pioneer 9071	194	
Pioneer 9092	252	
Ciba 3144	231	
Terra TS195E	150	
Chiangmai 2	108	Supanimit *et al.* 2013
Chiangmai 60	70	
Sukhothai 3	188	
Sukhothai 1	65	
SJ 5	144	
KKU 35	165	
BRS 246	52.9	Jonatas *et al.* 2021
BRS 317	42.67	
BRS 294	33.6	

Isoflavone content of soybean cultivars based on maturity group

Soybean varieties are divided into 00 to IX maturity groups depending on the length of the growing season. Kassem (2021) reported that isoflavone content significantly varied in soybean seeds depending on maturity group. The maturity groups 00 being for the shortest growing season and IX being designed for the longest growing season. Wang *et al.* (2000) tested isoflavone content among maturity group 0 to II soybeans using 210 soybean cultivars and results showed total isoflavone contents ranged from 1161 to 2743 μg/g and maturity group I had the higher total isoflavones content compared to maturity group 0. Zhang *et al.* (2014) examined the isoflavone Content of Soybean Cultivars from maturity group 0 to VI and found significant differences in total isoflavone content among the maturity groups. Maturity groups V and VI showed notably higher isoflavones than maturity groups 0-IV. Besides, the average value of isoflavone content for MG 0 varieties was 2225.21l μg g^{-1} of soybean seed, while isoflavone content for MG VI was 3569.41lμg g^{-1} of soybean seed, resulting in early mature cultivars content of lower isoflavone compared with late mature cultivars.

Isoflavone-related genes and quantitative trait loci (QTL)

At present time, the genetic parameter is the most priority topic of research. The major genes and QTLs are the main genetic parameters of the crops. Chen *et al.* (2011) experimented with isoflavone-related gene expression using various soybean cultivars and reported 14 key genes (PAL, CHS1, CHS3, CHS5, CHS6, CHS8, CHR, CHI1A, CHI1B1/1B2, CHI2, CHI3, CHI4, IFS1 and IFS2) and gene homologs encoding enzymes related with isoflavone synthesis as well as observed that gene expression among plant parts varied notably based on the cultivars. Cultivar (AC Orford) showed relative gene (CHS1) transcripts levels were highly visible in leaves, intermediate in flowers and stems, and slightly in seeds, pods and roots. Alternately, in cultivar (AC Proteina) showed expression levels of CHS1 were greatest in leaves and stems, and lower in the other parts. This result indicates that gene expression level varies regarding plant parts. Gutierrez-Gonzalez *et al.* (2010) stated that gene expression involved in isoflavone synthesis in soybean seeds varies throughout plant development, the stage at which maximum expression is observed based on the gene or gene homolog.

To find out the isoflavone-related QTL, Zeng *et al.* (2009) made a cross between two soybean cultivars Zhongdou 27 (high isoflavone content) and 'Jiunong 20 (low isoflavone content). This author reported that three QTL (QDZF_1, QDZI_1, QDZK_1) were associated with daidzein content, four (QGTA2_1, QGTC2_1, QGTF_1, QGTM_1) with genistein content, three (QGCI_1, QGCM_1, QGCO_1) with GC glycitein content, and five (QTID2_1, QTIF_1, QTIG_1, QTIO_1, QTIM_1) with total isoflavone content. For all QTL detected the beneficial allele was from cultivar Zhongdou 27. QTL were located on three daidzein, three glycitein, four genistein and five total isoflavone molecular linkage groups. A novel QTL was detected with marker Satt144 on linkage group F that was associated with daidzein, three glycitein and total isoflavone across the various environments. Hui-zhen *et al.* (2010) identified QTL for isoflavone and reported that six QTLs content were localized in linkage groups J, N, D2, and G. Above mentioned discussion will help to molecular breeding of soybean.

