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The distribution of seeds, seedlings, and established plants of Arrow Arum (*Peltandra virginica* (L.) Kunth) in a freshwater tidal wetland[1]

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WHIGHAM, D.,[1] R. SIMPSON,[2] and M. LECK.[2] ([1] Chesapeake Bay Center for Environmental Studies, Smithsonian Inst., P.O. Box 28, Edgewater, MD 21037 and [2] Biol. Dept., Rider Coll., Lawrenceville, NJ 08648). The distribution of seeds, seedlings, and established plants of arrow arum (*Peltandra virginica* (L.) Kunth) in a freshwater tidal wetland. Bull. Torrey Bot. Club 106: 193–199. 1979.—Arrow arum is a widely distributed perennial in Delaware River freshwater tidal wetlands. The disjunct distribution of established arrow arum plants and the rather cosmopolitan distribution of seeds within the Hamilton Marsh freshwater tidal wetland suggests that factors which determine where seedlings become established are most important in controlling its population structure. Established plants were absent and seed mortality was high on stream banks, which suggests that water velocity may limit seedling establishment. The almost complete absence of arrow arum from all but the littoral fringe of ponds suggests that light is also an important factor in limiting the establishment of seedlings. Buried seed studies showed that the seeds were distributed throughout the wetland, but that densities were greatest on the high marsh. Allelopathy may be an important factor in controlling seed germination.

Peltandra virginica (L.) Kunth. (Arrow arum) is a widely distributed perennial in eastern North American wetlands (Blackwell 1972) and has been reported to occur in almost all types of freshwater to low salinity coastal tidal wetlands (Whigham *et al.* 1978). In contrast to many perennial emergent macrophytes, *Peltandra* is dispersed almost exclusively by seeds and, once established, there is little asexual propagation except by occasional fragmentation of plants. Dispersal is hydric and, in New Jersey, occurs from late summer until well into the winter. Fruit dispersal is affected by decomposition of the spathe and resultant release of ripe berries. The berries, which usually contain one seed, are dispersed throughout the wetland because they are buoyant when released. Seeds will not germinate until the fruit wall is disrupted (West and Whigham 1976). The fruit then loses its buoyancy because of imbibition of large amounts of water by a gelatinous mass that lies between the fruit wall and the seed (West and Whigham 1976).

The dispersal of *Peltandra* fruits is especially obvious in freshwater tidal wetlands where incoming and outgoing tidal waters transport them individually or on rafts of litter to all areas of the wetland. Like McCormick (1970), McCormick and Ashbaugh (1972), and Good and Good (1975), we noted that established plants of arrow arum did not seem to occur in all habitats and/or vegetation types of the Hamilton Marshes even though we observed that fruits seemed to be uniformly dispersed throughout the wetland in the fall and winter. The purpose of this paper is to report results of studies on the relationship between the distribution of *Peltandra* seeds, seedlings, and established plants as well as studies on temporal changes that occur in *Peltandra* seed populations in adjacent habitats during the time period between

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Table 1. Habitats and vegetation types sampled. NS indicates that those areas were not sampled.

Habitat	Tidal characteristics	Vegetation types	Number of sites sampled	Number of quadrats sampled	Physiognomically dominant plants
I. Pond	Continuous inundation	A. Yellow water lily	1	9	*Nuphar advena, Polygonum punctatum*
II. Pond-like	Standing water always present Tidal amplitude @ 1 m	A. Arrow arum	1	3	*Peltandra virginica, Polygonum punctatum, Zizania aquatica* var *aquatica, Pontederia cordata*
		B. Cattail	1	3	*Typha latifolia, Peltandra virginica*
		C. Purple loosestrife	1	3	*Lythrum salicaria, Polygonum punctatum, Pontederia cordata*
		D. Wild rice	NS	NS	*Zizania aquatica* var *aquatica, Polygonum punctatum, Peltandra virginica*
		E. Yellow water lily	1	3	*Nuphar advena, Polygonum, punctatum, Pontederia cordata, Zizania aquatica* var *aquatica*
III. High marsh	4–6 hours of inundation	A. Arrow arum-mixed	7	21	*Peltandra virginica, Acorus Calamus, Sagittaria latifolia, Bidens laevis, Polygonum arifolium, Polygonum sagittatum*
		B. Cattail	3	9	*Typha latifolia, Typha angustifolia, Peltandra virginica, Polygonum arifolium*
		C. Purple loosestrife	1	3	*Lythrum salicaria, Peltandra virginica, Polygonum arifolium*
		D. Wild rice	NS	NS	*Zizania aquatica* var *aquatica, Polygonum arifolium*
IV. Stream bank	6–8 hours of inundation	A. Wild rice	1	3	*Zizania aquatica* var *aquatica, Polygonum arifolium, Pontederia cordata*
	At least 6–8 hours inundation	B. Yellow water lily	3	3	*Nuphar advena, Acnida cannabinus, Polygonum punctatum*

