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Potential for Hydrilla Dispersal by Sexual Means in North Carolina Surface Waters

by

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ABSTRACT

Flowering and seed production by monoecious hydrilla populations in three North Carolina (USA) lakes was studied, and eleven populations of monoecious and dioecious hydrilla in the United States were karyotyped. Flowering did not occur when plants were maintained in a phytotron for two months under various day lengths and temperature regimes. Staminate and pistillate floral initiation occurred in the field during early July suggesting a long-short-day flowering response. Mature hydrilla seeds were only observed in Lake Wheeler where seed density ranged from three to thirty per square meter in 1984 and 1985, respectively. Seed viability ranged from 30% to 5.0% when seeds were collected 01-06-86 and 10-15-86, respectively. Seedling vigor was observed to be low compared to hydrilla cloned from the parent population. Only one seedling exhibited apparently normal growth. The triploid number of 24 chromosomes was observed in somatic cells of hydrilla from all populations and it is suggested that this is the cause for low seed and seedling viability. Karyotypes of monoecious and dioecious populations were similar to each other and similar to previously published hydrilla karyotypes. However, discrepancies as to the ploidy of monoecious hydrilla populations from Washington D.C., Virginia, and Maryland suggests chimeras or a population of individuals with different ploidy.

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INTRODUCTION

Hydrilla [Hydrilla verticillata (L.f.) Royle] is a submersed aquatic plant of African origin. Unique and highly specialized physiological and biological adaptations allow hydrilla to invade a wide variety of aquatic habitats and to competitively exclude native and more beneficial aquatic plants (Haller and Sutton, 1975; Van et al. 1978). Because of its growth habit and prolific reproductive capabilities, hydrilla can cause detrimental impacts to sport fish populations (Colle and Shireman, 1980) and may severely limit recreational, domestic, industrial, and agricultural water use (Shireman and Haller, 1982). Hence expensive measures to manage the plant are necessary. For example, up to 12 million dollars are spent annually for hydrilla management in the state of Florida.

Two small hydrilla populations were discovered at separate locations in Florida (USA) in 1959. By the late 1960's hydrilla was causing severe problems in major water bodies of every watershed throughout the state. Hydrilla is currently distributed throughout the Southeastern United States as far north as Delaware, and as far west as California (Haller, 1982).

Hydrilla biology and ecology have recently been reviewed by Cook and Luond (1982) and by Pieterse (1981). Hydrilla is highly polymorphic. Geographically isolated populations often have dissimilar leaf and stem form, general stature, and sexual

expression. Hydrilla observed in Washington, D.C., Delaware, and North Carolina tends to have narrower leaves, smaller diameter stems, and a generally less robust growth habit than that observed in most of Florida and other more southerly locations. Several Florida populations, however, vary from this generality and have morphological characteristics similar to the more northern hydrilla populations (personal observations).

On a worldwide scale, hydrilla is usually monoecious in tropical regions and dioecious in more temperate climates (Cook and Luond, 1982). The pattern is reversed in the United States. In the subtropical climate of Florida, where hydrilla has been studied for 25 years, staminate flowers have never been observed, and it was believed that only dioecious, pistillate hydrilla existed in the United States. However, staminate flower production by hydrilla that had been collected from Washington, D.C. (Vandiver et al. 1982), and Delaware (Steward, 1983, personal communication) was reported under experimental conditions in Florida. Likewise, in the summer of 1983, profuse staminate flower production was observed in monoecious hydrilla populations in North Carolina (USA) lakes (Langeland and Schiller, 1983).

Hydrilla populations have been compared genetically by chromosome number and by isoenzyme analysis with electrophoresis. Hydrilla collected from Washington, D.C. had several isoenzyme characteristics that differed from hydrilla collected from other areas of the United States (two California collections, three Florida collections and one from Texas) (Verkliej et al. 1983).

