CHAPTER

45

Drought and Heat Stress Effects on Soybean Fatty Acid Composition and Oil Stability

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CHAPTER POINTS

- Higher oleic acid and lower linoleic and lower linolenic fatty acids are desirable for oil stability, long shelf storage, and processing.
- Fatty acid profiling is significantly affected by genotype and environmental factors, especially drought and high heat.
- To ensure the stability of a desired fatty acid trait across environments, further research on genotype and environment interactions is needed.
- Breeders and biotechnology researchers continue to develop soybean with high levels of healthy oils such as oil with *trans*-fat free, reduced saturated fat soybean oil, and increased stability for food processing.
- Advances in genetic modifications continue, and soybeans with designed fatty acid profile in seed oil may dominate the market in the future.

INTRODUCTION

Soybean is a major source of vegetable oil in the world, and soybean oil represents 56% of world production (Soystat, 2008). Oil concentration in soybean seeds ranges from 8.3 to 28%, with a mean of 19.5% (Wilson, 2004). Soybean oil contains five major fatty acids, two saturated fatty acids (palmitic, C16:0; stearic, C18:0) and three unsaturated fatty acids (oleic, C18:1; linoleic, C18:2; linolenic C18:3). The concentration of saturated fatty acids in soybean oil ranges from 10–12% for palmitic acid and 3–5% for stearic acid. The concentration of unsaturated fatty acids in oil is about 24% for oleic acid, 54% for linoleic acid, and 8.0% for linolenic acid. Lower saturated fatty acids and higher unsaturated fatty acid contents are desirable for human health, although higher oleic acid and lower linolenic acids are desirable for oil stability, long shelf-storage, and processing because a higher concentration of oleic acid contributes to oxidative stability. An oxidation reaction with polyunsaturated fatty acids such as linoleic and linolenic acids occurs when they are exposed to oxygen, forming oxygenated species such as hydroperoxide and subsequent degraded products. The level of oil degradation depends on the fatty acid composition of the parent oil.

Soybean oil with higher linoleic and linolenic acid contents and lower oleic acid requires an additional industrial process, hydrogenation, to increase saturation and improve oil stability and utility properties. It is now known that the process of hydrogenation produces *trans*-fatty acids, as opposed to the naturally occurring *cis* fatty acids. *Trans*-fatty acids have negative effects on human health, increasing the risk of coronary heart disease and are associated with higher LDL-cholesterol and lower HDL-cholesterol (Federal Register, 2003). The partial hydrogenation converts polyunsaturated fatty acids such as linolenic acid to oleic and stearic acids, reducing polyunsaturated fatty acids to about 18% and linolenic acid to below 2% (Clemente and Cahoon, 2009). This has increased demand for low-linolenic soybean oil that allows food processors to reduce the need for hydrogenation, thus reducing *trans*-fatty acids from oil in foods.

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DROUGHT EFFECTS ON SEED OIL, FATTY ACID COMPOSITION, AND OIL STABILITY

Drought stress during seed-fill (R5-R6) stage can alter chemical composition of soybean seed, and severe drought can result in up to12.4% lower total oil (Dornbos and Mullen, 1992). These authors also indicated that drought stress increased stearic acid, but decreased oleic acid (Dornbos and Mullen, 1992), and the decrease or increase in oil may depend on the level of drought (Specht *et al.*, 2001). Lee *et al.* (2008) studied the effects of irrigation on elevated oleic acid, and/or reduced linolenic acid genotypes under field conditions. They found that irrigation did not significantly affect unsaturated fatty acid concentration in soybean genotypes with modified higher oleic acid and/or modified low linolenic acid. When comparing irrigated with non-irrigated soybean genotypes, Lee *et al.* (2008) indicated that oleic acid tended to increase and linolenic acid tended to decrease in genotypes with high oleic acid and low linolenic acid. They concluded that near optimum irrigation during the growing season could result in the highest levels of oleic acid and lowest levels of linolenic acid. Boydak *et al.* (2002) reported that cultivar Asgrow 3935 had higher linoleic acid and lower oleic acid when soybeans were irrigated every 12th day after emergence. Table 45.1 shows that seed of soybean varieties (maturity group MG IV) grown in drought stressed (−90 to −100 kPa soil water potential) conditions (Bellaloui *et al.*, 2011) had higher oil and oleic acid concentrations and lower linoleic and linolenic concentrations compared with irrigated soybeans (−15 to −20 kPa soil water potential). The alteration of fatty acids depended on genotype (Table 45.1) and MG (Figure 45.1). List *et al.* (1980) reported that poor quality oil, extracted from soybean seed damaged in the field or exposed to frost, heat, and moisture, resulted in low refining oil quality, poor refined-bleached color, lower flavor, and oxidative stability. In addition, drought caused shrinking and cracking, making dehulling much more difficult and less efficient for processing. For example, Brumm and Hurburgh (1990) reported that in the Midwest USA drought in 1988 resulted in soybeans with shriveled and wrinkled seed coats, and processors expressed concerns about the processing of the seed due to size and shape. Carrera *et al.* (2009) investigated the effect of water deficit on soybean seed protein, oil, and fatty acids during the reproductive period, and found that when precipitation minus potential evapotranspiration was less than 70 mm oil increased linearly with the increase of the average daily mean temperature during seed-fill and with increase in water deficit. They concluded that water stress during seed-fill stage is important due to its effects on the inverse relationship between oil and protein with temperature. Scherder *et al.* (2008) studied the stability of soybean lines with modified elevated oleic acid, combined with modified low saturated fatty acids, 1% linolenic acid, or both low saturates and 1% linolenic acid. They found, when these lines were grown in 11 environments (one in Missouri and four in Iowa, USA) in a 2-year experiment, that the mean oleic concentration was 590 g/kg in elevated oleic acid and low saturated fatty acid lines, 521 g/kg in elevated oleic acid and 1% linolenic acid lines, and 557 g/kg in elevated oleic acid and low saturated fatty acids and low linolenic acid lines, and 269 g/kg for conventional/normal cultivars. They found that the lines with the highest concentration of oleic acid generally had the most variation across environments, but the lines with the highest mean of oleic acid were most probably meeting or exceeding 500 g/kg across environments. Gao *et al.* (2009) evaluated the effect of precipitation on soybean oil and fatty acid composition, and found that oleic acid and linoleic acid contents were significantly affected by seasonal precipitation, but palmitic, stearic, and linolenic contents were relatively stable. They also found that oil quality ratio of oleic/(linoleic + linolenic) had

