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Impact of altitude on grain yield, oil, and protein content of soybean

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Abstract

Soybean (*Glycine max* (L.) Merrill) is one of the most important commodities in the world, with grains that show variations in their chemical composition, mainly in oil and protein content. These variations can be related to genotype (G), environment (E), and G × E interaction. Thus, the objectives of this study were to determine the environments which maximize oil and protein yields, and to identify potential soybean cultivars that have increased grain yield, and oil and protein content in high-and low-altitude environments. Twenty-eight soybean cultivars were evaluated at high (846–963 m, *Cfb* climate) and low (336–480 m, *Cfa* climate) altitude environments, in the 2017/18 and 2018/19 crops, for grain yield, thousand grain weight, and oil and protein contents and yields. Growing environment affected the chemical composition of soybean grains. Altitude had a positive effect on protein content and a negative effect on oil content. The high-altitude environment increased the protein content by 6.15% (380 g kg^{-1}), whereas the low altitude environment promoted an increase of 5.58% in oil content, with a mean value of 220 g kg^{-1}. We identified soybean cultivars with potential for greater oil and protein yields in high-and low-altitude environments. Knowledge of the associations between environments and the chemical composition of soybean grain is valuable for developing direct breeding efforts, recommending cultivars and growing locations, in order to meet the demand of the oil and protein market.

Keywords: *Glycine max* Merrill; low- and high-altitude environment; genotype x environment interaction.
Abbreviations: ABL, Abelardo Luz; CAM, Campos Novos; E, environment; G × E, environment x genetics interaction; G, genetics; GY, grain yield; GUA, Guarapuava; MED, Medianeira; OIL, oil content; OILY, oil yield; PAL, Palotina; PROT, protein content; PROTY, protein yield; RLZ, Realeza; TGW, thousand grain weight.

Introduction

Soybean (*Glycine max* (L.) Merrill) is one of the main agricultural commodities in the world. In the 2019/20 growing season, the world production was estimated in 337.3 million tons, and Brazil leads the world soybean production, with ~126 million tons annually (FAO, 2020). Because of its high oil and protein content, soybean is used for human and animal feed, and it is an important renewable and sustainable resource for vegetable oils for human consumption and biodiesel production (Wu et al., 2013; Leite et al., 2019). Soybean represents ~27% of vegetable oil produced, and currently approximately 77% of biodiesel is produced from vegetable oil (OECD/FAO, 2020). In 2020, the Brazilian biodiesel production was estimated at 6.3 billion liters, with soybeans accounting for 71% of this production (USDA, 2020).
The oil content in soybean grains ranges from 17% to 24%, whereas the protein content varies from 37 to 42% (Patil et al., 2017). Several studies measuring the chemical composition of grains reported greater oil and protein concentrations in soybeans from Brazil than those from the USA and Argentina (Matei et al., 2018; Rotundo et al., 2016; Ibáñez et al., 2020). Concentrations of 21% of oil and 39% of protein are desirable for soybean crushing and the meal market (Stobaugh et al., 2017). The variation in grain quality can be attributed to the environment (E), genetics (G), and G × E interactions. Environmental factors such as temperature, radiation, water availability, soil characteristics, and crop management affect grain composition, particularly in relation to the oil and protein content (Vollmann et al., 2000; Choi et al., 2016; Silva et al., 2017; Assefa et al., 2018; Anda et al., 2020). Brazil has an extensive latitudinal range, and soybean is cultivated from the south to north region (30 ºS to 5 °N), which creates challenges for cultivation at different altitudes and environmental conditions. Altitude and temperature are strictly related in the subtropical and tropical climate regions; temperature decreases at high altitudes, and small changes in altitude affect environmental conditions (Alvares et al., 2013). In Paraná State, the relationship between temperature and altitude is approximately 1 ºC/126 m (Fritzsons et al., 2008). The effect of temperature on soybean grain quality has been reported in other studies (Pípolo et al., 2004; Rotundo & Westgate, 2009; Choi et al., 2016; Mourtzinis et al., 2017; Hossain et al., 2019; Alsajri et al., 2020), and high-temperature conditions have generally been shown to increase oil and decrease protein content. Currently, soybean prices are based on quantity, although the economic system is shifting to payment for quality, guaranteeing more predictability (Martin, 2015; Xing et al., 2018). Thus, when confronted with the increase in oil, protein, and biodiesel demand for

the next decade (OECD-FAO, 2020), a strong alternative for supply would be cultivar recommendations from specific growing regions, in order to maximize oil and protein production and improve farmer profitability. The processing industries have thereby been challenged to develop a general model of environmental effects on grain composition, to predict growing regions and/or environmental conditions that provide high-quality soybean production (Rotundo and Wesgate, 2009).