Hydrilla collected from Washington, D.C., Maryland, and Delaware also differed by having 16 (2n) chromosomes compared to 24 (3n) for all other U.S. collections except one from Alabama which had 32 (4n) (Verkleij et al., 1983; Verkleij et al., 1983). It was assumed that hydrilla populations in North Carolina, which are similar in morphology and sexual expression (monoecious) to populations centered around Washington D. C., were of the same strain. However, Harlan et al. (1983) reported that hydrilla collected from North Carolina (Lake Wheeler) was triploid (3n=24). Likewise, Wain (1983) reported insignificant differences in isoenzyme banding patterns from hydrilla collected from several Florida locations.

Chromosome numbers of 42 hydrilla plants had been documented, worldwide, as of 1981. Of these, 21 were diploid (2n=16), 20 were triploid (3n=24) and 1 was tetraploid (4n=32) (Cook and Luond, 1982). Diploid and triploid populations have been on record since 1929 (Sinoto, 1929), whereas the tetraploid was recently reported (Davenport, 1980).

Published idiograms of diploid hydrilla have 6 short, 4 medium and 6 long chromosomes. Triploid karyotypes are apparently less consistent (Cook and Luond, 1982). One published triploid karyotype records 15 long and 9 short chromosomes (Sinoto, 1929), while another states that the triploid idiogram corresponds with the diploid aside from the extra set of chromosomes (Czapik, 1978). Metaphase chromosomes range in length from 2.3 to 2.5 um for the smallest to about 7.5 to 8.0 um for the longest (Pieterse, 1981; Sharma and Bhattacharyya, 1956; Czapik, 1978).

Sinoto (1929) suggested that an unequal pair of chromosomes (XY sex chromosomes) was responsible for sexual expression. However, there has been no subsequent evidence for the presence of sex chromosomes (Cook and Luond, 1982). Likewise, there has been no verification of a relationship between vegetative morphology or ecology and karyotype (Verkleij et al. 1983; Chauduri and Sharma, 1978; Czapik, 1978) as was suggested by Misra (1966,1971).

Prolific vegetative reproduction has allowed rapid spread of hydrilla aided by man's transportation of vegetative material. This means of dispersal is most effective over short distances under natural conditions. Viable seed production is a natural mechanism for long distance dispersal whereby seeds may be consumed by waterfowl and transported. The question arose whether the monoecious hydrilla populations were genetically capable of producing viable seed after Harlan et al. (1984) reported that the North Carolina populations have a chromosome number of 24 (3n). This implied that the North Carolina hydrilla populations cannot produce viable seed because triploid organisms often have defective sex cell formation and are usually sterile. Conant et al. (1984), however, observed seed production and germination under experimental conditions by hydrilla collected from Delaware and North Carolina. More recently, hydrilla was observed to produce viable seed in North Carolina lakes (Langeland and Smith, 1984). The purpose of this study was to determine the potential for dispersal of monoecious hydrilla by measuring seed production capabilities and viability and environmental parameters necessary for seed production.

Karyotypes of various southeastern hydrilla populations were compared as a possible explanation for the ability or inability to produce viable seed.

MATERIALS AND METHODS

Environmental Stimuli for Flower and Seed Production

The Southeastern Plant Belt Environmental Laboratories NCSU Phytotron was used for controlled environment studies to identify parameters that induce flower and seed production by hydrilla. Hydrilla tubers were sterilized with 10% bleach, allowed to sprout in distilled water, and plants with uniform growth were selected for the studies. Sprouted tubers were planted in sterilized one-gallon glass jars or in 30 gallon aquaria that contained sterilized sandy loam. Hydrilla from North Carolina (monoecious) and Florida (dioecious) was planted in an aquarium and the two populations were separated by a glass barrier. Aquaria were maintained in phytotron A-chambers for 2 months under short- or long-day photoperiods and day/night temperatures of 30/26, 26/22, 22/18, and 18/14 C. Jars were placed in phytotron C-chambers under constant long day photoperiod with day/night temperature of 26/22 C, long day photoperiod with day/night temperature gradually decreasing from 26/22 C to 22/18 C, or long day gradually approaching short day at the above temperature regimes.