TABLE 45.1 Effect of Drought Stress Conditions (−90 to −100 kPa Soil Water Potential) on Soybean Seed Total Oil and Fatty Acids Composition (g/kg) in Genotypes of Maturity Group IV Under Greenhouse Conditions[a]

	Watered Soybean						Drought Stressed Soybean					
Variety	**Oil**	**C16:0**	**C18:0**	**C18: 1**	**C18: 2**	**C18: 3**	**Oil**	**C16: 0**	**C18: 0**	**C18: 1**	**C18: 2**	**C18: 3**
Hutcheson	209 c	124 a	43 a	244 b	556 b	69 b	238 ab	111 b	46 a	266 b	488 a	54 bc
DT97-4290	211 c	117 c	41 b	243 b	565 a	68 b	234 b	111 b	45 ab	267 b	468 b	52 c
AG 4403	218 b	118 c	43 a	247 ab	560 ab	67 b	239 a	120 a	43 b	280 a	482 a	57 a
AG 4903	225 a	121 b	44 a	251 a	536 c	74 a	239 a	118 a	38 c	278 a	457 b	57 a

Drought stress soybeans were grown at −90 to −100 kPa soil water stress and compared with watered soybean grown at field capacity at −15 to −20 kPa, according to Bellaloui *et al.*, (2011). Soybeans were grown under greenhouse conditions similar to those in Bellaloui *et al.* (2011). Values are means of four replicates. Values within columns sharing a letter are not significantly different ($P > 0.05$) using Fishers' test.

[a] *Seed composition analysis was conducted at harvest maturity (R8 stage) according to Bellaloui et al. (2009).*