The objective of this study was to determine the environments that maximize oil and protein yields, and identify potential soybean cultivars that increase grain yield, and oil and protein content in high-and low-altitude environments.

Results

Genotype x environment interaction on the evaluated traits

The daily mean temperature and precipitation in high-and low-altitude environments are shown in Figure S1. The high altitude environment showed daily mean temperatures of 20.6 and 19.8 ºC, and accumulated precipitation of 1378 and 1294 mm in the 2017/18 and 2018/19 crop seasons, respectively. The daily mean temperatures reported in the low-altitude environment were 24.4 °C and 24 °C, with precipitation of 1582 and 1346 mm during the 2017/18 and 2018/19 crop seasons, respectively. Thus, a daily mean temperature range of 4 ºC was observed between the high and low environments. During grain filling growth stage R5 (Fehr and Caviness, 1979), the daily mean temperature was 3.5 °C and 4 ºC, higher at low altitudes than high altitude environments.

The significate interaction between environment x cultivars were observed to all evaluated traits (Table S1). The overall mean grain yield (GY) at high and low altitudes was 3832 and 4105 kg ha^{-1}, respectively, with an increase of 7.13% in the low-altitude environment (Table S2). At low altitude there was an increase of 5.5%, 13.82% and 1.85% of oil content (OIL), oil yield (OILY) and protein yield (PROTY), respectively. In contrast, the thousand-grain weight (TGW) was 5.43% greater at high altitudes, and the protein content (PROT) was 6.15% greater at high altitudes than at low altitudes.

Seed quality attributes

According to the mean and stability analysis, it was possible to identify the individual performance of soybean cultivars in each environment evaluated. At high altitudes, the cultivar TMG 7062 IPRO (28) showed higher GY, and AS 3610 IPRO (1) was the most stable (Figure 1a, Table S2). At low altitude, higher GYs were observed for 50I52RSF IPRO (8) and NS 5445 IPRO (18), and the most stable cultivars were NS 5445 IPRO (18) and NS 6601 IPRO (21) (Figure 1b).

The cultivar TMG 7062 IPRO (28) showed the best performance for TGW, with a high mean and great stability in both environments (Figure 1c, 1d). In addition, at high altitude, the cultivars 50I52RSF IPRO (8) and 68I70RSF IPRO (5) presented higher mean values, and the more stable cultivars were 5958RSF IPRO (9), AS 3610 IPRO (1), and 50I52RSF IPRO (8) (Figure 1c). In low-altitude environment, higher TGW values were observed for 68I70RSF IPRO (5), followed by TMG 7062 IPRO (28), NS 5445 IPRO (18), and NS 6909 IPRO (24), and the more stable cultivars for TGW were M6410 IPRO (16), M5917 IPRO (13), and 58I60RSF IPRO (6) (Figure 1d, Table S2).

In the high-altitude environment, NS 6006 IPRO (20) and NA 5909 RG (17) showed higher values for OILY and greater stability (Figure 2a). At low altitude, the cultivar 50I52RSF IPRO (8) presented the best performance, followed by NS 5445 IPRO (18), 68I70RSF IPRO (5), and 95R51 IPRO (27) (Figure 2b). The more stable cultivars in this environment were NS 5445 IPRO (18), M6410 IPRO (16), and NS 6601 IRPO (21). Mean OILY at high and low altitude were 788 and 897 kg ha^{-1}, respectively, showing 13.82% higher at low altitude (Table S2).

The cultivar M5838 IPRO (12) showed the greatest value for PROTY in the high-altitude environment, followed by NA 5909 RG (17), NS 6006 IPRO (20), and M5730 IPRO (11). The more stable cultivars were M5730 IPRO (11), M5947 IPRO (14), and M5730 IPRO (10) (Figure 2c). At low altitude, the higher PROTY cultivars were NS 5445 IPRO (18), 50I52RSF IPRO (8), 5855RSF IPRO (3), M5947 IPRO (14) and 95R51 IPRO (27); whereas the most stable cultivar was NS 7300 IPRO (25), followed by M5917 IPRO (13), NA 5909 RG (17) and AS 3730 IPRO (2) (Figure 2d, Table S2). Mean values for PROTY were greater at high-altitude, ranging from 581 to 2333 kg ha^{-1} (Table S2). For OILY and PROTY, each environment featured the best cultivar for mean and stability performance, evidencing the expressive G × E interaction effect on these traits.