Seed Production

Hydrilla was collected from four replicate $0.1m^2$ quadrats in three locations in Lake Wheeler (North Carolina) November 1, 1984; five $0.1m^2$ quadrats in Lake Wheeler, Lake Raleigh, and Big Lake (North Carolina) on November 1, 7, 14, 27, 1985; and five $0.1m^2$ quadrats from Lake Wheeler October 15 and 31, 1986. Fruits were collected from the vegetation and opened to determine the number of mature seeds contained within. Mature seeds were brown in color and hard as compared to green immature seeds that could be crushed between the fingers with slight pressure.

Seed Viability

Sixty-two mature hydrilla seeds were collected from Big Lake January 6, 1986. Twenty of these were placed immediately on Petri dishes that contained soil mix consisting of 2 redi-earth: 1 sterilized topsoil: 1 sand and 20 seeds were placed immediately in Petri dishes without rooting media. Petri dishes were placed in aquaria that contained filtered water from Lake Wheeler, and maintained in a long day greenhouse. Twelve seeds were stored in darkness, in distilled water at 5.0 C for 14 weeks and placed in a Petri dish with soil as described. Forty hydrilla seeds were collected from Lake Wheeler October 15, 1986 and placed on soil as described. Seeds were observed daily for germination and seedling viability.

Karyotyping

Hydrilla collected from eleven geographically separate

populations in the United States (Table 1) was cultured in a greenhouse and root tips were collected from these cultures for karyotyping. Root tips were harvested between 7 and 9 am for obtaining maximum metaphase images. Root tips were pretreated in 8-hydroxyquinoline for 2-4 hours. After pretreatment the root tips were rinsed in distilled water and placed in Farmers fluid (3:1 ethanol/acetic acid) at room temperature for a minimum of 4-24 hours. Root tips were then macerated in 10% HCl at 60 degrees for approximately 10 minutes, and rinsed. DNA was stained by soaking root tips overnight in Leuco-basic fuchsin and then rinsing in distilled water. A root tip section 1 mm in length was placed on a microscope slide with a drop of 45% acetic acid. A cover slip was placed on the slide and the eraser end of a pencil was used for initial spread of the cells. The slide was then pressed at 5000 psi on a Carver lab press. A dry ice method was used to make permanent slides.

Cells that were photographed and used for karyotyping were catalogued by recording the slide and negative frame number on the film. Chromosome images were cut from the prints and visually arranged into eight groups of homologues (n=8). Arm lengths were measured on prints and corrected for magnification. Total chromosome lengths, arm ratios (short arm length/long arm length), centromere indices (short arm length/total chromosome length), and standardized lengths (chromosome length/longest chromosome length in the cell) were calculated. Chromosome groups were then plotted by standardized length and arm ratio to detect and correct inaccuracies in visual groupings. Homologous

Table 1. Collecting locations, collectors, and numbers of cells counted for karyotyping hydrilla populations in the United States.

Location	Collector-Date	Total No. of cells counted
Constitution Gardens Washington D.C.	R. R. Yeo- [1]	10
Dyke Marsh, VA	C. F. Reed-11/85	2
Fort Lauderdale, FL (culture)	D. L. Sutton-9/84	2
Guntersville, Resovoir Jackson Co. AL	E. R. Burns-10/84	1
Kenilworth Aquatic Gardens, Washington, D.C.	K. A. Langeland-10/85	3
Lake Kerr, FL	K. A. Langeland-12/84	2
Lake Raleigh, NC	C. B. Smith-10/84	2
Lake Wheeler, NC	C. B. Smith-10/84	5
Lilypons Aquatic Gardens, MD	K. A. Langeland-10/85	1
Lilypons Aquatic Gardens, TX	W. T. Haller- [2]	2
Violets Lock, MD	R. R. Yeo- [1]	1

[1]Received 5/85, collection date uncertain.

[2]Received 12/84, collection date uncertain.

groups were compared among populations with respect to standardized length and arm ratio using multivariate analysis(SAS 1985).

RESULTS AND DISCUSSION

Environmental Stimuli for Flower and Seed Production

Floral production did not occur under any of the environmental conditions tested in the phytotron. Competition between filamentous algae and hydrilla, encountered throughout the study, despite attempts to sterilize tubers, aquariums, and growth media precluded evaluation of this portion of the study.

