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Ecotypic Differentiation in Response to Photoperiodism in Several Species of *Amaranthus*¹

E. L. McWILLIAMS², R. Q. LANDERS³, J. P. MAHLSTEDT⁴

Abstract. *Amaranthus retroflexus*, *A. hybridus* and *A. powellii* were grown in a uniform garden at Ames from seed collected over a wide geographic area. Intraspecific variability in flowering response to photoperiod was studied. There was a significant correlation between date of flowering and the collection site.

Amaranthus retroflexus L., *A. hybridus* L. and *Amaranthus powellii* Wats., commonly called pigweeds, are wide ranging weedy species. They are often difficult to identify. Examination of these species for variability has been made by growing plants in a uniform garden at Ames, Iowa, from seed collected over a wide geographic area. This report considers the responses of collections to photoperiod.

It may be accepted as fact that wide ranging plant species, in general, show genetically based ecological differentiation in morphological as well as physiological characteristics (Heslop-Harrison, 1965). Hiesey and Milner (1965) have stated recently that many ecological races and species of diverse plant groups differ in photoperiodic responses. This phenomenon was first demonstrated by the work of Olmsted (1944) on races of *Bouteloua curtipendula* distributed over 17 degrees of latitude. Larsen (1947), and more recently McMillan (1965), have demonstrated regional differentiation in photoperiodic responses of other wide-spread perennial grasses.

Photoperiodic responses of *Chenopodium quinoa* and *Amaranthus caudatus*, two annual species, have been studied by Fuller (1949), and reexamined by Zabka (1961). In a similar study to ours, Davidson (1965) observed that flower initiation in populations from Iowa and Texas of *Froelichia floridana*, an annual species in Amaranthaceae, is promoted by short-day photoperiods and retarded by long-day photoperiods. However, the degree of long-day retardation was less for northern than for southern plants. Davidson considered that these photoperiodic differences were adaptive. Allard and Garner (1940) reported that photoperiodic responses in *Amaranthus* species were indeterminate, although no attempt was made to compare responses in ecological races.

METHODS

Seeds of *Amaranthus retroflexus* L. were requested from 40

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state and Canadian seed laboratories and many foreign botanical gardens and herbaria. Many seed analysts pointed out that *Amaranthus* species are practically indistinguishable on the basis of seed morphology; as a result many species were received in these seed samples.

The seeds were planted in steam-treated soil on April 15, 1965, in 2½ inch "Jiffy Pots" in a greenhouse under a 16-hour photoperiod. The seedlings were maintained under a 16-hour photoperiod until June 5, 1965, at which time they were planted (4-6 leaf stage) at the Iowa State University Horticulture Farm. The rows were spaced 6 feet apart, and the plants were spaced 2 feet apart within each row. The planting was a completely randomized design, and replications for each geographical location varied from 1 to 10 plants depending upon the number of seeds available. Most locations were represented by three plants.

Because the soil contained indigenous *Amaranthus* seeds, precautions had to be taken to maintain the identity of the planted seedling. Each plant was carefully labeled, and each pot was surrounded by a two inch layer of "perlite" extending 3-4 inches from the pot. The area was hand-weeded weekly.

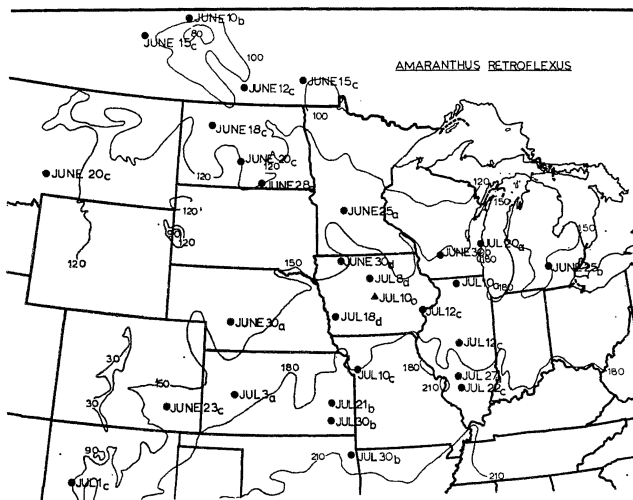


Fig. 1. Flowering dates and isotherms of the average length of the frost free season for U. S. and Canadian collections of *Amaranthus retroflexus* grown at Ames (indicated by triangle) Iowa, during 1965. Subscript letters indicate the number of plants observed for each location a=1 d=4.