thawing of the wetland surface and seedling establishment.

The studies were conducted in the Hamilton Marshes, which form the northernmost freshwater tidal wetland in the Delaware River estuarine system. The wetlands have been the location of several recent studies (Simpson *et al.* 1978; Whigham and Simpson 1975, 1976a, 1976b, 1977, 1978; Whigham *et al.* 1978).

Methods. The frequency of occurrence and density of *Peltandra* within the wetland was determined by performing a stratified random sampling of vascular plants during the 1973 growing season. The wetland was divided into four major habitats and six vegetation divisions (Table 1) based on our preliminary reconnaissance of the wetland and the earlier work of McCormick (1970) and McCormick and Ashbaugh (1972) who had divided other Delaware River freshwater tidal wetlands into separate habitat and vegetation types. The habitats were selected to represent major physical units within the wetland while the vegetation types were defined on the presence of physiognomically dominant plant species. A more detailed description of the habitats and vegetation types can be found in Whigham and Simpson (1975, 1976a, 1977). The distribution of *Peltandra* was determined by sampling vegetation in randomly positioned quadrats (1 m^2) in each vegetation type. Three quadrats were located in each area and they were sampled on four occasions between 6 June and 15 August, 1973. In addition to counting all individuals, both seedlings and larger established plants, in each quadrat, we counted the number of *Peltandra* fruiting spathes within each quadrat.

From preliminary work, it appeared that the most obvious disjunction was the almost total lack of *Peltandra* along stream banks and its dominance on areas of the high marsh that were immediately adjacent to the stream bank. The distribution of seeds was examined in detail in 1974, when we conducted a survey to quantify temporal changes that occurred in *Peltandra* seed populations in a high marsh vegetation type and an adjacent stream bank habitat. Three quadrats (2 m × 2 m) were established in each of the two habitats. The two areas

Table 2. Values in the table are frequency of occurrence of arrow arum in the areas sampled during the 1973 vegetation survey. A dash (—) indicates which vegetation types did not occur in the habitats studied. A plus (+) indicates that the vegetation type occurs in the Hamilton Marshes, but was not examined during this study.

	Habitat type			
Vegetation type	Pond	Pond-like	Stream bank	High marsh
Arrow arum	+	100	—	—
Arrow arum-mixed	—	—	—	57
Cattail	—	100	—	56
Purple loosestrife	+	67	—	67
Wild rice	—	+	0	+
Yellow water lily	0	67	0	—

were 10 m apart and the quadrats within each habitat were separated by 5 m. The number of seeds in each quadrat was counted on six occasions between 15 March and 26 April, and each seed was examined to determine whether or not (1) the fruit wall was intact, (2) the seed had germinated, and/or (3) there were any signs of grazing on the seed.

