RESEARCH ARTICLE

Extending the range of an ancient crop, *Salvia hispanica* L.—a new ω3 source

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Abstract Chia, *Salvia hispanica* L., was well
developed into a cultivated crop and an important
component of Mesoamerican cultures and nutrition.
Early Mesoamerican breeders produced lines with
well developed agronomic characteristics including
good, uniform seed yield and retention. Seed reten-
tion in particular is disadvantageous for survival in
the wild. Maize, beans and squash were developed
into important crops concomitant with chia in Mes-
oamerica but unlike these other crops lack of
photoperiodic variability in floral induction limited
the spread of chia cultivation into North America.
There has been renewed interest in chia as an
excellent source of ω3 fatty acids and dietary fiber
for healthy diets. Such highly unsaturated oils also
are useful starting materials for many renewable
chemicals. Further we find chia grows very well in
Midwestern and Eastern USA but flowers too late in
the season for seeds to mature before killing frosts.
We set out to develop the genetic diversity in floral
induction to provide germplasm for production in the
US and other temperate areas of the world. We
demonstrate that new early flowering lines are able to
flower under a photoperiod of 15 h under greenhouse
conditions. In field conditions, some selected new
lines flowered at a photoperiod of 14 h and 41 min
during the 2009 growing season in Kentucky and can
produce seeds in a range of environments in temper-
ate areas.

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Introduction

Chia, *Salvia hispanica* L., has long been cultivated
and domesticated (Cahill and Ehdaie 2005). It was
widely used in pre-Columbian Mesoamerica as a
major commodity and its seeds were valued for food,
medicine and oil. Cultivation of chia was drastically
reduced after Spanish colonization due to cultural

conflicts. Chia has recently been revived as a new crop particularly due to its high oil and highest ω-3 fatty acid content among productive oilseeds (Cahill 2003; Cahill 2004). Chia also may be the best source of healthful fiber known (Ayerza 1995; Cahill 2003).

Mesoamerica is one of the main centers of crop domestication providing maize, common beans and squash among other important crop plants. Cultivation of maize (Buckler, et al. 2009), common beans and squash was spread over much of North America in pre-Columbian times. Two hypotheses are related to plant domestication pattern and process: 1) Photoperiodic sensitivity constrained the diversity of cultivated chia (Salvia hispanica L.) to its center of origin of domestication; and 2) Altering photoperiod sensitivity has been a successful strategy in expanding patterns of dispersal of Mesoamerica crops to temperate regions in part due to the syndrome of traits that resulted from the Mesoamerican plant domestication process.

The historic patterns of dispersal of domesticated chia in Mesoamerica are obscured by the association of chia by pre-Columbian cultures with the food of warriors and others who traveled. For example, in 1581, Fray Diego Duran wrote of numerous instances of chia seeds being moved in times of war and forced migrations (Duran 1994). A significant portion of the pre-Columbian Mesoamerican diet constituted seeds of the domesticated crop plant chia (Harvey 1991; Rojas-Rabiela 1988). Figure 1 shows the historic geography of chia cultivation and dispersal in pre-Columbian Mesoamerica based on ethnohistorical data from Aztec tribute records, colonial cultivation records, and linguistics. Aztec tribute records include the 'Matricula de los Tributos' believed to be pre-contact and the 'Codex Mendoza' of 1541 both of which detail the amount of tribute including chia seeds and chia flour paid to the Aztec capital from throughout the empire (Berdan and Anawalt 1996; Durand-Forest 1980). More regionally specific manuscripts such as the 'Matricula de Huexotzinco' of 1,560 confirm the levels of chia tribute and offer more geographic specificity on within province chia production (Perm and Carrasco 1974). The majority of provinces contributed chia with the exception of provinces restricted to lowland coastal tropics or deserts. Chia production during the early Spanish colonial period declined in quantity, however the scope of geography of cultivation was maintained