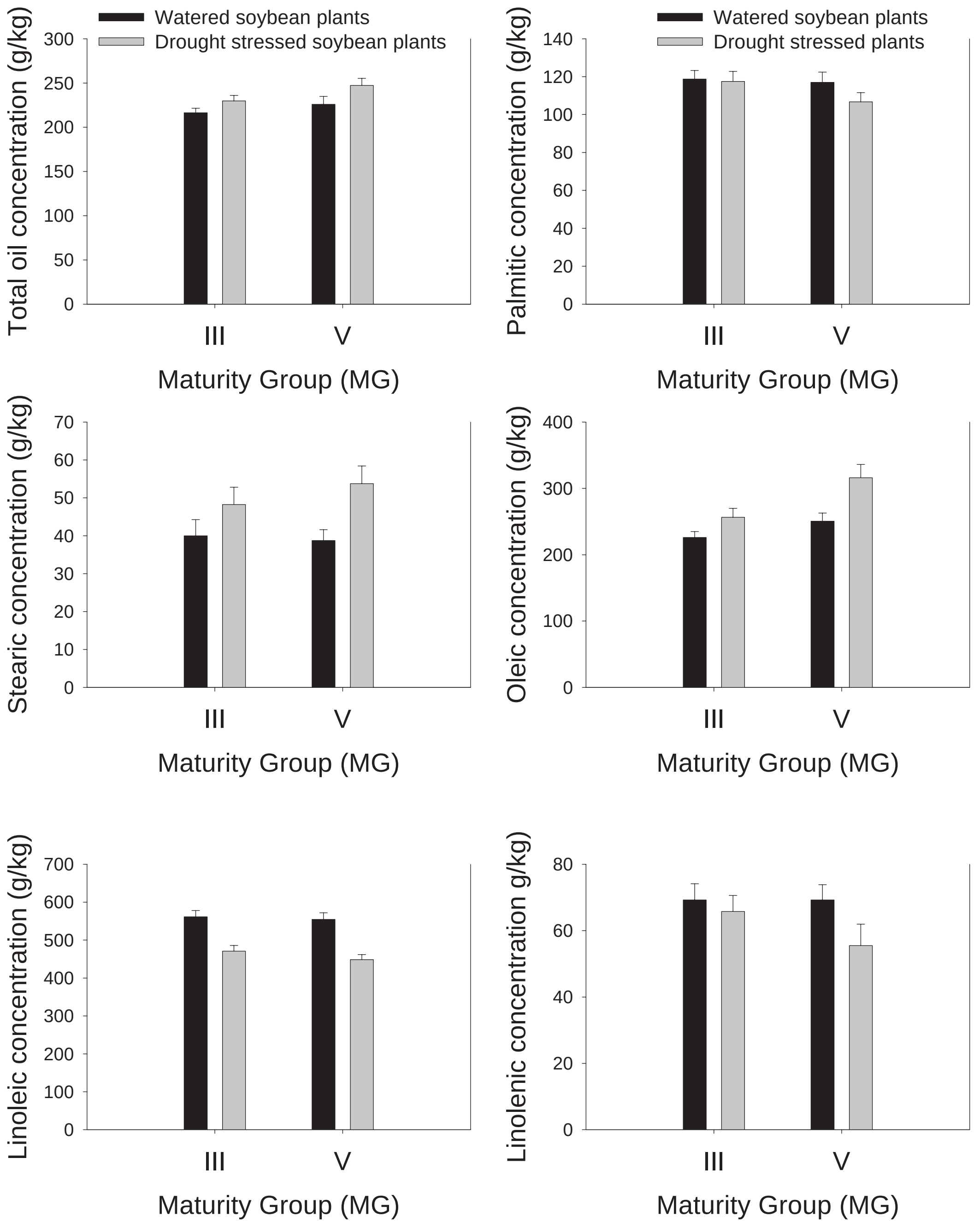

FIGURE 45.1 Effects of high temperature on oil composition in maturity group (MG) III and V soybean genotypes. The graph shows the alteration of oil composition by temperature "Unpublished." Values are mean of four replicates ± SE. Seed composition analyses were conducted on harvest maturity seed (R8 stage) according to Bellaloui *et al.* (2009).

a quadratic relationship with precipitation. These studies showed that drought decreases total oil (Dornbos and Mullen, 1992), alters fatty acid composition (Gao *et al.*, 2009), and affects oil stability and oil processing (Brumm and Hurburgh, 1990). Therefore, development of drought tolerant soybeans with stable high oleic and low linolenic acid genes across geographical locations is critical to maintain the stability of oil production and desirable fatty acid composition.

EFFECT OF HEAT STRESS ON TOTAL OIL, FATTY ACID COMPOSITION, AND OIL STABILITY

The wide range of oil concentration in soybean seed is due to genotype, the environmental factors under which soybeans grow, and geographic location. It was found that genetics and temperature during seed-fill stage (Oliva *et al.*, 2006; Bellaloui *et al.*, 2009) and drought

TABLE 45.2 Effect of Normal (25/20°C) and Warmer (26/28°C) Temperature on Soybean Seed Total Oil and Fatty Acids Composition (g/kg) in Genotypes of Maturity Group IV Under Growth Chamber Conditions[a]

	25/20°C						36/28°C					
Variety	**Oil**	**C16:0**	**C18:0**	**C18:1**	**C18:2**	**C18:3**	**Oil**	**C16:0**	**C18:0**	**C18:1**	**C18:2**	**C18:3**
Hutcheson	195 c	125 b	39 bc	213 a	561 a	80 b	233 b	114 b	44 a	268 b	461 b	50 c
DT97-4290	205 a	126 a	43 a	218 a	482 c	76 c	245 a	113 b	44 a	306 a	482 a	45 d
AG 4403	198 bc	114 c	40 b	213 a	545 b	75 c	242 a	119 a	35 c	276 b	476 ab	55 b
AG 4903	201 ab	114 c	38 c	201 b	560 a	87 a	242 a	117 a	39 b	278 b	472 ab	61 a

In heat stress experiments, soybean genotypes were grown under growth chamber conditions with photon flux density of about 1000 µmol•m^{-2}•s^{-1}, supplied with a combination of 10 high pressure sodium and metal halide lights, each of 400 W. Values are means of four replicates. Values within columns sharing a letter are not significantly different (P > 0.05) using Fishers' test.

[a]*Seed composition analysis was conducted at harvest maturity (R8 stage) according to* Bellaloui et al. (2009).