Additional studies were conducted in 1976 and 1977 when, as part of a larger study of buried seed populations (Leck and Graveline, In prep.), we examined the horizontal and vertical distribution of *Peltandra* seeds in several vegetation and/or habitat types in most of the areas studied in 1973 and 1974. Between December 10–16, 1976, 10 substrate samples (10 × 10 × 10 cm) were collected from each of the following areas: (1) Stream bank habitat, (2) High marsh habitat with arrow arum-mixed vegetation, (3) High marsh habitat with ragweed (*Ambrosia*) vegetation, (4) Stream bank habitat with wild rice (*Zizania*) vegetation, (5) High marsh habitat with cattail (*Typha*) vegetation. The samples were divided into three layers (0 to 2, 4 to 6, and 8 to 10 cm) that were then cut in half. The halves were combined to form duplicate composite samples for each site. The samples were then stored until January 21, 1977 at 5°C for afterripening and then placed in aluminum pans in the greenhouse where they were watered daily. Cumulative counts were made of the number of seedlings of all species that germinated in each pan with seedlings being removed after they were counted. The experiment was repeated using substrate samples that were collected in March, 1977, from the arrow arum-mixed and cattail vegetation types of the high marsh habitat as well as the wild rice vegetation of the stream bank habitat. The samples received treatments similar to those collected in December, 1976 with the exception that one pair of each composite sample was maintained in a continually flooded condition.

Additional field studies included noting seedling presence on 14 April and 6 May, 1977 at the five sites where sediments were collected for the buried seed study. Additionally, seedling counts were made in the field on May 23, 1977 using five (25 × 25 cm) quadrats at each site.

Results. Results of the vegetation survey are shown in Tables 2 and 3. *Peltandra* was recorded in two of the four habitats

Table 3. Density (individuals m²) of arrow arum in the Hamilton Marshes based on the 1973 vegetation survey. Values are means ± 1 standard error. A dash (—) indicates which vegetation types did not occur in the habitats studied. A plus (+) indicates that the vegetation type occurs in the Hamilton Marshes, but were not examined during this study.

	Habitat type				
Vegetation type	Pond	Pond-like	Stream bank	High marsh	$\bar{X}$ frequency of vegetation type
Arrow arum	+	5.3 ± 2.6	—		5.3 ± 2.6
Arrow arum-mixed	—	—	—	1.8 ± 0.5	1.8 ± 0.5
Cattail	—	3.0 ± 0	—	2.4 ± 1.6	2.6 ± 1.2
Purple loosestrife	+	0.7 ± 0.3	—	3.0 ± 1.7	1.8 ± 0.9
Wild rice	—	+	0	+	0
Yellow water lily	0	0.7 ± 0.3	0	—	0.2 ± 0.2
$\bar{X}$ density of habitat type	0	2.4 ± 0.8	0	2.1 ± 0.5	
$\bar{X}$ density in wetland					1.5 ± 0.3

Table 4. Results of the 1974 study of temporal changes in *Peltandra* seed populations on a stream bank and adjacent high marsh habitat. Values are means ± 1 standard error.

	Seed conditions				
Date	Seeds/m²	% Germinated[1]	% With fruit wall intact	% With broken fruit wall	% Grazed
		I. High Marsh			
March 15	22.5 ± 2.6	0	9.8 ± 1.8	90.2 ± 1.8	0
29	20.1 ± 1.6	0	11.8 ± 2.8	88.2 ± 2.8	3.3 ± 1.7
April 5	21.4 ± 4.5	1.8 ± 0.3	11.5 ± 1.8	88.5 ± 1.8	6.2 ± 3.4
12	23.8 ± 5.0	14.2 ± 2.6	4.0 ± 2.2	96.0 ± 2.2	9.4 ± 1.6
19	17.2 ± 2.9	37.4 ± 5.6	5.6 ± 0.8	94.4 ± 0.8	16.2 ± 2.0
26	16.1 ± 2.0	53.3 ± 7.0	1.2 ± 1.2	98.8 ± 1.7	14.8 ± 1.9
		II. Stream bank			
March 15	16.7 ± 1.8	0	19.8 ± 5.2	80.2 ± 5.2	0
29	15.9 ± 1.0	0	22.6 ± 5.7	77.4 ± 5.9	1.2 ± 1.2
April 5	11.8 ± 0.9	12.5 ± 1.6	16.7 ± 1.3	83.3 ± 1.3	7.2 ± 3.6
12	10.2 ± 1.1	35.6 ± 1.5	12.2 ± 7.2	87.8 ± 7.2	16.4 ± 3.2
19	7.8 ± 1.2	45.0 ± 2.9	5.7 ± 2.9	94.4 ± 2.9	11.7 ± 6.0
26	5.0 ± 1.4	63.3 ± 3.3	5.6 ± 2.9	94.4 ± 2.9	14.3 ± 9.8

[1] None of the germinated seedlings were rooted in the substrate during the period of observation.

and five of the six vegetation types sampled. Frequency values were almost the same for pond-like and high marsh habitats and there was a similar frequency distribution in the arrow arum-mixed, cattail and purple loosestrife (*Lythrum*) vegetation types of the high marsh habitat. Density was variable (Table 3) and averaged between 1.8 and 2.6 plants m² in the three vegetation types where it was frequently found. The average density for the wetland was 1.5 ± 0.3 plants m².