according to analyses of chia cultivation records (Acuña 1986). Domesticated populations in Guatemala exhibit genetic and phenotypic similarity to domesticated and wild populations in Mexico and do not differ in photoperiodic sensitivity (Cahill 2004). The range of cultivation is contiguous with Mexico. Populations of domesticated chia in Nicaragaua exhibit a unique photoperiodic sensitivity of later flowering and likely represent a pre-Columbian dispersal from Mexico. Such domesticates are well beyond the range of wild chia and exhibit genetic and phenotypic similarity to domesticated populations in Mexico (Cahill 2004). According to Bolaños, Salvia hispanica had medicinal uses in pre-Columbian Nicaragua and was known by the common name "chia" in Pipil, an indigenous language (Bolaños 1974). The common name "chia" or "chian" was also used for S. hispanica in the Nahuatl language spoken by the Aztecs and the Spanish later applied the name to other species with similar uses throughout New Spain (Molina 1970; Sandoval 1989). Salvia hispanica is not known as chia in any other indigenous languages of Central America and many of the indigenous languages of western Mexico. Nahuatl and Pipil languages are both derived from Proto-Yutoaztecan, and began segregating with the well documented migration of the Pipil people and language from Central Mexico to Nicaragua around 800 A.D. (Léon-Portilla 1996). Although the timing of dispersal of domesticated chia to Nicaragua is obscured, these populations likely represent a pre-Columbian dispersal beyond the center of diversity and the only known example of divergence in photoperiodic sensitivity (Fig. 1).

While photoperiod insensitivity may be the most essential trait for expansion of dispersal, domestication syndrome traits also facilitate successful expansion beyond the Mesoamerican center of crop diversity. Chia is no exception exhibiting the results of human selection for, among other traits: yield components, vigor, plant architecture, uniform maturation, and non-shattering, the latter achieved by calyxes that remain closed at seed maturity effectively eliminating natural dispersal and confining domesticated varieties to human cultivation (Cahill 2005).

Chia is a short-day flowering plant. It is cultivated in Argentina, Australia, Bolivia, Colombia, Guatemala, Mexico and Peru. Chia has also been reportedly cultivated in Southeast Asia and naturalized in the

Fig. 1 Chia cultivation and dispersal. The area shaded in *blue* represents the traditional area of chia cultivation from N. central Mexico into Guatemala. A second apparently pre-Columbian cultivation area is known in southern Honduras and Nicaragua (*green*). The areas shaded in *yellow* indicate areas in which traditional chia lines can be grown in the US (with irrigation). The area in red represents areas where the new early flowering chia genotypes reported herein could be grown for seed production
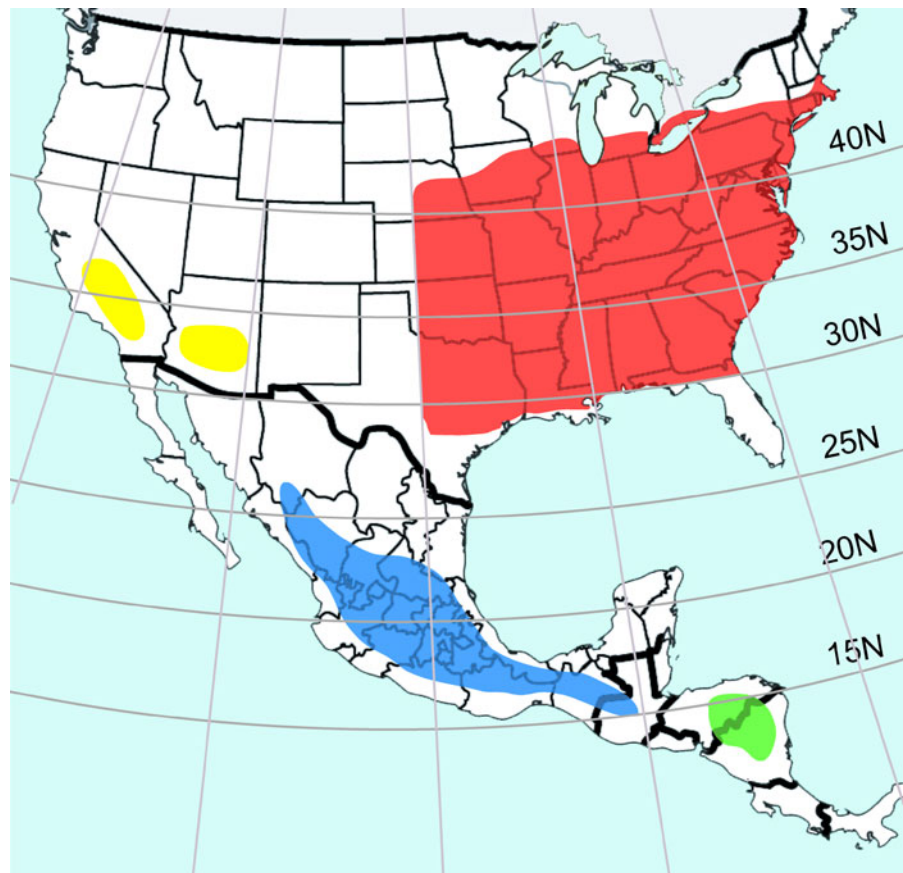
Caribbean (Epling 1940; Jansen et al. 1991; Perry and Metzger 1980). At higher latitudes such as Choele-Choele (39°11′S) Argentina and Tucson (32°14′N), Arizona, USA, the plant cannot produce seeds since it is killed by frost before flowers set (Ayerza and Coates 2005). Chia grows well in Kentucky and has low requirement for pesticides, fertilizer and irrigation. It produces flower buds in short days of October and is killed by frost before seeds set. Seed production cannot be attained in most areas of North America. As there was no source of natural long day chia available we set out to develop such early flowering chia germplasm.