Staminate and pistillate floral initiation were observed in lakes during early July during this study, and previously by Harlan et al. (1985). This suggests a long-short-day flowering response by monoecious hydrilla compared to a day-intermediate response by dioecious, pistillate hydrilla in Florida (Haller, 1978). These two apparent strains of the same species have evolved different flowering responses. The flowering responses do not represent a temporal separation to crossing because floral initiation in monoecious hydrilla continued until senescence November-December.

Seed Production

Viable seed production was only observed in Lake Wheeler during this study whereas immature seeds were found in Lake Raleigh and Big Lake, and no seed production was documented in

Lake Benson. Average seed density in Lake Wheeler ranged from 3-30 mature seeds and 5-74 immature seeds m^{-2} (Table 2). Immature seeds did not germinate but these seeds could have been fertilized/maturing, or unfertilized/non-viable. Numbers of mature seeds did not increase appreciably during the four consecutive sampling periods in 1985, and only one mature seed was found per seed pod throughout this study, hence the immature seeds were probably unfertalized/nonviable. Cook (1982) observed that "those [fruits] that do set seed usually have one, two or three, rarely four and very rarely five or six seeds" for hydrilla populations in South India.

Annual hydrilla seed production rate is difficult to estimate because fruits are difficult to find without removing vegetation from the water column and because the fruits reportedly fall from the parent plant when mature (Cook and Luond 1982). Although hydrilla seed production is low relative to that of many terrestrial plants the numbers are adequate to provide a source of sexual propagules for dispersal by waterfowl or other agents, provided they are viable and can survive after consumption and or desiccation.

Seed Viability

Viability of hydrilla seed collected from Lake Wheeler was low under all conditions tested (Table 3). Germination rate ranged from 30% (January) to 5% (October). Although it was not possible to collect enough seeds to statistically test for a difference between planting immediately and cold treatment, there

Table 2. Fruit and seed production by monoecious hydrilla in Lake Wheeler (NC).

Date	Fruits	Seed		$\bar{n}$
		Mature	Immature	
	Average (range)			
11-01-84	6 (0-10)	3 (0-10)	5 (0-10)	12
11-01-85	-	8 (0-30)	-	5
11-07-85	-	8 (0-40)	-	5
11-14-85	-	16 (0-20)	-	5
11-27-85	-	10 (0-30)	-	5
10-15-86	68 (0-110)	30 (0-70)	74 (0-190)	5
10-31-87	32 (10-70)	18 (0-50)	16 (10-30)	5

was no apparent effect. The large difference between germination rate of seeds collected in January vs. October may reflect differences in collection dates, however; tests were not designed to test this effect.

Seeds collected in January germinated over a period of 7-43 days but no seeds collected in October germinated after 23 days. Of the seeds that germinated, only one seedling continued to grow at a rate visibly similar to vegetative clones from Lake Wheeler. All others attained a length of 2-4 cm with one to several branches and roots but did not elongate further. None of these stunted seedlings survived longer than 214 days. Low viability and seedling vigor may be attributable to the triploid nature of North Carolina hydrilla populations.

Karyotyping

The triploid chromosome number of 24 was observed in all populations in this study. This corroborates Harlan et al. (1984) who reported that monoecious hydrilla collected from Lake Wheeler, NC was triploid (3n=24). However, our observations conflict with those of Verkleij et al. (1983) who described diploid (2n=16) hydrilla collected from "Washington D. C., Reflecting pool; Washington D. C., Kenilworth Gardens; and Maryland, Lilypons Gardens". These were most likely representatives of the same populations used in our study. This discrepancy may suggest the existance of mixed populations of diploid and triploid organisms and, or chimeras. In the former case, random collections could result in obtaining either diploid

Table 3. Germination (percent) of hydrilla seed collected from Lake Wheeler (NC) when placed in aquaria under long-day photoperiod.