OBSERVATIONS

As growth of seedlings progressed, it became obvious that considerable variation existed. This variation could be attributed to the fact that several *Amaranthus* species were received, to

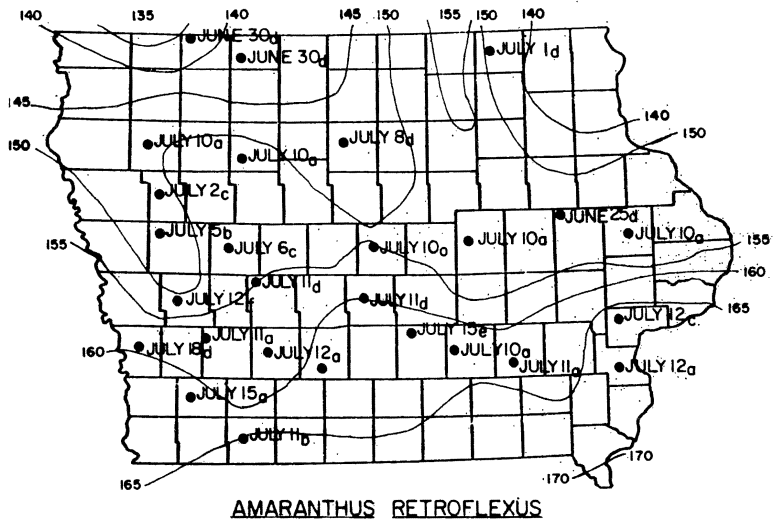


Fig. 2. Flowering dates and isotherms of the average length of the frost free season for Iowa collections of *Amaranthus retroflexus* grown at Ames, Iowa during 1965. Subscript letters indicate the number of plants observed for each location a=1 d=4.

intraspecific differences between geographical collections, and to random variation. Intraspecific differences were most obvious at the onset of flowering. The date was recorded when the floral primordia were macroscopically visible on each plant. The range of variation in the date of flowering for a collection usually was less than ± 5 days.

Dates of flowering and average length of the frost free season are compared for some of the U.S. and Canadian collections of *Amaranthus retroflexus* in figure 1, for Iowa in figure 2, and for Illinois in figure 3. Dates of flowering are compared with frost free season for some of the United States collections of *A. hybridus* in figure 4, and for Iowa and Illinois collections, respectively, in figures 5 and 6. Climatic data were obtained from "Climates of the States" (1959). A weather station near each collection site provided us with data on mean date of first fall frost, mean date of the frost free season, and the mean summer temperature.

A multiple regression was determined for date of flowering, latitude, first fall frost, frost free season and average summer temperature for *A. hybridus* and *A. retroflexus*. For *A. hybridus*, the correlation between date of flowering and latitude was significant at the 1 per cent level. All collections of *A. hybridus* are from the mid-continental area of the United States except for two collections from Virginia. For *A. retroflexus*, the cor-

