Genetic Variation in Jerusalem Artichoke (*Helianthus tuberosus* L.) Flowering Date and Duration

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Additional index words. plant breeding, inulin, bulking agent, fructose

Abstract. Increased interest in the Jerusalem artichoke (*Helianthus tuberosus* L.) stems from the high level of inulin, a straight chain fructan, found in the tubers that has a number of current and potential industrial applications. Deficiencies in existing cultivars have underscored the need for a pragmatic breeding program. Since synchronization of flowering has a pronounced influence on genetic crosses that can be made, we assessed the flowering date and duration of 190 clones with selected clones similarly monitored for two additional growing seasons. Substantial genetic variation in the date and the duration of flowering were found with the onset of flowering ranging from 69 to 174 days after planting (DAP). Flowering duration ranged from 21 to 126 days. The onset of flowering was substantially affected by planting date and to a lesser extent by location. The results suggest that at lower latitudes flowering date for some clones can be manipulated by planting date; at higher latitudes, growth under controlled conditions may be required to synchronize flowering of some clones.

Inulin, a β -(2-1) linked straight chain fructan, is found in low levels in a wide cross-section of food crops and in high concentrations in Jerusalem artichoke tubers (*Helianthus tuberosus*). About 8 to 12 g·d⁻¹ of inulin from a wide variety of sources is consumed in Western diets (Fuchs, 1996). Inulin has four major attributes that have stimulated considerable research in Europe (Fuchs, 1993).

- 1) Inulin is a dietary fiber, the consumption of which confers a number of health advantages [i.e., lowers blood cholesterol level; promotes Bifido bacteria in the large intestine; reduces blood sugar, low-density lipoprotein, and triglyceride levels; and is beneficial to certain heart diseases (Farnsworth, 1993; Hirayama and Hidaka, 1993; Sakun, et al., 1996; Varlamova et al., 1996)].
- 2) Inulin is little digested by humans and as a consequence, has potential utility as a bulking agent in low calorie formulated foods.
- 3) Longer chain length inulin (average dp ~25) can be used for fat replacement in foods.
- 4) Inulin can be hydrolyzed to produce a high purity fructose syrup which can be used in soft drinks and a wide range of other products. Because of these attributes, production of inulin in Europe has increased in an exponential manner where it is used primarily to produce fructose syrups and as a low-calorie, high-fiber food additive (Fuchs, 1996). Inulin is, likewise, a component of a growing number of foods produced and/or marketed in the United States.

The Jerusalem artichoke, native to North America, represents an excellent source of inulin. The crop is not, however, without certain deficiencies (e.g., tuber size and shape, stolon length, certain leaf and root diseases) which can only be resolved through the development of new cultivars. Synchronization of flowering between male and female parents in a plant breeding program is, therefore, an essential requisite. Both flowering and tuberization are modulated by photoperiod and it is interesting to note that some of the early research on photoperiodism used the Jerusalem artichoke as a model (Garner and Allard, 1923). Subsequently, there have been a diverse array of basic and applied photoperiodic studies on the crop (Allard and Garner, 1940; Czajlichian, 1937; Hackbarth, 1937; Hamner and Long, 1939; Nitsch, 1965; Schiebe and Müller, 1955; Tincker, 1925; van de Sande Bakhuyzen and Wittenrood, 1950, 1951; Wagner, 1932).

The critical day length for a cross-section of Jerusalem artichoke clones is between 13 and 13.5 h (Allard and Garner, 1940; Hamner and Long, 1939; Zhou et al., 1984). Short day clones exposed to photoperiods of ≥ 14 h stay vegetative. Data on the minimum length of exposure to inductive conditions varies, though a relatively short duration (16 to 17 d) (Hamner and Long, 1939; Zhou et al., 1984) appears to be more likely than longer periods that have been proposed (Schiebe and Müller, 1955). Both short day and day neutral clones for flowering have been reported (Hackbarth, 1937).