Date collected	Placed on rooting medium	No rooting medium	Cold treated, no rooting medium
01-06-86	30	15	25
10-15-86	5	-	-

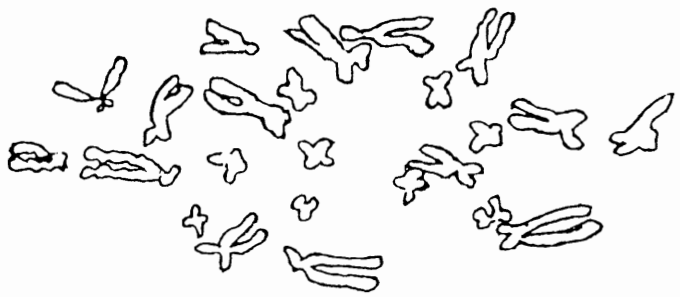
or triploid karyotypes. Although the probability is low, it is possible for triploid parent plants in the populations to produce diploid progeny, in addition to progeny with other ploidies. Diploid progeny would be viable, whereas embryos with one to several extra chromosomes would probably not be viable, or produce low vigor seedlings, such as those observed in this study. In the latter case, either the diploid or triploid chromosome number (or other ploidy) could be observed in the same collection if entire chromosomes sets are duplicated in the chimera. Chimeras have previously been suggested in the hydrochacitaceae (Sharma and Bhattacharyya, 1956).

Since it is well documented that the triploid number for hydrilla is 24, with each homologue represented three times in somatic cells at metaphase, it was possible to construct an idiogram for each cell that consisted of eight groups of three homologues (Figure 1, Table 4); to compare the chromosomes among populations. Chromosomes within groups were not significantly different among populations with respect to standardized length and arm ratio according to Wilks' lambda, Pillai's trace, Hotelling-Lawley trace, or Roy's maximum root (SAS, 1985). Therefore, we concur with Chadhuri and Sharma (1978) that karyotypes are not correlated with morphology or ecology. Differences in length with respect to ecology, as suggested by Misra (1966, 1971) would be difficult to demonstrate because of the variability in chromosome length within the same population and root tip. For example, in this study the length of the longest chromosome in a cell ranged from 4.25 um to 8.38 um in

the same root tip. These differences are a result of the degree of condensation of chromosomes that was affected by the stage of metaphase and the fixation process.

Since chromosomes were not significantly different between populations, morphological characteristics of chromosomes were combined and grouped among populations into a karyotype that was common to all populations (Figure 1, Table 4). Chromosome groups 1 and 5 (Figure 1) are distinctly acrocentric (arm ratio < 0.33) and separate distinctly from other groups by size (standardized length) and arm ratio (Figure 1 and 2, Table 4). Groups 2-4 appear as a single natural grouping (Figure 2) but they were separated into three separate groups to attain eight groups of three homologues among the 24 chromosomes (Figure 1). Group 2 tends to be longer than Groups 3 or 4 and less acrocentric than Group 3 (Figure 2, Table 4). Group 3 tends to be longer and more acrocentric than Group 4 (Figure 2, Table 4). The nine chromosomes of groups 6-8 are similar in size but, despite some overlap, these groups appear to be destinct considering differances in arm ratio (Figure 2, Table 4). Groups 6 and 8 are submetacentric (0.33 < arm ratio < 1.00), with group 6 having a smaller arm ratio (Figure 2, Table 4). Group 7 is metacentric (arm ratio = 1) (Figure 2, Table 4). Secondary constrictions, described by Sharma and Bhattacharyya (1956) or a pair of unequal chromosomes suggested by Sinoto (1929), were not identified in this study or by other researchers.

Chromosome morphology observed in this study was similar to that reported by others. Groups 1-5 and 6-8 correspond,



Group 1 2 3 4

Group 5 6 7 8

Figure 1. Early metaphase, somatic chromosomes of hydrilla [Hydrilla verticillata (L.f.) Royle] collected from Lake Wheeler, North Carolina, 10/84.

Table 4. Chromosome morphology of hydrilla collected from various populations in the United States (n=93).