Different performances of soybean cultivars were observed for OIL in high-and low-altitude environments. At high altitude, 7166RSF IPRO (7) and 68I70RSF IPRO (5) had the greatest oil concentration and stability for OIL (Figure 3a, Table S2). The cultivar 50I52 RSF IPRO (8) presented the higher OIL at low altitude (241 g kg^{-1}), followed by M6210 IPRO (15), and NA 5909 RG (17) (Figure 3b).

In general, soybean cultivars have low oil content and high protein content. The cultivar AS 3730 IPRO (2) showed high PROT in both altitude environments, with mean values of 401 and 374 g kg^{-1} at high and low altitudes, respectively. At high altitude NS 7709 IPRO (26), NS 6828 IPRO (22), and M5917 IPRO (13) were highlighted by their excellent performance (Figure 3c). The 5958RSF IPRO (9), NS 6906 IPRO (23), and 5855RSF IPRO (3) cultivars presented higher mean and stability at low-altitude environment (Figure 3d).

Associations between seed quality characteristics and production environment

The oil content ranged from 208 g kg^{-1} to 220 g kg^{-1} at high and low altitude, respectively, with an increase of 5.58% at low altitude (Table S2, Figure 4d). PROT was superior at high altitudes (380 g kg^{-1}) over low altitudes (358 g kg^{-1}) by 6.15% (Table S2, Figure 4d). Among the soybean cultivars evaluated, 7166RSF IPRO (7) expressed a favorable performance potential because of the strong positive correlation with OIL in both environments (Figure 4a, b). Furthermore, AS 3730 IPRO (2) and 5855RSF IPRO (3) were positively associated with PROT in high-and low-altitude environments (Figure 4a, b, Table S2). These cultivars show greater stability to OIL and PROT, and are less affected by the growth environment.

The cultivars M5838 IPRO (12), M5730 IPRO (11), and NS 6909 IPRO (24) were positively associated with PROTY at high-altitude (Figure 4a); whereas, at low altitude, 68I70RSF IPRO (5), NS7300 IPRO (25), and NS 6909 IPRO (24) presented positive correlation with PROTY (Figure 4b). Strong associations were observed between OILY and 68I70RSF IPRO (5), M5705 IPRO (10), and NS 6006 IPRO (20) at high altitude (Figure 4a). In contrast, at low altitudes, 50I52RSF IPRO (8), NS 6006 IPRO (20), and 95R51 RR (27) showed strong correlation with OILY (Figure 4b).

Test locations classified as high altitude (CAM, ABL, and GUA, see Table S1) presented a positive association with PROT. ABL expressed the stronger correlation (Figure 4c). Furthermore, positive associations were observed between TGW and test locations at high altitude, which corroborate the results in Table S2, whereas the test locations classified as low altitude (MED, PAL, RLZ) were positively associated with OIL (Figure 4c). We also highlight the negative association observed between the OIL and PROT. There was a positive linear relationship between altitude and PROT, with a rate of increase of 0.0343 g kg^{-1} m^{-1} (R^2: 0.73^*) (Figure 4d). Therefore, a negative relationship between altitude and OIL was reported, with a rate of decrease of 0.0242 g kg^{-1} m^{-1} (R^2: 0.56^{ns}). Thus, this relationship suggests that an increase of 100 m in altitude results in an increase of 3.43 g kg^{-1} for PROT and a decrease of 2.42 g kg^{-1} for OIL.

Discussion

There was a G × E interaction effect (altitude) on grain yield (GY), thousand grain weight (TGW), oil (OIL), protein content (PROT), oil yield (OILY), and protein yield (PROTY). Several studies have reported the genotypic and environmental effects on the yield and chemical composition of soybean grains (Matei et al., 2018; Umburanas et al., 2018; Assefa et al., 2019).