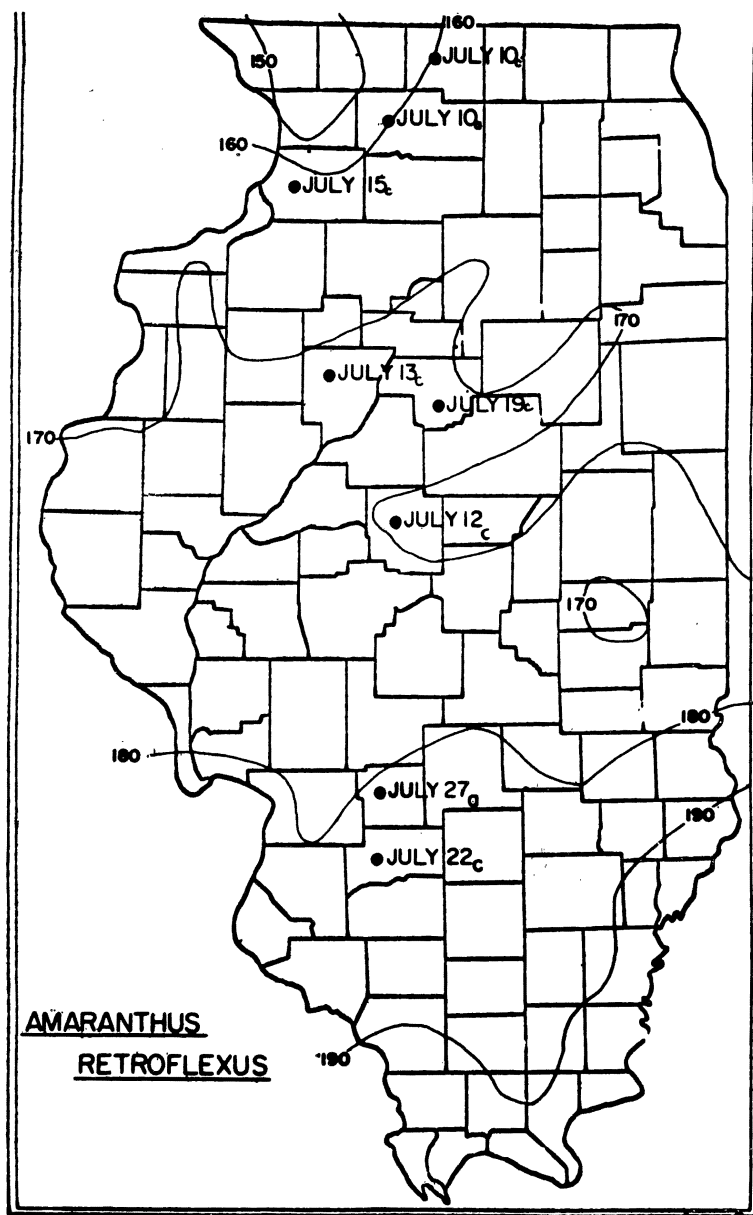


Fig. 3. Flowering dates and isotherms of the average length of the frost free season for Illinois collections of *Amaranthus retroflexus* grown at Ames, Iowa, during 1965. Subscript letters indicate the number of plants observed for each location a=1 d=4.

relation between date of flowering and latitudes approaches significance at the 5 per cent level. When the collections from the