(Bellaloui *et al.*, 2011) play a major role in oil deposition and oil composition. Previous research has shown that concentrations of linoleic and linolenic acids in soybean seed developed under higher temperature decreased, but oleic acid concentrations increased (Dornbos and Mullen, 1992). Oliva *et al.* (2006) studied the effects of average temperature over the final 30 days of the reproductive period on oleic and linolenic acids in 17 normal and modified fatty acid genotypes across 10 environments. They found that the concentration of oleic acid in modified mid-oleic genotypes were less stable than in those of reduced oleic acid, but found mid-oleic (50–60% oleic acid) lines, N98-4445A and N97-3363-4 with stability coefficients of 3.28 and 2.53, respectively, were the most unstable genotypes, and the elevated oleic acid line M23 (up to 80% oleic acid) was the most stable (stability coefficient of 0.13). Conversely, studying the stability of linolenic acid concentration in reduced linolenic acid genotype IA 3017 (a line with 1% linolenic acid), Oliva *et al.* (2006) found that linolenic concentration was the most stable across environments, and the higher linolenic acid genotypes were less stable. They concluded that soybean lines with stable oleic acid and linolenic acid across environments could be used as a source of crops with desirable fatty acids composition. In an experiment, where normal (Century cultivar) and low-linolenic soybean genotypes (C1640 and 9509: genotypes differ in linolenic acid due to alleles at the fan locus), Wilcox and Cavins (1992) found that palmitic acid concentration tended to decrease and stearic acid tended to increase with later planting, and linolenic acid was more sensitive to this change than other fatty acids due to temperature changes coinciding with late planting.

Howell and Collins (1957) found that linolenic acid concentration decreased from 105 to 66 g/kg as daytime temperatures in the greenhouse increased from 21 to 29°C. Linolenic acid decreased from 164 to 50 g/kg, linoleic acid decreased from 558 to 403 g/kg, and oleic acid increased from 131 to 387 g/kg as day/night temperature increased from 18/13 to 33/28°C (Wolf *et al.*, 1982). There were no changes in palmitic and stearic acids with temperature changes (Wolf *et al.*, 1982). Our research showed that seed of similar and different MGs, with different genotypes grown at normal (25/20°C, day/night) and at warmer temperature (36/28°C) had higher total oil and oleic acid concentrations and lower linoleic and linolenic concentrations at warmer temperature compared with those grown at normal temperatures (Table 45.2; Figure 45.2). Therefore, alteration of fatty acids depended on both MG and genotype (Table 45.2; Figure 45.2). Rennie and Tanner (1989) evaluated fatty acid concentration in five low-linolenic acid lines, and found at day/night temperatures ranging from 15/12 to 40/30°C, a decrease in linoleic and linolenic acids, increase in oleic acid, and relatively stable palmitic and stearic acid concentrations in the five lines. It was also reported that growing soybean cultivars near the northern range of their adaptation resulted in 10 to 20 g/kg higher linolenic acid concentration and 30 to 60 g/kg higher linoleic acid than those grown at the southern range of their adaptation (Collins and Sedgewick, 1959), reflecting influences of temperature and geographical location.

The instability of conventional cultivars and mid-oleic acid germplasm across environment created a challenge, mainly due to temperature changes that influence the enzymes controlling biosynthesis of soybean seed fatty acids, especially at seed-fill stage (Wilcox and Cavins, 1992; Bachlava and Cardinal, 2009). The explanations of the effects of temperature on oleic and linolenic acid were that temperature may affect oleate and linoleate desaturases (Burton, 1991), decrease oleyl and linoleyl desaturase activities at 35°C (Cheesbrough, 1989), and ω-6 desaturase enzyme, encoded by the FAD2-1A gene, was degraded at high growth temperatures of 30°C (Tang *et al.*, 2005). Studying the transcript level of the functional GmFAD2 isoforms, FAD2-1A, FAD2-1B, FAD2-2B, and FAD2-2C, Schlueter *et al.* (2007) found that only significant increase in expression was observed in FAD2-2C when soybean was grown at 18/12°C day/night during the pod development stage. Upchurch and Ramirez (2010)