A lower altitude environment and higher mean temperature (24.2 °C) showed increase in GY (Table S2). Alsajri et al. (2020) found that a higher GY was reached at ~25º °C, which is considered the optimal temperature for soybean growth and development. The increase in temperature can benefit GY, approaching the ideal for the culture; however, if this temperature is exceeded, there is a negative impact on soybean yield (Qiao et al., 2019; Alsajri et al., 2020).

In high-altitude environments with low mean temperatures, the cultivars showed higher TGW (Table S2; Figure 1c), similar to the results of other studies (Choi et al., 2016; Alsajri et al., 2020). Jumrani and Bhatia (2018) studied soybean high-temperature stress and reported that an increase of 4 °C deceased the TGW by approximately 12%. In the present study, we observed a decrease of ~5.4% in TGW in low-altitude environments, and a negative relationship between TGW and low altitude test locations (Table S2, Figure 4c). According to Taiz et al. (2017), higher temperatures can result in shorter soybean development cycles and increased respiration rate of plant tissues, consequently reducing carbon reserves, grain weight, and yield.

The soybean cultivar ranges for OIL (176 to 263 g kg^{-1}) and PROT (299 to 445 g kg^{-1}), corroborate the results of Matei et al. (2018) for Brazilian soybean cultivars. In the USA, Assefa et al. (2019) reported ranges of 132–246 g kg^{-1} and 273–454 g kg^{-1} for OIL and PROT, respectively. Rotundo et al. (2016) studied regional and temporal variations in soybean seed composition across the USA and found protein concentrations ranging from 320 to 374 g kg^{-1}, and seed oil from 167 to 205 g kg^{-1}. In general, the chemical composition and nutritive value of soybean are affected by the country of origin. According to Ibáñez et al. (2020), soybean from Brazil had the greatest crude protein content, followed by the USA, India, and Argentina.

The ideal cultivar should have a high oil and protein yield, and therefore a high oil and/or protein content, in addition to high grain yield. In this study, the best cultivars for OILY were 50I52RSF IPRO (8) and NS 5445 IPRO (18) with 1110 and 978 kg ha^{-1}, respectively, in a low-altitude environment. For PROTY, maximized in a high-altitude environment, the best cultivars were M5838 IPRO (12) and NA 5909 RG (17), with 1560 and 1473 kg ha^{-1}, respectively (Figure 1a, 4a, Table S2). Assefa et al. (2018) found that for each 1 Mg ha^{-1} in GY there was an increase of 0.35 Mg ha^{-1} for PROTY and 0.20 Mg ha^{-1} for OILY.

According to Taiz et al. (2017), protein is composed of amino acids formed from nitrogen molecules. Loss in photosynthesis activity results in a decrease in soluble protein in leaf tissue, and in C3 mechanism plants, rubisco is degraded during leaf senescence and used as the main source of protein and nitrogen translocated to the grain. Thus, when this translocation occurs, the rubisco activity and photosynthetic rate are reduced, and there is improvement in grain quality over grain yield. This mechanism can explain the negative relationship between protein content and grain yield in soybean, as observed in this study (Fig 5c) and by other authors (Assefa et al., 2018; Assefa et al., 2019; Matei et al., 2018).

Regarding OIL, higher values were reported in low-altitude environment (Table S2; Figure 4c). In these environments, the daily mean temperature observed was 4 °C above that of the high-altitude environments during the soybean development cycle. Higher temperature had a positive effect on OIL, which was also reported in several studies (Ren et al., 2009; Bellaloui et al., 2017; Matei et al., 2018; Umburanas et al., 2018). Bellaloui et al. (2017) and Umburanas et al. (2018) found that mild temperatures during grain filling can reduce oil content, corroborating the results obtained in this study. Ren et al. (2009) reported significant increases in oil and oleic acid content at high temperatures (30/37 ºC), and Anda et al. (2020) found higher oil content in soybean grains grown under dry and hot conditions. In light of the expressive search for renewable fuel sources and soybean use in biodiesel production, recommending cultivars from growing regions with lower altitudes and higher temperatures during grain filling could increase the oil content in soybean grains. This correlation has been reported in several studies (Carrera et al., 2011; Mourtzinis et al., 2017; Kohler et al., 2019; Qiao et al., 2019).