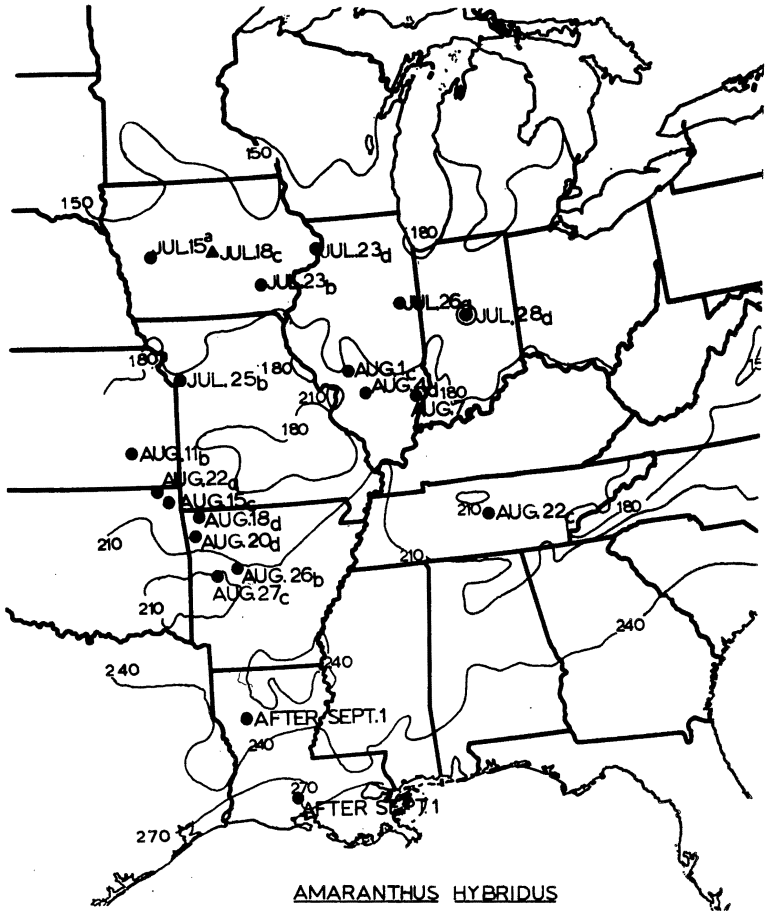


Fig. 4. Flowering dates and isotherms of the average length of the frost free season for collections of *Amaranthus hybridus* grown at Ames (indicated by triangle) Iowa during 1965. Subscript letters indicate the number of plants observed for each location a=1 d=4.

Rocky Mountain states are removed from the regression, the correlation between date of flowering is significant at the 1 per cent level. In mountainous areas flowering is more a function of altitude than latitude.

For both *A. hybridus* and *A. retroflexus* the correlation between date of flowering and first fall frost gave the second best measure of fitness although it was not statistically significant.

DISCUSSION AND CONCLUSIONS

McMillan (1965) noted early flowering in prairie community transplants of northern origin and late flowering in those of

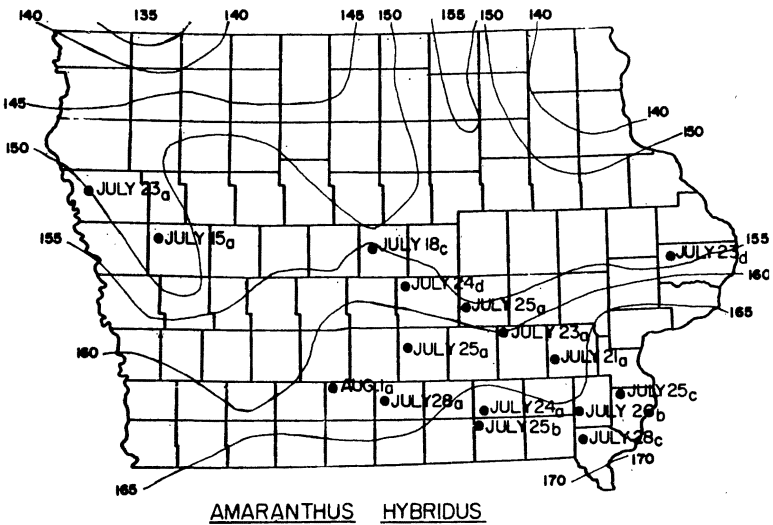


Fig. 5. Flowering dates and isotherms of the average length of the frost free season for Iowa collections of *Amaranthus hybridus* grown at Ames, Iowa, during 1965. Subscript letters indicate the number of plants observed for each location a=1 d=4.

southern origin when grown in a uniform garden. He noted further that the ecological variation resulting from natural selection included early maturity within northern and montane populations. We observed similar effects of the climate on the date of flowering of the *Amaranthus* collections of the montane regions, the coastal regions, and the Lake Michigan region as shown in figures 1 and 4. Collections from coastal regions and the Lake Michigan region exhibited a later maturity date than did mid-continent collections from the same latitude.

A flowering gradient or cline extending from Canada to Kansas was observed for collections of *A. retroflexus*, from Iowa to Louisiana for *A. hybridus*, and from Canada to Iowa for *A. powellii*. On the basis of these observations it is hypothesized that the first fall frost is an important factor of the environment acting upon the genetic variability controlling the photoperiod response mechanism. A population is maintained which is a compromise between large, late flowering plants capable of producing many seeds and smaller plants which almost always produce some seeds before frost. In those regions where the growing season is longer because of large bodies of water the compromise allows a later date of floral induction.