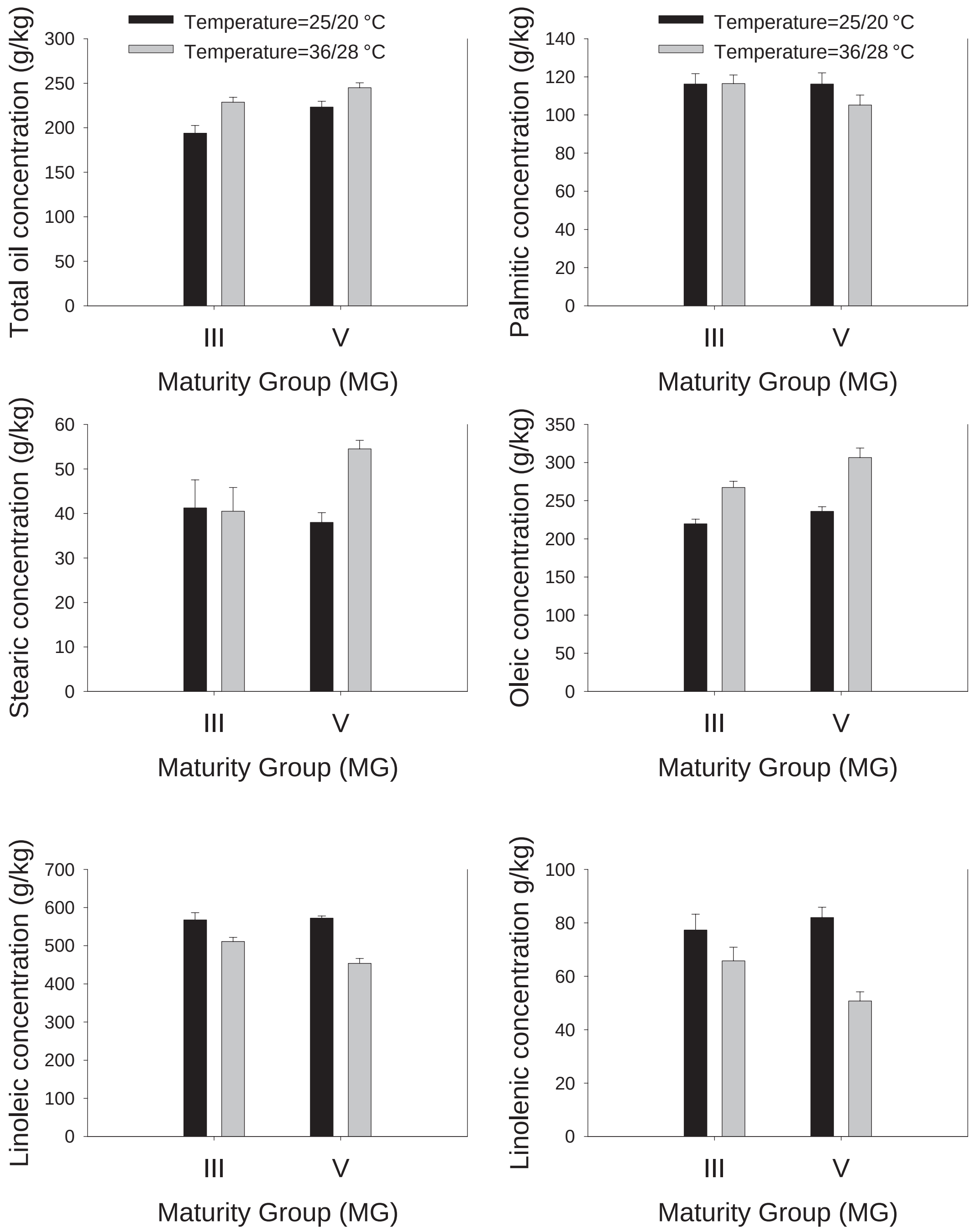

FIGURE 45.2 Effects of drought stress on oil composition in maturity group (MG) III and V soybean genotypes. The graph shows the drought stress (−90 to −100 kPa soil water potential) effects on total oil and fatty acids composition "Unpublished." Watered soybeans were grown under field capacity conditions (−15 to −20 kPa soil water potential). Values are mean of four replicates ± SE. Soybeans were grown according to Bellaloui *et al.* (2011). Seed composition analyses were conducted on harvest maturity seed stage (R8) according to Bellaloui *et al.* (2009).

studied the expression levels of ω-6 desaturase GmFAD2 genes and genes that determine seed oleic acid concentration in modified mid-oleic acid soybean mutant M23 (a deletion of GmFAD2-1A, an allele of the microsomal ω-6 oleate desaturase gene) with 50–60% oleate. They found that there were lower expressions of GmFATB1a, GmFAD2-1A, GmFAD2-1B, GmFAD2-2, and GmFAD2-3 and higher expression of GmSACPD-C. They suggested that several soybean genomic loci known or suspected could be involved in oleic acid phenotype, and some may encode genes involved in regulation of oleate biosynthetic genes.

Pham *et al.* (2010), through their breeding program, were able to create and identify high oleic acid trait of

80% oleic acid concentration in soybeans seed by identifying and combining mutations in two delta-twelve fatty acid desaturase genes, FAD2-1A and FAD2-1B. They found three polymorphisms in the FAD2-1B alleles of two soybean lines. The mutant FAD2-1B alleles were associated with an increase in oleic acid concentration, but the FAD2-1B mutant alleles alone could not produce high oleic unless the existing FAD2-1A mutations were combined with the novel mutant FAD2-1B alleles. This combined mutation resulted in high (80%) oleic acid that was recovered only for lines which were homozygous for both of the mutant alleles. The developed conventional soybean lines with 80% oleic acid were stable in two production environments (Lee *et al.*, 2012). Therefore, heat stress is a major environmental factor that affects total oil and alters fatty acid composition. Further research is needed to establish that non-GMO or GMO soybeans with desirable fatty acid composition do not compromise production and other seed quality traits across environments and geographic locations.