Due to the importance of the timing and duration of flowering in a breeding program, these traits were determined for a large cross-section of Jerusalem artichoke clones. In addition, the developmental sequence and timing of individual flowers of selected clones are presented.

Three single plant replications of 190 clones were grown at the University of Georgia Horticulture Farm near Watkinsville (33° 57' N) during the summer of 1999. Individual tubers or tuber pieces of 30 g were planted on March 24. The plants were grown in a Cecil sandy clay loam and fertilized with 1,121 kg·ha⁻¹ of 10-6.5-8.3, one half applied before planting. Within row and between row spacings (0.5 × 5 m) were selected to minimize plant to plant competition and to facilitate fungicide applications (mancozeb at 2.24 kg·ha⁻¹). The dates of anthesis of the first flower and senescence of the last flower per plant were recorded at weekly intervals from planting until frost. Very little variation in flowering was found among replicates for individual clones. Data on flowering date were also collected in southeastern Missouri (35° 3' N; planted 1 Mar.) in 1998 and in Watkinsville in 1997 (planted 29 Apr.) but on fewer clones and at wider recording intervals. These data are not included, though comparisons among selected clones were made for each year.

The clones tested (Table 1) were from the following sources: a private collection in Farmington, Maine; the U.S. Department of Agriculture Plant Introduction Station, Ames, Iowa; Agriculture & Agri-Food Canada, Morden, Manitoba; The Royal Veterinary & Agricultural University, Taastrup, Denmark; Lehr- und Versuchsanstalt für Integrierten Pflanzenbau, Güterfelde, Germany; Federal Centre for Breeding Research on Cultivated Plants, Braunschweig, Germany; and commercial sources. The name assigned to each clone was as received. In some instances, clones with the same name but from different sources were present.

Results and Discussion

The results demonstrate a tremendous range in flowering response within the Jerusalem artichoke genepool. Anthesis of the first clone to flower (NC10-85) occurred on 24 May, only 62 d after planting (DAP). When plotted as a frequency distribution (Fig. 1), most clones began flowering between 1 June (69 DAP) and 15 July (114 DAP). After 15 Aug. (145 DAP), the number of clones flowering declined markedly. The last clones to flower, began flowering on 13 Sept., 174 d after planting.

The relationship among individual clones in the number of DAP until the onset and completion of flowering is presented in Fig. 2. The data illustrate clones in which crosses could be attempted (i.e., both clones in flower at the same time) and the time interval over which this could occur. In addition, the approximate time intervals at 33°57' N latitude for crosses between specific clones are presented. Clone 1 (NC10-85) had the longest time interval (126 d) during which flowers were available, while clone 182 ('Cross Bloomless') had the shortest (21 d). Clone 1, with its exceptionally long period of flowering, could potentially be crossed with each of the other clones in the study. In contrast, clone 75 and clones >172

Received for publication 12 Nov. 2004. Accepted for publication 1 May 2005. The authors would like to thank Will Bonsall, Mary Brothers, Ferdinaud Kiehn, Susanne Klug-Andersen, Josef Zubr, B. Honermeier, and Lothar Frese for their contribution of clones and Gerald Williams, Brad Williams, Robert Walkup, and Betty Schroeder for their technical assistance.

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could not be crossed without artificially manipulating the flowering date in some manner. While all clones began flowering before the end of the study, some clones were lost before completion of flowering due to the incidence of *Sclerotium rolfsii* Sacc. during the latter part of the growing season. The incidence of *S. rolfsii* in Georgia is common and the organism appears to represent the primary impediment to culture of the Jerusalem artichoke in the southern part of the southeastern U.S. (Mc-

Carter and Kays, 1984). Consequently, it was not possible to determine the flowering duration for several of the clones listed in Table 1, however, the timing of the onset of flowering can be determined from a clones numerical position relative to adjacent clones in Fig. 2. Table 1 lists the clones in the order of flowering date (earliest first) and secondarily by the duration of flowering (shortest first).