Materials and methods

Mutagenesis

S. hispanica cv. 'Pinta' seeds were soaked in EMS solutions for 6 h at room temperature with shaking.

For gamma radiation seed samples were treated with 500 Gy.

Screening for early flowering mutants

In order to screen for early flowering or long-day mutants, M_2 seeds were planted in bulk in the field of Spindletop farm in Lexington, KY (38°1′47″N, 84°29′41″W, 298 m above sea level). There were 209 plots of M_2 EMS-mutagenized plants, 232 plots of M_2 gamma-mutagenized plants and 11 plots of non-mutagenized plants. Early flowering plants were transferred to a greenhouse before the killing frost on the third week of October. Early flowering plant M_3 seeds were collected.

Floral induction study

M_3 seedlings were grown under a photoperiod of 14.5 h until having at least six nodes. Daylengths were then set to 12, 13, 14 and 15 h with

approximately the same daily light irradiance integral. Each light treatment contained 16 experimental units. One experimental unit consisted of six M_3 plants from one M_2 line. Each experimental unit was randomized for a placement in a light treatment. Because irradiance can impact flowering in several *Salvia* species (Mattson and Erwin 2005) the floral induction experiment with chia held total daily light integrals nearly the same by covering all plants after 12 h of daylight and the daylength was only varied with incandescent bulbs under the covering.

Forty M_3 full sib families (20 EMS mutagenized lines and 20 gamma mutagenized lines) from self-pollinated M_2 plants were planted in the field in Lexington, KY on May 20 2009 when the day length was 14 h and 43 min.

Results and discussion

The geography of the genetic and phenotypic diversity of both wild and domesticated populations of chia encompasses the semi-temperate and temperate highlands of western Mexico and eastward across the trans-volcanic belt to Puebla, generally between 1,400 and 2,200 m.s.n.m. (Cahill 2004; Hernández Gómez and Miranda Colín 2008; Miranda 1978). In general, the domesticated chia variety 'Pinta' now dominates cultivation with only a few rare interspersed domesticated populations that exhibit human selected traits to a lesser degree (Cahill 2005). Domesticated chia germplasm has a floral induction photoperiod of about 12 h (Table 1), so in the northern hemisphere, chia begins flowering in

Table 1 Flowering of different M_3 mutant lines under different photoperiods compared to non-mutagenized plants

L	TM	SC	Photoperiod											
			12 hours			13 hours			14 hours			15 hours		
			3W	4W	5W	3W	4W	5W	3W	4W	5W	3W	4W	5W
A	NMF	C			❀									
B	NMR	C			❀			❀						
C	NMR	W			❀			❀						
D	EMS	C	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀
E	EMS	C	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀
F	EMS	C		❀	❀		❀	❀			❀			
G	EMS	C	❀	❀	❀	❀	❀	❀		❀	❀		❀	❀
H	EMS	W	❀	❀	❀	❀	❀	❀		❀	❀		❀	❀
I	EMS	W	❀	❀	❀	❀	❀	❀	❀	❀	❀			❀
J	γ	C	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀
K	γ	C	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀
L	γ	C	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀
M	γ	C	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀
N	γ	C	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀
O	γ	W	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀
P	γ	W	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀	❀

L: line; TM: type of mutagenesis; NMF: non-mutagenized family; NMR: non-mutagenized plants from random seeds; EMS: EMS-mutagenized line; γ: gamma ray-mutagenized line; SC: seed coat color; C: charcoal seed coat; W: white seed coat; 3W: at the third week of induction; 4W: at the fourth week of induction; 5W: at the fifth week of induction; ❀: flowering