GENOTYPE × DROUGHT × HEAT STRESS INTERACTIONS ON OIL QUALITY AND STABILITY

The effects of genotype × environment interactions on total oil and fatty acids are major concerns because of their influence on oil level and fatty acid composition. Although seed oil level and composition are genetically controlled, environment plays a major role in altering the level and composition of oils. Since drought and temperature are major environmental factors altering seed oil level and composition, we will discuss the environment effects in the context of drought and temperature and how drought and temperature interact with genotype or maturity group (MG). The effect of environment on seed composition has been extensively studied (Piper and Boote, 1999; Dardanelli *et al.*, 2006). However, the reasons for the variability of oil under different environments are still not completely understood. Hou *et al.* (2006) evaluated fatty acids composition in a recombinant inbred line (RILs) population, developed from a cross between a modified low palmitic acid line and a high stearic acid parent. They conducted this experiment for two years and in three environments in Canada, and found that linolenic acid was more sensitive to the environment, and year effects were greater than the effects of location in palmitic, stearic, and oleic acid concentration. However, location was more important for the relative concentrations of linoleic, and linolenic acids. Dardanelli *et al.* (2006) evaluated oil level in six MG (II–III, IV, V, VI, VII, VIII–IX) in 14 to 24 environments from 2000–2003 in Argentina, using water deficit and temperature data from 1970–2003 for each location. They found that the oil variations among environments depended mainly on MG, and showed that oil concentrations were higher in MG II, III, and IV in every environment than in other groups in every environment, suggesting broad adaptations of early MG, and that high temperature during seed-fill could explain the consistent pattern of higher oil concentration across seasons and environments in early MGs. Another example of the environmental and geographical influences on oil concentration in soybean seed is that oil concentration in the northern and western growing area in the USA is greater than in those of southern USA (Hurburgh *et al.*, 1990), which is the opposite trend of seed protein due to the inverse relationship between oil and protein (Dornbos and Mullen, 1992; Bellaloui *et al.*, 2009). This suggests that oil level and its composition can be altered by protein also.

Serretti (1993) reported that oil concentration increased 6.7 g/kg/°C with the increase of mean temperature, and Kane *et al.* (1997) found that oil concentration increased 5.2–6.6 g/kg/°C among six cultivars. In growth chamber and greenhouse experiments, Gibson and Mullen (1996) and Dornbos and Mullen (1992) found that oil concentration increased with increasing temperature with an optimum at 25–28°C, above which the oil concentration declined. It was concluded that oil concentration increased linearly with the increase of mean temperature (Gibson and Mullen, 1996; Wolf *et al.*, 1982). Recently, Bellaloui *et al.* (2009) investigated the effect of genotypic background and environment and their interactions on seed oil in two sets of near isogenic lines (Clark and Harosoy isolines), where each set has the same genotypic background, but differ in maturity genes. Clark (e1 E2 E3 e5) and Harosoy (e1 e2 E3 e5) are different only in the E2/e2 locus for the maturity genes. Bellaloui *et al.* (2009) found that year, maturity, and year × maturity interactions were significant ($P < 0.0001$) for seed oil in the Clark isoline set, but in the Harosoy isoline set there was no year × maturity effect for oil, suggesting that the response of the two genotypic backgrounds to the environmental factors in each growing season was different. They also found that E-gene (maturity genes), E-gene × genotypic background, and E-gene × year were the major contributors to oil variability. The physiological and biochemical mechanisms of how these variables interact with each other and their effects on seed composition are still not understood (Bellaloui *et al.*, 2009).

ALTERED SOYBEAN FATTY ACIDS AND OIL ON THE HORIZON

Private and public sectors have been conducting intensive research to develop soybean with desirable fatty acids profile. Pioneer, a DuPont company, is developing soybean using accelerated yield technology under the brand Plenish™ with high oleic acid, low linolenic acid, less saturated fat, and high monounsaturated fat compared to commodity soybean oil. The Plenish™ high oleic soybean oil has zero *trans*-fat with high stability for extended high temperature use with nutritional benefits. The Plenish™ high oleic soybean is currently in the field and oil testing phase and was projected for a limited launch in 2012 (Pioneer, 2012). Monsanto has developed through traditional breeding techniques and launched Vistive® low linolenic soybean with low levels of linolenic acid and low *trans*-fat in processed oil which increase shelf life and flavor stability in processed foods. Monsanto is currently developing Vistive® Gold soybeans with *trans*-fat free and reduced saturated fat soybean oil with increased stability for food processing. The ultra-low linolenic acid (1%) non-GMO varieties IA2096, IA2097, IA3042, and Roundup Ready variety A2098RR, and low non-GMO saturated fatty acids varieties IA1024 and IA2095, were also developed (Warner and Fehr, 2008; Healthier Soybean Oils, 2008). Monsanto is also developing stearidonic acid (SDA) ω-3 soybeans rich with SDA, which the body converts to heart-healthy 1 eicosapentaenoic acid (EPA), one of the three ω-3 fatty acids used by the body. Both Vistive Gold and SDA ω-3 soybeans are developed through biotechnology and are currently in phase IV of the research and development pipeline, and are not commercially available yet (Monsanto, 2012). As advances in genetic modifications continue, it is more than likely that soybeans with designed fatty acid profile in seed oil could dominate the market in the future.