Within any given location where all three species are present, the order of flowering is usually as follows: *A. powellii*, *A. retroflexus* and *A. hybridus*. Nougarede *et al.* (1965) considered *A. retroflexus* to be a quantitative short-day plant rather

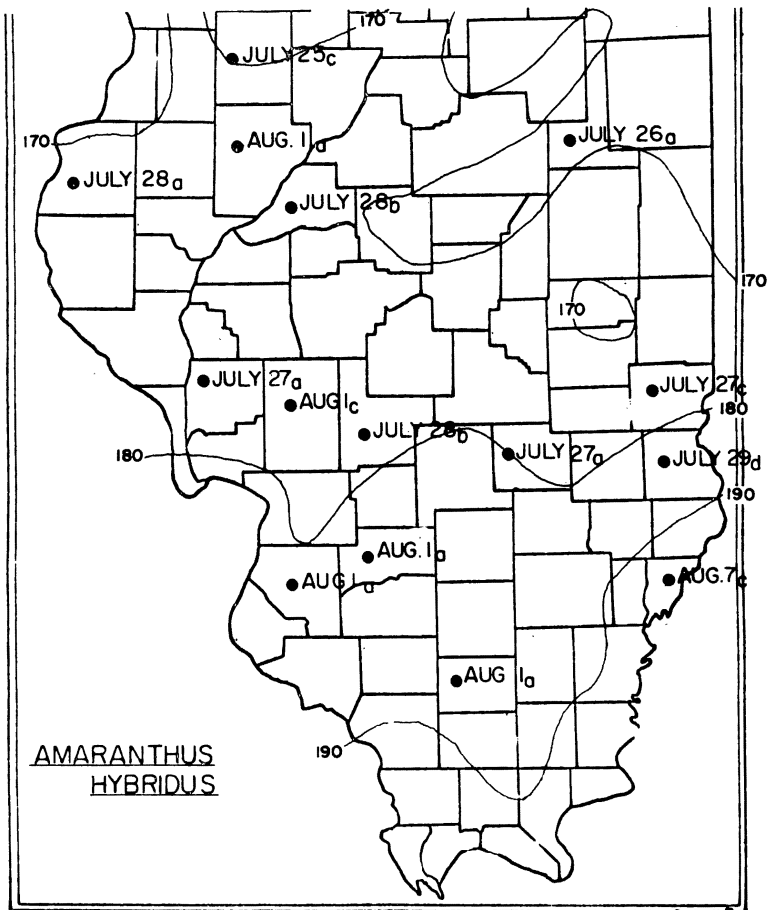


Fig. 6. Flowering dates and isotherms of the average length of the frost free season for Illinois collections of *Amaranthus hybridus* grown at Ames, Iowa, during 1965. Subscript letters indicate the number of plants observed for each location a=1 d=4.

than an indeterminate plant as described by Allard and Garner (1940). Our study indicates that the northern collections of *A. retroflexus* and *A. hybridus* are quantitative short-day plants, although plants grown from seeds collected in Louisiana were unable to flower before frost in Iowa. Therefore, the type of photoperiodic response of a wide ranging species may depend to a large extent on the collection site.

Davidson (1965) stated that one may suspect that to the north of the present distribution of *Froelichia floridanus* the selective pressure associated with photoperiod and length of growing season is too demanding to have been overcome by the narrow limits of the current gene pool. This would appear to apply to

our information on the northern range of *A. hybridus* which appears to be presently limited in the midwest at the latitude of northern Iowa.

Despite the continual mixing of genotypes of these weed populations by agricultural practices and seed introductions, it appears that these three species have evolved genetically adapted populations in response to different environments throughout their ranges.

ACKNOWLEDGMENTS

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Notes on Prairie Species in Iowa. I. Germination and Establishment of Several Species

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Abstract. Information is given concerning the germination and early establishment of 30 prairie species. A stratification treatment was included for all seeds, and scarification was also used for the legumes. Germination percentage in greenhouse flats was generally higher than in field plots with variation in germination ranging from 96% in compassplant, *Silphium laciniatum*, to zero in some such as *Rosa suffulta* and *Gentiana puberula*. Seedlings in field plots were subjected to five levels of competition throughout the growing season. Establishment, measured by numbers of seedlings and vigor in September, was most successful on weed free treatments, least successful on cover crop treatments.

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