October. Wild populations do not significantly deviate. Chia germplasm competent to flower under long day conditions is unknown among diversity of collected domesticated and wild populations. The one outlier is domesticated populations from Nicaragua that have a floral induction photoperiod of about 10.5 h and lack the uniformity in maturity present in wild and domesticated material from Mexico (Cahill 2005). There is high phenotypic similarity with respect to traits associated with domestication such as non-shattering and large seeds, however the Nicaraguan populations are generally more adapted to tropical biomes having increased calyx pubescence to repel moisture and protect mature seed as well as greater fungal tolerance. Otherwise, these populations exhibit high phenotypic and genetic similarity to domesticated populations from western and central Mexico (Cahill 2004, 2005). The geographic boundaries of patterns of diversity for domesticated chia across its traditional range in Mesoamerican are in large part defined by photoperiodic sensitivity. The northern boundary is limited by the lack of long day flowering types necessary for maturity of seeds prior to frost, whereas human selection for later flowering enabled the expansion of the southern boundary into tropical areas where the growing season extends longer into short days. Although genetic and phenotypic patterns of diversity for domesticated chia are centered in Mexico, the pattern of diversity in photoperiodic sensitivity instead correlates more to the pattern of dispersal.

Efforts to breed for chia a floral induction photoperiod of longer than 12 h utilizing parents with maximum genetic distance and very slight variation in photoperiodic sensitivity failed (Cahill unpublished data). The development of multiple chia lines through chemical mutagenesis characterized herein as flowering under long day photoperiods of about 12–15 h has significant potential to expand the range of production to regions with shorter growing seasons as shown in Fig. 1. Breaking the barrier of photoperiodic sensitivity and the agronomic advantage of existing domesticated traits makes chia a strong candidate for crop introduction beyond its Mesoamerican origin.

The patterns of dispersal of chia have analogies with those of other Mesoamerican domesticates. The dispersal to temperate regions has been dependent on deliberate and indirect human selection as well as natural selection resulting in crops capable of maturing prior to killing frost. In American cottons, pre-Columbian human selection for altered photoperiod sensitivity enabled dispersal of *Gossypium barbadense* L. in South America and *G. hirsutum* L. from Mexico to Central America (Smith and Cothren 1999; Westengen and Huaman 2005). In the 1800's, development of the sea island cultivars of *G. barbadense* and subsequent dispersal inland to shorter growing seasons in the U.S. cotton belt culminated in cultivars that flowered in longer days (Smith and Cothren 1999). Induced mutation has also proven effective in generating photoperiod insensitive lines of wild types for introgression with domesticated cotton (Abdurakhmonov et al. 2007). In maize, dispersal from central Mexico to cold temperate regions ranged in latitude from $\sim 45°$ N in Canada to $\sim 40°$ S in Chile. Temperate maize flowering is controlled by complex genetic photoperiod triggers and accumulation of a given amount of vegetative biomass (Buckler et al. 2009). The latter is not present in chia and may have eased the selection necessary for the wide dispersal of maize. These patterns of dispersal suggest that the chia lines described herein having long-day floral induction photoperiods can be successfully adapted and introduced to temperate biomes (Fig. 1).

Uniform maturation following floral induction is essential for a temperate biome where just prior to killing frost it is necessary to maximize yield in a shorter growing season. Novel long-day flowering chia lines described herein have altered photoperiod sensitivity but maintain the uniformity in maturation preferable for dispersal into temperate biomes. These novel chia lines are exemplary of the unending nature of plant domestication and are a congruent extension of the examination of historical patterns of dispersal and domestication of chia and other Mesoamerican domesticated crops. The success in altering photoperiod sensitivity combined with the domestication syndrome traits and the inherent health benefits of chia seed and oil make chia a strong new complement to existing oilseed crops in temperate regions.

Flower buds of the earliest flowering mutants formed 55 days after planting when the day length was 12 h and 16 min. No flower buds were found in control plots and in non-mutagenized border rows on that date (Supplemental Fig. 1). 0.013% early flowering plants were found in approximately 165,000 M_2 EMS-mutagenized plants and 0.024% of the

approximately 185,000 gamma-mutagenized plants. The rest of the field started to flower in the second week of October at 82 days after planting. Non-mutagenized plants were killed before blooming (petal opening).