Results of the study of temporal changes in seed populations in the high marsh and stream bank sites are shown in Table 4. The majority of fruit walls were broken by 15 March and most were disrupted by 26 April. Patterns of seed herbivory and the phenology of seed germination were similar in both habitats. The major difference was in the size of the seed population which was always higher in the arrow arum-mixed vegetation of the high marsh habitat. Seed density declined temporarily in both habitats, but the decline was more rapid on the stream bank habitat. Seed density on the high marsh was three times that on the stream bank by 26 April.

Results of the buried seed studies are shown in Table 5. Arrow arum only germinated from the top 2 cm of substrate and there were distinct differences between habitats. Two hundred and ninety and 260 seeds per m² germinated from sediments collected from the arrow arum-mixed vegetation compared to 10 seeds per m² from the stream bank habitat, 20 seeds per m² from the ragweed vegetation type, and 0 to 40 seeds per m² from the wild rice vegetation types. No seeds germinated from sediments collected in the cattail vegetation or sediments collected from the stream bottom. Seedling counts made in May (Table 5) show that seedlings were present in all areas except the wild rice vegetation type. Seedling density (9.6 ± 3.9 per m²) in the cattail vegetation and on the stream bank (6.4 ± 3.9 per m²) was less than those found for the arrow arum-mixed and ragweed vegetation types which were 25.6 ± 13.0 and 19.2 ± 6.0 seedlings per m² respectively.

Discussion. The distribution of emergent macrophytes within a wetland is a consequence of the interaction of several factors. Once initially established, a species has the potential for intrawetland dispersal by the production and dissemination of asexually produced plant parts and/or seeds. The rate at which the species spread would be variable. It would be optimum if species could be free of significant predators and produce numerous sexual and/or asexual propagules that would be uniformly disseminated followed by rapid and successful establishment. At the other end of the spectrum would be species that spread very

Table 5. Results of the 1977 buried seed (I) and seedling count (II) studies. All values are numbers of seeds per m^2 or seedlings per m^2 $\pm$ 1 standard error. NS indicates that no samples were collected. A plus (+) indicates seedlings were present while a dash (—) indicates that they were absent.

	Habitat and vegetation type																
	Stream bottom	Stream bank: no vegetation			Stream bank: wild rice			High marsh: arrow arum-mixed			High marsh: ragweed				High marsh: cattail		
Soil depth (cm)		0–2	4–6	8–10	0–2	4–6	8–10	0–2	4–6	8–10	Litter	0–2	4–6	8–10	0–2	4–6	8–10
	I. Buried seed study																
December	0	10	0	0	0	0	0	290	0	0	20	0	0	0	0	0	0
March	NS		NS		40	0	0	260	0	0		NS			0	0	0
	II. Seedling study																
April 14	NS		—			—			+			—				—	
May 6	NS		—			—			+			+				+	
May 23	NS		6.4 ± 3.9			—			25.6 ± 13.0			19.2 ± 6.0				9.6 ± 3.9	

slowly because they produce few seeds that are not widely dispersed and/or because they either do not reproduce asexually or their asexual propagules do not spread rapidly. Unlike most macrophytes (Hutchinson 1975), *Peltandra* must rely on seedling establishment because it lacks, with the possible exception of occasional fragmentation or dislodging of entire plants, any means of asexual propagation. Its dispersal seems to be efficient because of the production of buoyant and numerous fruits that are uniformly dispersed throughout the wetland by tidal waters.