Higher altitudes are associated with a greater protein content in soybean grains (Pípolo et al., 2004; Rotundo and Westgate, 2009; Matei et al., 2018), which was also observed in the present study (Table S2; Figure 4c). Temperature affects the chemical composition of soybean grains, and a higher temperature during the maturation growth stage results in a decrease in protein content (Kohler et al., 2019; Bellaloui et al., 2011; Mourtzinis et al., 2017). Carrera et al., (2011) found that low temperature promotes increased soybean protein cultivation, corroborating the results obtained here (Table S2, Figure 4c, 4d).

During embryogenesis, the carbon flux is shared between oil and protein. In general, when increase of 1% in oil content occur, there is a decrease of 2% of protein content (Saldivar et al., 2011). There is a rapid increase in oil content during the earlier stages of grain filling, while the protein content is synthesized in the subsequent stages. Thus, when the cycle

Table 1. Environment (Env), test locations, edaphoclimatic regions (ECR), geographical coordinates (latitude, longitude, and altitude), and crop season of soybean cultivars

Env	Test location	ECR	Lat	Long	Alt (m als)	Crop Season	
						2017/18	2018/19
High-Altitude	Abelardo Luz - SC	102	26.53 S	52.29 W	846[1]	x	x
	Campos Novos - SC	103	27.40 S	51.23 W	963[1]	x	
	Guarapuava - PR	103	25.46 S	51.67 W	950[1]	x	x
Low-Altitude	Medianeira - PR	201	25.26 S	54.08 W	414[2]	x	x
	Palotina - PR	201	24.34 S	53.83 W	336[2]	x	
	Realeza - PR	102	25.77 S	53.53 W	480[2]	x	x

[1]*Cfa*: Humid subtropical, oceanic climate, without dry season, with hot summer; [2]*Cfb*: Humid subtropical, oceanic climate, without dry season, with temperate summer, according to Köppen's classification (Alvares *et al.*, 2013).

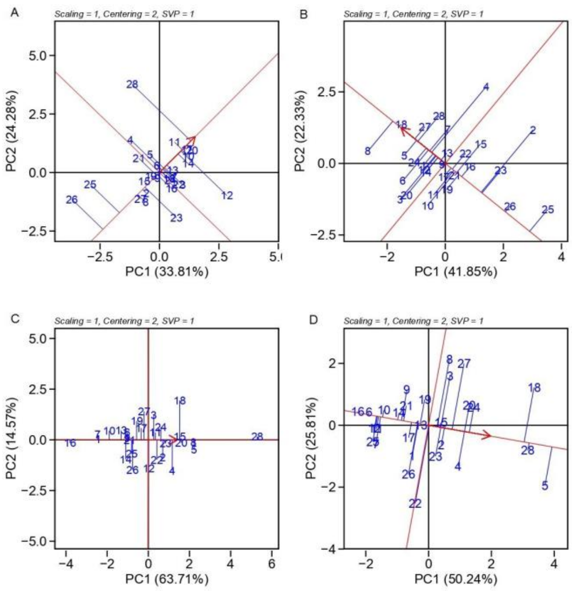

Fig 2. Mean and stability in the set of 28 soybean cultivars for grain yield (GY, kg ha^{-1}) performed at (A) high and (B) low altitude; and thousand grain weight (TGW, g) performed at C) high and (D) low altitude. PC, principal component; SVP, singular value partition. See Table S1 for a full description of soybean cultivars.

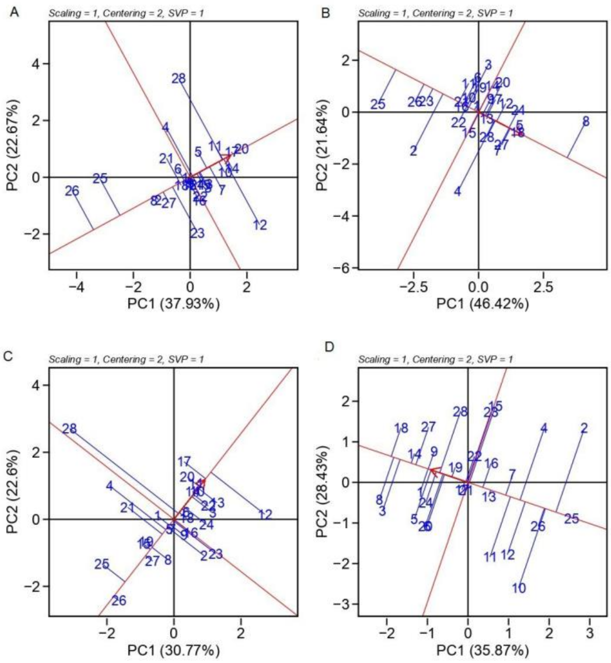

Fig 3. Mean and stability in the set of 28 soybean cultivars for oil yield (OILY, kg ha^{-1}) performed at (A) high and (B) low altitude; and protein yield (PROTY, kg ha^{-1}) performed at C) high and (D) low altitude. PC, principal component; SVP, singular value partition. See Table S1 for a full description of soybean cultivars.