A frequency distribution for the duration of flowering among the clones tested is presented

in Fig. 3. Most clones were in flower between 70 and 100 d. The range, however, was from 21 to 174 d, indicating substantial genetic variation for the trait.

Some variation in flowering response was found among several clones listed as the same cultivar. For example, clones 19, 39, and 83 which were identified as 'Fuseau', differed in the timing of the onset of flowering by 28 d and the completion of flowering by 14 d. There are several possible explanations for this variation.

Table 1. Jerusalem artichoke clones tested in 1999 arranged in order of flowering date (earliest first) and length of flowering (shortest first).^z Clones which succumbed to *Sclerotium rolfsii* Sacc. before flowering was complete.

1. NC10-85	61. PI 503274	126. 'Castro' ^z
2. NC10-8	62. NC10-52	127. 'Totman' ^z
3. NC10-9	63. NC10-83	128. 'Cowell's Red' ^z
4. NC10-15	64. NC10-84	129. 'Olds' ^z
5. NC10-16	65. HEL 63 'Gibrid'	130. 'Skorospelko' ^z
6. NC10-18	66. 228-62	131. 'Clearwater' ^z
7. NC10-24	67. 2071-63	132. 'Refla' ^z
8. NC10-25	68. 'Leningrad'	133. 'Vanlig' ^z
9. NC10-28	69. 'Dave's Shrine'	134. 'Swenson'
10. NC10-32	70. 'Long Red McCann'	135. Hybrid 120
11. NC10-34	71. 'Grem Red'	136. 'Monteo'
12. NC10-35	72. No. 9	137. 'Freedom'
13. NC10-48	73. 'Mari'	138. 'Mulles Rose'
14. NC10-88	74. PI 503272 ^z	139. NC10-22
15. BBG 2	75. PI 503279	140. 'Challenger'
16. 'Gute Gelbe'	76. PI 503283	141. BT4
17. 'Waldspindel'	77. NC10-29	142. dwarf
18. 'Waldoboro Gold'	78. NC10-40	143. 'Drushba'
19. 'Fuseau'	79. NC10-70	144. 'Sunrise'
20. 'Magenta Purple' ^z	80. NC10-81	145. 'Susan's Yard'
21. 'Waldspindel' ^z	81. 'Deutsche Waldspindel'	146. 'Gurney's Red'
22. 'Jack's Copperskin'	82. 'Medius'	147. 'Swenson'
23. PI 547227	83. 'Fuseau 60'	148. 'Wilton Rose' ^z
24. NC10-5	84. 'Nahodka'	149. 'Reka' ^z
25. NC10-7	85. 'Onta'	150. 'Cody Miller'
26. NC10-14	86. D19-63-122	151. PI 503266
27. NC10-26	87. D19-63-340	152. NC10-94
28. NC10-41	88. 'Nakhodka'	153. NC10-99
29. NC10-62	89. 'Grem White'	154. 'Firehouse'
30. NC10-78	90. 'Volga 2'	155. 'Sodomka'
31. 'Mahlow rot'	91. 'Nescopeck'	156. 'Boston Red'
32. 'Bela'	92. 'Southington Pink'	157. 'Whitford'
33. 2327	93. 'Austrian Wild Boar' ^z	158. 'Jack's Copperskin'
34. 'Stampede' ^z	94. 'Fuseau' ^z	159. K 24 ^z
35. NC10-73	95. D 19 ^z	160. 'Leningrad'
36. 'Waldoboro Gold'	96. PI 503265	161. PI 503271
37. PI 503276	97. 'Gold Nugget'	162. 'Boyard'
38. PI 503277	98. 'Clearwater'	163. 'Jack's White'
39. 'Fuseau' (Idaho)	99. NC10-44	164. 'Silverskin'
40. NC10-4	100. NC10-100	165. NC10-76
41. NC10-6	101. BBG 1	166. 'Kierski Beli'
42. NC10-11	102. 'Mahlow Gelb'	167. 'Sugar Ball'
43. NC10-13	103. 'Tambovski Krasnyi'	168. 'Drown's Long Red'
44. NC10-46	104. 'Sachalinski Krasnyi'	169. 'Flam'
45. 'Stampede'	105. HEL 53 ^z	170. 'Draga' ^z
46. 'Remo'	106. 'Roza' ^z	171. 'Sunchoke' ^z
47. 'Columbia'	107. 'CR Special' ^z	172. 'Garnet'
48. 'Top'	108. 'Skorospelka'	173. PI 503275
49. 'Novost'	109. 'CR Special'	174. NC10-90
50. KWI 204 ^z	110. PI 503262	175. NC10-92
51. 12/84 ^z	111. PI 503280	176. 'Challenger'
52. 952-63 ^z	112. NC10-75	177. HEL 69
53. 'Dwarf Sunray' ^z	113. NC10-82	178. Hybrid 120
54. 'Orrington' ^z	114. Unknown	179. 'Beaula's'
55. 'Miles #1'	115. 'Brazilian White'	180. 'Karina'
56. 'Urodny'	116. 'Sunchoke'	181. 'Bianca'
57. 'Nora'	117. D 19	182. 'Cross Bloomless'
58. C 2071-63	118. 'Violet de' Rennes'	183. 'Vadim'
59. 'Nakhodka'	119. 'Parlow Gelb'	184. 'Schmoll' ^z
60. PI 503269	120. 'Gro& Beerens'	185. J.A. 61 ^z
	121. 'Neus'	186. PI 503264 ^z
	122. 'Maikopski'	187. 'Roter Topinambur'
	123. HEL 68	188. 'Lucien's Painting'
	124. 'Medius'	189. 'White Crop'
	125. BT3	190. 'Kiev White'