Chromosome Group No.	Total Length (u)		Standardized[1] Length		Arm Ratio[2]	
	Average	Range	Average	Range	Average	Range
1	5.54(0.11)[3]	3.32-8.37	0.94(0.01)	0.77-1.00	0.22(0.00)	0.16-0.31
2	5.47(0.10)	3.32-7.50	0.93(0.01)	0.80-1.00	0.53(0.01)	0.43-0.65
3	4.97(0.10)	2.93-7.00	0.84(0.01	0.69-0.95	0.41(0.01)	0.29-0.58
4	4.39(0.08)	2.54-6.12	0.75(0.01)	0.59-0.85	0.51(0.01)	0.32-0.70
5	3.51(0.06)	2.00-5.00	0.60(0.00)	0.44-0.74	0.26(0.00)	0.17-0.38
6	2.18(0.04)	1.30-3.25	0.37(0.00)	0.29-0.53	0.61(0.01)	0.42-1.00
7	2.12(0.04)	1.20-3.00	0.36(0.01)	0.26-0.53	0.98(0.00)	0.80-1.00
8	1.69(0.03)	0.90-2.25	0.29(0.00)	0.20-0.41	0.80(0.01)	0.50-1.00

[1]Chromosome length/length of longest chromosome in cell.

[2]Short arm length/long arm length.

[3]Numbers in parentheses are standard errors of means.

respectively, to the 15 long and 9 short chromosomes reported by Sonoto (1929) for hydrilla from Itikawa, Japan; and groups 1-3, 4-5, and 6-8 correspond, respectively, to the 9 long, 6 medium, and 9 short chromosomes of female triploid plants from Japan. Our idiogram is similar in appearance to that published by Harada (1955). However, chromosome morphology was not quantified in that idiogram. Czapik (1978) quantified the idiogram of diploid hydrilla from Irish lakes and a triploid from Poland. Neither of these populations were observed to flower, but it was assumed that they were female because their idiograms were similar to those of female plants reported by Sinoto (1929). The chromosomes of the triploid, with 12 acrocentric, 9 submetacentric, and 3 metacentric chromosomes, corresponded closely with the diploid. The average size of chromosomes in the United States populations (1.67 um - 5.54 um; Table 4) was somewhat smaller than that of the diploids from Irish lakes (2.46 um - 7.79 um). Chromosomes of the triploid from Poland were reportedly more condensed than the diploids which may explain the apparent smaller size chromosomes from the United States populations. The size of chromosomes in the Irish lake populations compare well with those of the United States populations in that the group sizes of both idiograms compare proportionately, and the sizes of those from the Irish lakes fall within the ranges observed in the United States populations. Although our idiogram differ slightly from the Polish triploid (6 acrocentric, 15 submetacentric and 3 metacentric chromosomes) we feel that inaccuracies in visualizing and measuring chromosomes