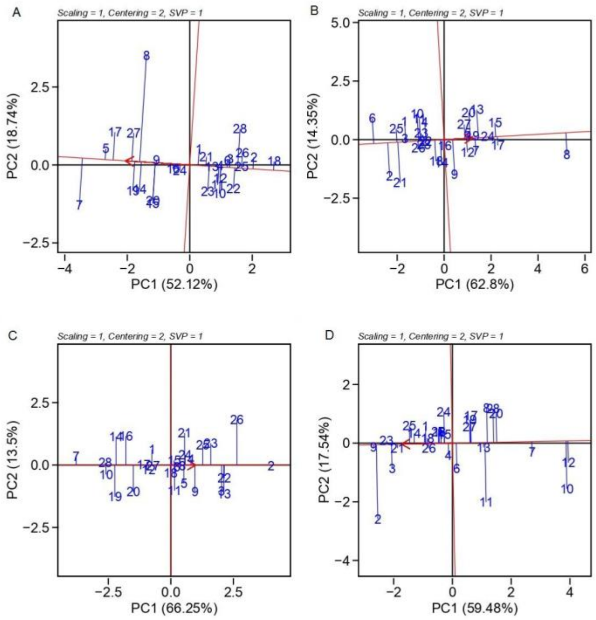

Fig 4. Mean and stability in the set of 28 soybean cultivars for oil content (OIL, g kg^{-1}) performed at (A) high and (B) low altitude; and protein content (PROT, g kg^{-1}) performed at C) high and (D) low altitude. PC, principal component; SVP, singular value partition. See Table S1 for a full description of soybean cultivars.

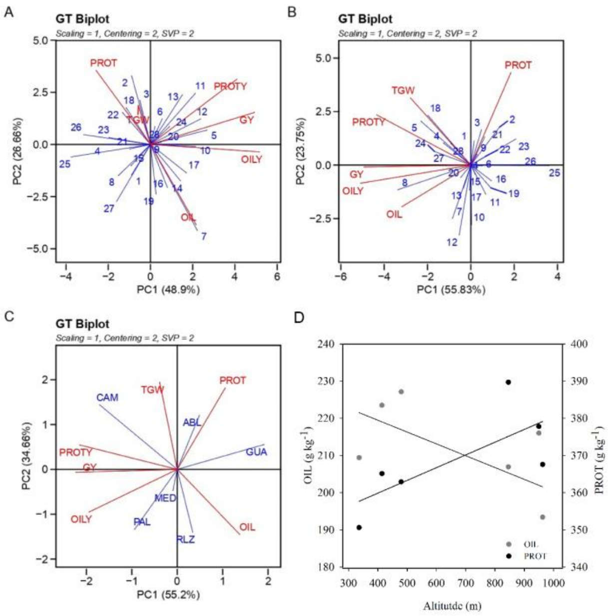

Fig 5. Association between evaluated traits with soybean cultivars grown in a) high and b) low altitude. C) Association between traits and test locations. D) Effect of altitude on oil and protein content in soybean grains. Traits: GY: grain yield, kg ha^{-1}; TGW: thousand grain weight, g; OIL: oil content, g kg^{-1}; PROT: protein content, g kg^{-1}; OILY: oil yield; PROTY: protein yield, kg ha^{-1}. See Table S1 and Table 1 for a full description of soybean cultivars and test locations, respectively.