Fig. 1. Frequency distribution of Jerusalem artichoke clones for the date of flowering (planting date 24 Mar. 1999).

The Jerusalem artichoke has been used and improved much more extensively in Europe than in North America, its site of origin. During the last 400 years, desirable clones have been moved extensively from one country to another, starting with the first introduction of the crop into France in 1607 (Lescarbot, 1609). As clones are moved into locations with different languages, there is a tendency to rename them. This also occasionally occurs when commercial sources of propagation material desire a unique name for marketing purposes. In addition, selection pressure on a clone grown in diverse environments can, over a number of generations, result in a shift away from the original type. This is a common occurrence in the sweetpotato [*Ipomoea batatas* (Lam.) L.], another asexually propagated crop (Villordon and LaBonte, 1996). As a consequence, the authenticity of a clone is not always definitive and the uniqueness and degree of relatedness of individual clones tested await amplified fragment length polymorphism analysis or another molecular means of assessment.

Control of flower induction varies depending upon the type of photoperiodic response operative within the clone (i.e., short day versus day neutral) as well as other factors. Thus, when a diverse cross-section of the germplasm is assessed, a wide range in flowering dates can be found (Fig. 2). Current thinking is that the early flowering clones represent day neutral types in which the induction of flowering is controlled by the stage of development of the plant (Denoroy, 1996) rather than photoperiod. In contrast, short day (late flowering) clones are dependent upon receiving the appropriate photoperiodic response (Hackbarth, 1937; Steinrücken, 1984; van de Sande Bakhuyzen and Wittenrood, 1950; Zhao et al., 1984).