Isoflavone-related genes in soybean during environmental stress

Abiotic stress alters the normal function of a gene. Juan *et al.* (2010b) reported that in well-watered conditions CHS7, CHS8 and IFS2 are associated with isoflavone levels. Surprisingly, IFS2 showed down-regulated and highly correlated with isoflavone accumulation under both water deficit and well-watered conditions, resulting in IFS2 as the main contributor to isoflavone reduction under drought. Jia *et al.* (2017) examined the salt stress soybean gene (GmIFS1) expression and isoflavone accumulation and reported that salt stress induced GmIFS1 expression increased isoflavone accumulation.

Chennupati *et al.* (2012) observed the key genes involved in isoflavone synthesis under temperature stress. High-temperature stress reduced the expression of the CHS8 gene at the R5 stage, CHS7 and IFS1 at the R6 stage as well as CHS7, CHS8, IFS1, and IFS2 at the R7 stage in the seed. In pods, high-temperature stress affected the expression of CHS7 and IFS2 genes at the R6 stage and CHS7, CHS8, IFS1, and IFS2 genes at the R7 stage. At the R6 stage, the high temperature increased the expression of CHS7 and IFS2, whereas at the R7 stage the expression of CHS7, CHS8, IFS1, and IFS2 genes was reduced. Therefore, it can be concluded that high-temperature stress affects negatively isoflavone gene expression in soybean.

Effect of location on isoflavone content in soybean

It has been reported that there is a significant difference in isoflavone content in soybean when planted in different locations using the same cultivars and conditions (Lee *et al.* 2003a). Supanimit *et al.* (2013) have grown Chiangmai 60 have grown in 2010 at 4 different research centres and reported that isoflavone varied significantly from 1.22 ± 1.24 to 2.75 ± 0.33 mg/g. Wang and Murphy (1994) tested vinton 11 varieties at a different location in Iowa, USA and stated that the isoflavone variations were 1.18 to 1.75 mg/g. Ain *et al* (2022) stated that isoflavone content in soybean varied widely with location. Ultimately, isoflavone content in soybean differs based on growing location.

Effect of crop year on isoflavone content in soybean

Crop production is highly sensitive to crop year due to the variation of climate from the year to year. Wang and Murphy (1994) have grown 8 American and 3 Japanese verities from 1989 to 1991 and reported the variation of total isoflavone content varied greatly regarding year. Supanimit *et al.* 2013 conducted an experiment using Chiangmai 60 cultivar and reported variations of isoflavone were 1.05 to 1.21 mg/g in 2008, and 2.27 to 2.95 mg/g in 2009, and 1.79 to 3.17 mg/g in 2010. Regarding above mention discussion, it can be concluded that there is a remarkable effect of different crop years on isoflavone content in soybean.

Effect of temperature on the isoflavone content in soybean

Temperature affects many parameters of soybean including isoflavone. Charles *et al.* (2005) determined the effect of temperature of the isoflavone content using a growth chamber and reported temperature increasing during seed development from 18°C to 23°C, resulting in decreased total isoflavone content by about 65%. Similarly, again 5°C increase from 23°C decreased the total isoflavone content by about 90% in soybean. Chennupati *et al.* (2011) experimented to determine the effects of high-temperature stress imposed at different development stages using two cultivars (AC Proteina and OAC Champion) in growth chambers with stress conditions of 33/25°C (day/night temperature) and control conditions of 23/15°C. The result showed the total isoflavone concentration was reduced by an average of 85% compared to the control. Therefore, it could be stated that temperature stress may change the isoflavone content of soybean.

Effect of drought on the isoflavone content in soybean

Drought is one of the most important severe environmental factors that affect crop production. Lozovaya *et al.* (2005) reported drought may alter the isoflavone content and composition. Variations in isoflavones content in soybean varieties subjected to drought stress were investigated by Akitha and Girdhar (2015) and reported that little enhancement in total isoflavone content was found in cultivar KHSb-2 (3.44%) and JS 335 (2.84%) increase in seeds subjected to mild stress; this report also indicated severe drought stress diminished the total isoflavone content in both varieties JS 335 (52.02%) and KHSb-2 (46.4%). Therefore, drought stress negatively affects isoflavone assimilation in soybean.