Chia shows a short-day response to flowering (Table 1). Under controlled conditions, non-mutagenized plants were only able to flower when the daylenth was less than 14 h. This suggests a critical daylength between 12 and 13 h. All but one early flowering chia line flowered under a 15 h photoperiod (Table 1). In addition, all but one new chia line flowered within 3 weeks of moving to the 12 h photoperiod compared to non-mutagenized plants that required 5 weeks at 12 h to initiate flowering. Time to flowering was unaffected in most of the early flowering mutants, which all flowered after 3 weeks regardless of daylength. Four other mutants took longer to flower at the 14 and 15 h photoperiods compared to the 12 h photoperiod. In several *Salvia* species, flowering requires a critical photoperiod to initiate flowering as well as for flower development. For example, *S. leucantha* Cav. requires a 12 h photoperiod for flower induction and a 10 h photoperiod for continued flower development (Armitage and Laushman 1989). Although, the critical daylength for continued floral development was not evaluated in the current study for wild type chia plants, it appears that the majority of chia mutants were altered for daylength floral induction as well as floral development as flower formation appeared to be normal under the 15 h photoperiod.

Forty early flowering M_3 chia lines were planted in spring 2009 (May 20, 2009 when the day length was 14 h and 23 min) at Lexington, KY. Flower buds were first noticed on mutant lines on July 7, 2009, 47 days after planting at a daylength of 14 h and 41 min. Petal opening was observed starting on July 17, 2009. Flower buds were not found on non-mutagenized plants. Most of tested mutant lines had petal opening by July 24, 2009. However, there were some lines that opened petals later and some lines that did not form flower buds until induced by much shorter days. Most of the new early flowering chia lines set seed and matured by early October, 2009. Some of the lines matured and produced harvestable dry seeds as early as September 16, 2009 when the daylength was 12 h and 23 min (Fig. 2).

This is the first report on induction of early flowering chia mutants. Although genetic variation for many traits can be induced via mutagenesis (Koche and Choudhary 2008) the genetic mechanisms of floral induction varies among plant species and it was not obvious that early flowering in chia

Fig. 2 Flowering of an early flowering chia line in the field in Lexington, KY, July 2009

could be achieved by mutagenesis as multiple genes could be involved. Indeed, with the range of early flowering chia lines we have produced with floral induction ranging from early July when the daylength was close to 15 h and late September when the daylength was shorter than 12 h indicates numerous floral induction genes involved in the different lines. However we see remarkable uniformity in flowering within most M_3 plants of the M_2 families with little segregation for flowering phenotype as illustrated in Fig. 2. This might suggest that many of the mutations are dominant but further studies will need to be conducted on the inheritance of these early flowering chia mutants.

Salvia is a large genus and has species that vary in their daylength requirements for flowering (Zanin and Erwin 2006). Several horticultural species of subgenus *Calospace* including the annuals *S. splendens* Sellow ex Wied-Neuw., and *S. farinaceae* Epling have been shown to be facultative long-day plants, *S. greggii* A. Gray, a perennial, is a facultative short-day plant, while other perennials are obligate short day plants as seen in *S. leucantha* Cav. and *S. elegans* Vahl. The annuals utilized for seed production such as *S. hispanica* and *S.* tiliifolia Vahl when planted in the spring of the northern hemisphere flower in the short days of September for seed harvest in late fall (Gentry et al. 1990). Numerous genes have been reported to influence floral induction in Arabidopsis and rice (Fornara et al. 2009; Koche and Choudhary 2008; Komiya et al. 2009; Ryu et al. 2009; Stangeland et al. 2009; Strasser et al. 2009; Yoshida et al. 2009). Hou and Yang 2009 (Hou and Yang 2009) describe two genes in orchids that regulate flowering. Thurling and Depittayanan 1992 (Thurling and Depittayanan 1992) report on the induction of early flowering mutants in spring rape (*Brassica napus* L.) by EMS mutagenesis although they also produced later flowering lines.

In plants, daylength is perceived by leaves through the influence of red, far red and blue light on phytochromes (Ishikawa et al. 2009) which induces a mobile signal known as florigen to move through the phloem to apical meristems. In the apical meristems florigen causes changes in the expression of genes which alters the developmental program of the meristems to produce flowers instead of leaves (Turck et al. 2008). Numerous genes have been reported to influence floral induction in Arabidopsis

and rice (Komiya et al. 2009). In a recent report on genes controlling flowering time in maize Buckler et al. (Buckler et al. 2009) report that numerous genes have small additive effects on flowering time. Kondo et al. (Kondo et al. 2010) found that DNA demethylation can induce flowering in the long-day plant *Silene armeria* L. and the short-day plant *Perilla frutescens* (L.) Britton. *P. frutescens* is in the same family as chia, Lamiaceae. Further studies are needed on the genetic control of flowering in chia and the genetic basis of the long-day flowering lines reported here. Chia is a diploid with only 12 chromosomes ($n = 6$) which will facilitate rapid genetic improvement of this new crop (Estilai et al. 1990).

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