In addition to the photoperiodic response, the date of flowering for individual clones will vary depending upon geographical location, timing of planting, production conditions, and other factors. Geographic location affects both the photoperiod as well as production conditions. *Helianthus tuberosus* is thought to have originated in the more northern latitudes of the United States where the photoperiod is favorable for extensive stem growth during the summer (long days) and is followed by photoperiods conducive to flower and tuber formation in the fall. Thus the location where the crop is grown has a significant impact of its development since long day conditions favor development of aerial plant parts. At mid-June the photoperiod at 60° N is >18 h, at 40° N 15 h, at 26° N 13.5 h, and at the equator 12 h. By October however, the light period has decreased to only 9.5 h at 60° N (10.5 h at 40° N; 11 h at 26° N) but remains 12 h at the equator. As

Fig. 2. Timing of the onset and duration of flowering for individual Jerusalem artichoke clones (clonal numbers correspond to Table 1). Clones in which the duration of flowering is missing succumbed to *Sclerotium rolfsii* Sacc. before flowering was complete.

Fig. 3. Frequency distribution of Jerusalem artichoke clones for the duration of flowering.

Table 2. Approximate^a time of flowering over three growing seasons for selected early, intermediate, and late flowering clones from 1999.

Clone ^b	Georgia 1999 ^a	Missouri 1998	Georgia 1997
Early			
3	31 May	Aug.–Sept.	Aug.
5	31 May	Sept.	Sept.
6	31 May	Aug.–Sept.	Aug.
8	31 May	Aug.–Sept.	Aug.–Sept.
Intermediate			
100	5 July	Sept.	Sept.
101	5 July	Sept.	Sept.
102	5 July	Sept.	Sept.
103	5 July	Sept.	Sept.
Late			
174	16 Aug.	Oct.	Sept.–Oct.
175	16 Aug.	Sept.	Sept.–Oct.
178	16 Aug.	Oct.	Sept.–Oct.
179	16 Aug.	Oct.	Sept.–Oct.

^aData on flowering during 1997–98 were taken less frequently and as a consequence, dates represent the general time interval in which the clone is in flower versus the date of initial anthesis in 1999.

^bClone numbers correspond to Table 1.

^cPlanting dates: 24 Mar. 1999, 1 Mar. 1998, and 29 Apr. 1997.

the production area moves progressively away from the equator, the amount of carbon fixed per day during the summer increases due to the longer photoperiod while the length of the growing season decreases. The photoperiod and length of the growing season at higher latitudes can result in short day (late flowering) clones failing to flower, hence the name ‘Cross Bloomless’ (clone 182). When grown in the southeastern United States, the clone flowers normally, though late in the season (Fig. 2).

When contrasting the date of flowering among years (Table 2), significant variation was evident. Early planting in Georgia (1999) resulted in earlier flowering for all clones whether early, intermediate, and late flowering, while maintaining more or less the same general chronology among clones. Early flowering clones in 1999 (Georgia) bloomed about 3 months later in 1997 (Georgia) even though the planting dates varied by only 36 d. For example, clone 3 bloomed on 31 May 1999 but not until 25 Aug. at the same location in 1997. When planted early (March 15) in a more northern location (Missouri), the timing of flowering was comparable to

delayed planting in Georgia (1997). If early flowering clones are in fact day neutral and flowering date is determined by heat units, then it is doubtful that flowering would be shifted so much later. The results suggest that there is a range in day length requirements and when planted early enough under conditions conducive to rapid growth, the plants reach a photoreceptive stage while the day length is still sufficiently short for photoinduction. The net effect is early flowering when planted early enough under photoinductive conditions but delayed flowering when planted later or under less favorable growing conditions. Regardless, it is evident that additional research is needed to clarify the mechanism(s) operative.

The results indicate the presence of a considerable genetic variation in the date of flowering among a large segment of the Jerusalem artichoke germplasm and in the duration of the flowering period. The date of flowering also appears to depend on the timing of planting and/or rate of growth early in the season relative to the photoperiod. Though dates for flowering reported are specific for the test location, they give an indication of the timing

and potential interrelationship among clones when grown elsewhere. The date of flowering of some clones can be manipulated in lower latitudes by planting date while higher latitudes require growing under controlled conditions to synchronize flowering.

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