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References

Bachlava, E., Cardinal, A.J., 2009. Correlation between temperature and oleic acid seed content in three segregating soybean populations. Crop Sci. 49, 1328–1335.

Bellaloui, N., 2011. Effect of water stress and foliar boron application on seed protein oil fatty acids and nitrogen metabolism in soybean. Amer. J. Plant Sci. 2, 692–701.

Bellaloui, N., Smith, J.R., Ray, J.D., Gillen, A.M., 2009. Effect of maturity on seed composition in the early soybean production system as measured on near-isogenic soybean lines. Crop Sci. 49, 608–620.

Boydak, E., Alpaslan, M., Hayta, M., Gercek, S., Simsek, M., 2002. Seed composition of soybeans grown in the Harran region of Turkey as affected by row spacing and irrigation. J. Agric. Food. Chem. 50, 4718–4720.

Brumm, T.J., Hurburgh, C.R., Johnson, L.A., 1990. Cracking and dehulling shriveled and wrinkled soybeans. J. Am. Oil Chem. Soc. 67, 750–756.

Burton, J.W., 1991. Recent developments in breeding soybeans for improved oil quality. Fat Sci. Technol 93, 121–128.

Carrera, C., Martínez, M.J., Dardanelli, J., Balzarini, M., 2009. Water deficit effect on the relationship between temperatures during the seed fill period and soybean seed oil and protein concentrations. Crop Sci. 49, 990–998.

Cheesbrough, T.M., 1989. Changes in the enzymes for fatty acid synthesis and desaturation during acclimation of developing soybean seeds to altered growth temperature. Plant Physiol. 90, 760–764.

Clemente, T.E., Cahoon, E.B., 2009. Soybean oil: genetic approaches for modification of functionality and total content. Plant Physiol. 151, 1030–1040.

Collins, F.I., Sedgwick, V.E., 1959. Fatty acid composition of several varieties of soybeans. J. Am. Oil Chem. Soc. 36, 641–644.

Dardanelli, J.L., Balzarini, M., Martinez, M.J., Cuniberti, M., Resnik, S., Ramunda, S.F., Herrero, R., Baigorri, H., 2006. Soybean maturity groups, environments, and their interaction define mega-environments for seed composition in Argentina. Crop Sci. 46, 1939–1947.

Dornbos Jr., D.L., Mullen, R.E., 1992. Soybean seed protein and oil contents and fatty-acid composition adjustments by drought and temperature. J. Am. Oil Chem. Soc. 69, 228–231.

Federal Register-68 FR 41433 July 11, 2003. Food labeling; trans fatty acids in nutrition labeling, consumer research to consider nutrient content and health claims and possible footnote or disclosure statements; final rule and proposed rule. Verified on October 7, 2012. http://www.fda.gov/food/labelingnutrition/labelclaims/nutrientcontentclaims/ucm110179.htm.

Gao, J., Hao, X., Thelen, K.D., Robertson, G.P., 2009. Agronomic management system and precipitation effects on soybean oil and fatty acid profiles. Crop Sci. 49, 1049–1057.

Gibson, L.R., Mullen, R.E., 1996. Soybean seed composition under high day and night growth temperatures. Ibid 73, 733–737.

Healthier Soybean Oils, Iwoa State University, 2008. Verified on October 12, 2012 , http://www.notrans.iastate.edu/.

Hou, G., Ablett, G.R., Pauls, K.P., Rajcan, I., 2006. Environmental effects on fatty acid levels in soybean seed oil. J. Am. Oil Chem. Soc 83, 759–763.

Howell, R.W., Collins, F.I., 1957. Factors affecting linolenic and linoleic acid content of soybean oil. Agron. J. 49, 593–597.

Hurburgh, C.R., Brumm, T.J., Guin, J.M., Hartwig, R.A., 1990. Protein and oil patterns in U.S. and world soybean markets. J. Am. Oil Chem. Soc. 67, 966–973.

Kane, M.V., Steele, C.C., Grabau, L.J., MacKown, C.T., Hildebrand, D.F., 1997. Early-maturing soybean cropping system: III. protein and oil contents and oil composition. Agron. J. 89, 464–469.