is shorter, there is a reduced time to synthesize oil in grains, promoting higher protein accumulation (Saldivar et al., 2011; Taiz et al., 2017). The relationship between the environment and protein content is complex, mainly related to precipitation and temperature (Rotundo et al., 2016). Several studies have attached this complex interaction to numerous protein content quantitative trait loci (QTL), with two main QTLs reported on chromosomes 15 and 20 (Diers et al., 1992; Prenger et al., 2019). Brzostowski and Diers (2017), using high-protein PI 407788A in crosses among elite cultivars, obtained an increase of 11 g kg^{-1} in PROT. Prenger et al. (2019) found an increase of 40 g kg^{-1} for proteins without grain yield loss. Apart from the negative correlation between PROT × OIL and PROT × GY reported in this study, the cultivars NS 6006 IPRO (20) and NA 5909 RG (17) could be recommended to high-altitude environments, and 50I52RSF IPRO (8) and NS 5445 IPRO (18) to in low-altitude; 7166RSF IPRO can be recommended for both altitude environments. It is worth mentioning that the soybean cultivars evaluated showed strong potential for use in biodiesel production, and as a protein source for animal nutrition, due to high OIL, PROT, and GY. Matei et al., (2018) and Woyann et al., (2019) highlighted the potential of soybean cultivars grown mainly in southern Brazil.

Soybean meal is one of the main protein providers, with an upward trend in demand expected for the next decade (OECD/FAO, 2020). Currently, soybean producer remuneration is based on quantity. However, a financial increase (premium) for the chemical composition of grain could enhance the quality of the products generated, ensuring greater profitability for farmers (Updaw et al., 1976; Stobaugh et al., 2018; Xing et al., 2018). The relationship between the environment and chemical composition of soybean grain thereby provides valuable information for soybean breeding programs that target grain quality to meet market demands. In summary, this study suggests that market demand could be supplied by soybean breeding efforts, crop management, and cultivar recommendations for growing regions in order to maximize oil and protein yields.

Material and Methods

Plant material and field experiments

Twenty-eight soybean cultivars available for cultivation in southern Brazil were evaluated (Table S1). These cultivars are recommended and they are representative for test locations. The field trials were conducted in the 2017/18 and 2018/19 crop seasons in six test locations, and combined in environments, classified as high (846–963 m asl) and low altitude (336–480 m asl) (Table 1). According to the Köppen climate classification (Alvares et al., 2013), high and low altitudes in this region are described as *Cfb* and *Cfa* climates, respectively.

The experimental design was a randomized complete block with three replications. The experimental plots consisted of four 5 m rows spaced 0.5 m apart, totaling 10 m², with a seed density of 34 plants m^{-2}. Cultural practices were performed in accordance with the technical recommendations for soybean crops (Embrapa, 2014).

Evaluated traits

Grain yield (GY, kg ha^{-1}) was assessed in the two central rows of each plot (5 m^2 area), with a grain moisture content of 13%. Thousand grain weight (TGW, g) was estimated using eight replications of 100 grains for each plot (BRASIL, 2009). The oil content (OIL, g kg^{-1}) and protein content (PROT, g kg^{-1}) were determined using a near-infrared reflectance spectroscopy (NIRS) model Perten® DA 7250. Oil yield (OILY, kg ha^{-1}) and protein yield (PROTY, kg ha^{-1}) were obtained from the products of GY and OIL, GY and PROT.

Statistical analysis

Graphical analysis of mean and stability was performed on all evaluated traits. All test locations and crop season were used to perform these analyses. The following parameters were used: data transformation (transform = 0, without transformation), data scale (scaling = 1, data scaled according to the standard deviation), data centering (centering = 2, focused on genotype + genotype × environment effects [G+GE]), singular value partition (SVP = 1, focusing on the genotype). The association analysis between traits and test locations was performed using the same parameters, except the singular value partition focused on the environment (SVP = 2). Mean and stability analysis was performed using the *gge()* function, and associations between traits and test locations were analyzed using the *gtb()* function, of the “metan” package (Olivoto and Lúcio, 2020) in R software (R Development Core Team, 2019).

Conclusions

The results showed that the environment affected the chemical composition of soybean grains. A high-altitude environment with low temperature promotes an increase of 6.15% in protein content. Low-altitude environments result in an increase of 5.58% in oil content. Furthermore, there was a positive effect of altitude on protein content and a negative effect on oil content. The cultivars NS 6006 IPRO (20) and NA 5909 RG (17) showed the best yield performance in high-altitude environments. At low altitudes, cultivars 50I52RSF IPRO (8) and NS 5445 IPRO (18) were superior. The cultivar 7166RSF IPRO exhibited excellent performance due to high oil yield in both high-and low-altitude environments.

Therefore, associations between the environment and chemical composition of soybean grain provide valuable information for developing direct breeding methods, and recommending cultivars and growing locations, in order to meet the demand of the oil and protein market.

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