Effect of planting date in the same crop year on isoflavone content in soybean

Basically, crop is highly responsible for the dates of planting. Supanimit *et al.* (2013) planted 14 soybean varieties under the same cultural practice on 19 December 2009, 26 December 2009, and 15 January 2010 and reported that mean isoflavone content with the cohort of 15 January 2010 generally showed a notability lower value than those of 19 December 2009 and 26 December 2009. Tsukamoto *et al.* (1995) reported a similar statement about the effect of planting date on isoflavone content in soybean. It can seem that the variation of isoflavone content occurred due to different climatic conditions.

Effect of soil nutrient on isoflavone content in soybean

Researchers want to increase isoflavones content in soybean differently; soil nutrient is one of them. Wang *et al.* (2019) reported that isoflavones concentration was more responsive to P fertilization and it increased isoflavone content in soybean. Tony *et al.* (2002) investigated potassium fertilization effects on isoflavone concentrations in soybean and reported that there is a positive effect of K fertilization on isoflavones accumulation in soybean. Thus, it can be stated that nutrient management could be an effective approach to increase isoflavone content in soybean.

Effect of UV-C on isoflavone content in soybean

The solar ultraviolet (UV) spectrum has three wavelength bands: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (200–280 nm). UV-C radiation contains shorter wavelengths and causes numerous injuries. The minor amount of UV-C may activate acclimation responses in plants along with the activation of enzymatic and non-enzymatic defense systems (Loyall *et al.* 2000; Rai *et al.* 20011). High doses of UV-C radiation id responsible for decreasing cell viability, and cell death. Karki *et al.* (2020) reported that UV-C irradiation of soybean leaves has been correlated with higher concentrations of isoflavone content. It can be concluded that UV-C exposure influences isoflavone concentrations in soybean plants.

CONCLUSION

This revision indicated that there is a big variation of isoflavone among the varieties and some varieties have low isoflavone, some varieties have medium isoflavone and some varieties have high isoflavone, as well as lower isoflavone concentration was exposed in early maturing cultivars rather than late. Furthermore, isoflavone content in soybeans varied considerably depending on 14 genes (PAL, CHS1, CHS3, CHS5, CHS6, CHS8, CHR, CHI1A, CHI1B1/1B2, CHI2, CHI3, CHI4, IFS1 and IFS2) and gene expression level varies regarding plant parts along with environmental stress affects negatively isoflavone gene expression in soybean. It is also documented that three QTL (QDZF_1, QDZI_1, QDZK_1) were associated with daidzein content, four (QGTA2_1, QGTC2_1, QGTF_1, QGTM_1) with genistein content, three (QGCI_1, QGCM_1, QGCO_1) with

GC glycitein content, and five (QTID2_1, QTIF_1, QTIG_1, QTIO_1, QTIM_1) with total isoflavone content. Regarding environmental factors, it could be stated that isoflavone content in soybean varies based on growing location and there is a notable effect of the different crop years on isoflavone content in soybean. Similarly, isoflavone assimilation was reduced by temperature stress in soybean and severe drought stress has a detrimental effect on the total isoflavone content in soybean. In conjunction with planting date even in the same year affect isoflavone content in soybean. In the case of the reformatory, soil nutrient management could be an effective approach to increase isoflavone content in soybean. And, UV-C irradiation of soybean leaves has been correlated with higher concentrations of isoflavone content. Based on this review, it may suggest that future study supposed to conduct, from a genetic point of view, targeting cultivars for high isoflavone concentration in soybean seeds. Ultimately, this review made advances the knowledge of genetics and environmental underlying isoflavone accumulation, which will help the breeder and agronomists to further improvement of isoflavone research in soybean.

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