Lee, J.D., Bilyeu, K.D., Pantalone, V.R., Gillen, M.G., So, Y.S., Shannon, J. G, 2012. Environmental stability of oleic acid concentration in seed oil for soybean lines with *FAD2-1A* and *FAD2-1B* mutant genes. Crop Sci. 52, 1290–1297.

Lee, J.D., Oliva2, M.L., Sleper, D.A., Shannon, J.G., 2008. Irrigation has little effect on unsaturated fatty acid content in soya bean seed oil within genotypes differing in fatty acid profile. J. Agron. Crop Sci. 194, 320–324.

List, G.R., Erickson, D.R., Pryde, E.H., Brekke, O.L., Mounts, T.L., Falb, R.A., 1980. Handbook of soy oil processing and utilization. AOCS Press, Champaign, Illinois 267–354.

Company, Monsanto, 2012. Soybean seeds. Available. Verified on October 18, 2012. http://www.monsanto.com/products/Pages/soybean-seeds.aspx.

Oliva, M.L., Shannon, J.G., Sleper, D.A., Ellersieck, M.R., Cardinal, A.J., Paris, R.L., Lee, J.D., 2006. Stability of fatty acid profile in soybean genotypes with modified seed oil composition. Crop Sci. 46, 2069–2075.

Pham, A.T., Lee, J.D., Shannon, J.G., Bilyeu, K.D., 2010. Mutant alleles of FAD2-1A and FAD2-1B combine to produce soybeans with the high oleic acid seed oil trait. BMC Plant Biol. 10, 195.

Pioneer, 2012. Plenish™ high oleic soybeans. Available. Verified on October 18, 2012. http://www.pioneer.com/home/site/about/products/product-traits-technology/plenish/.

Piper, E.L., Boote, K.J., 1999. Temperature and cultivar effects on soybean seed oil and protein concentrations. J. Am. Oil Chem. Soc. 76, 1233–1242.

Rennie, B.D., Tanner, I.W., 1989. Fatty acid composition of oil from soybean seeds grown at extreme temperatures. J. Am. Oil Chem. Soc. 66, 1622–1624.

Scherder, C.W., Fehr, W.R., Shannon, J.G., 2008. Stability of oleate content in soybean lines derived from M23. Crop Sci. 48, 1749–1754.

Schlueter, J.A., Vasylenko-Sanders, I.F., Deshpande, S., Yi, J., Siegfried, M., Roe, B.A., Schlueter, S.D., Scheffler, B.E., Shoemaker, R.C., 2007. The FAD2 gene family of soybean: Insights into the structural and functional divergence of a paleopolyploid genome. Crop Sci. 47, S14–S26.

Seed Today, 2012. Pioneer is positive about Plenish™ high oleic soybeans. Verified on 10/11/2012. http://www.seedtoday.com/articles/Pioneer__Is_Positive_About_Plenish_trade__High_Oleic_Soybeans-119615.html.

Serretti, C., 1993. Influence of high protein, genotype, and environment on protein quality of soybean. Master's Thesis. Kansas State University, Manhattan, Kansas.

Soystat, 2008. World soybean production 2007. United Soybean Board. Available at. Verified on 10/8/2012. http://www.soystats.com/2008/Default-frames.htm.

Specht, J.E., Chase, K., Macrander, M., Graef, G.L., Chung, J., Markwell, J.P., Orf, H.H., Lark, K.G., 2001. Soybean response to water: a QTL analysis of drought tolerance. Crop Sci. 41, 493–509.

Tang, G.Q., Novitzky, W.P., Griffin, H.C., Huber, S.C., Dewey, R.E., 2005. Oleate desaturase enzymes of soybean: Evidence of regulation through differential stability and phosphorylation. Plant J. 44, 433–446.

Upchurch, R.G., Ramirez, M.E., 2010. Gene expression profiles of soybeans with mid-oleic acid seed phenotype. J. Am. Oil Chem. Soc. 87, 857–864.

Warner, K., Fehr, W., 2008. Mid-oleic/ultra low linolenic acid soybean oil: A healthful new alternative to hydrogenated oil for frying. J. Am. Oil. Chem. Soc. 85, 945–951.

Wilcox, J.R., Cavins, J.F., 1992. Normal and low linolenic acid soybean strains: Response to planting date. Crop Sci. 32, 1248–1251.

Wilson, R.F., 2004. Seed composition. In: Boerma, H.R., Specht, J.E. (Eds.), Soybeans: Improvement, Production, and Uses. ASA Monogr. 16. ASA, Madison, WI, pp. 621–669.

Wolf, R.B., Cavins, J.F., Kleiman, R., Black, L.T., 1982. Effect of temperature on soybean seed constituents: Oil, protein, moisture, fatty acids, amino acids and sugars. J. Am. Oil Chem. Soc. 59, 230–232.