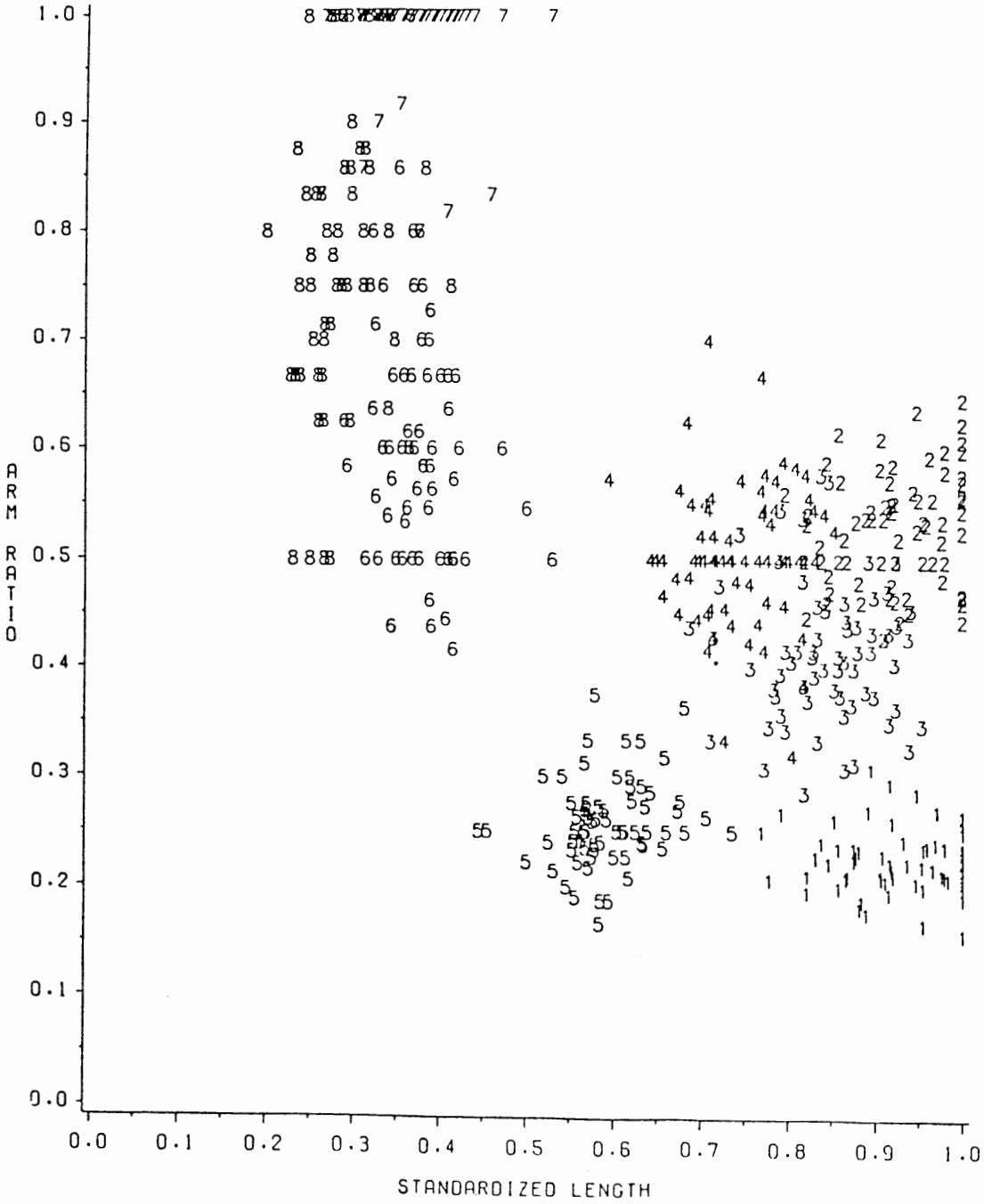


Figure 2. Scatter plot of arm ratios (short arm length/long arm length) and standardized lengths (chromosome length/length of largest chromosome in cell) of somatic chromosomes from eleven hydrilla populations [Hydrilla verticilla (L.f.) Royle] in the United States.

can explain these slight differences, and that the idiograms for hydrilla from Poland and the United States can be considered the same.

CONCLUSIONS

Hydrilla populations in North Carolina are monoecious and have the potential for producing viable seed. Based upon observations in this study, seed production is low and viability of seedlings that germinate from viable seeds is also low. Therefore, the potential for hydrilla dispersal by seed is low compared to dispersal by vegetative methods, especially when vegetative dispersal is assisted by cultural practices such as transport of plant material on boats and by the Aquarium plant industry. Precautions to limit the cultural spread of hydrilla such as posting of boat ramps and monitoring of the Aquarium plant industry should continue to be strictly imposed and the management program for hydrilla in North Carolina (Langeland, 1986) should be followed.

The triploid chromosome number of 24 was observed in somatic cells of hydrilla from North Carolina populations. This may explain the low seed and seedling viability observed. Karyotypes and chromosome numbers of hydrilla from North Carolina were not different from other monoecious populations in the Eastern United States. Discrepancies between chromosome numbers observed in previous studies and this research suggest chimeras in hydrilla or populations with individuals of differant ploidy. These possibilities should be researched further.

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