Although fruits are widely dispersed, results of the vegetation survey (Tables 2 and 3) show that the distribution of established plants is rather uniform throughout the high marsh and pond-like habitats, but is uncommon in ponds dominated by yellow water lily (*Nuphar*) and on stream banks that are dominated by wild rice and yellow water lily (Tables 2 and 3). Most likely, seedling establishment in the pond habitat is controlled by water depth with successful establishment only occurring in littoral areas that are flooded to a depth of 0.5 m or less (Hutchinson 1975). Within that zone, aphotic and anaerobic conditions are probably the most important factors in limiting seedling establishment (Hutchinson 1975). West (Unpublished manuscript) found that arrow arum seedlings had high light requirements immediately after they began to emerge from the seed and it seems likely that the littoral zone would be the only habitat within the pond where that condition would prevail. Because water in the pond habitat is anaerobic during the growing season (Simpson *et al.* 1978), it also seems likely that anoxic conditions would restrict arrow arum seedling establishment to the littoral fringe where the substrate would, at times, be exposed to the air. Edwards (1933) found that arrow arum seeds would germinate under anaerobic conditions but suggested that seedling establishment would be unlikely because seedling growth was minimal under those conditions and any increase in seedling size was due to maturation of embryonic cells rather than the production of new cells.

The absence of arrow arum from the stream bank habitat could be due to lack of seeds for regeneration, extensive herbivory of the seeds on the exposed mud banks, failure of seeds to germinate, or failure of seedlings to establish themselves. Our data (Table 4 and 5) show that seeds are not lacking in that habitat and there are no apparent differences in herbivory when we compared the stream bank with the adjacent high marsh. In addition, almost all seeds that were present on the stream bank were capable of germination because the fruit walls were broken (Table 4), a condition necessary for germination (West and Whigham 1976). In addition, results of the buried seed study (Table 5) show that a buried seed reservoir is present in the stream bank substrate and that seeds in the upper 2 cm are capable of germinating. Factors responsible for low rates of seedling establishment on stream banks, therefore, seem to be most important in controlling the population structure of *Peltandra*. The scouring effect of water obviously removes both germinated and ungerminated seeds (Table 4) from the stream banks. Garbisch and Coleman (1978) have shown that arrow arum seeds and seedlings placed at or below the mean tide line have significantly lower germination rates and were quite susceptible to removal by wave action and predation by fish. Light availability on the stream bank, as determined by length of tidal inundation, does not seem to be an important factor except perhaps in undrained stream bottoms. In the Hamilton Marshes, the tidal amplitude is so large (3 m) that the stream bank habitat is completely exposed for between four and six hours during each tide cycle (Table 1). In fact, inundation on the stream bank is of shorter duration than inundation in the pond-like habitat where arrow arum is a common species (Table 2 and 3). Composition of the substrate and desiccation during the ebb tide could also be important factors that restrict seedling establishment on the stream bank. Unfortunately, we do not know the specific substrate requirements of the seedlings nor do we know whether the seedlings are sensitive to dessication. It is known, however, that prolonged desiccation will decrease seed viability (West and Whigham 1976). Garbisch and Coleman (1978) have shown that seedlings growth rates are very slow in transplant beds and in the field and are not affected by substrate differences or fertilization. Our data show that the seeds are present and germinate, but establishment is very uncommon. Apparently, the very slow growth rate, combined with physical and biological stresses, determine that establishment occurs only occasionally.

Because of their ability to float, arrow arum seeds are capable of reaching each habitat and vegetation type. We would, therefore, expect to find a uniform pattern of seedling emergence. The only exception would be the stream bank habitat (Tables 4 and 5). Comparisons of data in Tables 2, 3, 4, and 5 show uniform distribution does not occur. The number of seedlings emerging from soils of the high marsh differ greatly; the lack of emerging seedlings in the cattail area is especially striking. The sediment samples were collected in the same areas that were studied in 1973. Using data from that survey, we calculate that arrow arum plants would produce an average of 35 seeds per inflorescence. With an average of 3.3 inflorescences per plant and a plant density of 2.4 individuals m^2 in the cattail areas, we calculate a seed production rate of 280 seeds m^2 year. Based on those calculations, there should be abundant seeds and seedlings in cattail areas. It is unlikely that all seeds produced within the cattail stand would be removed by tidal waters and there would be additional input from other areas. In fact, we would expect that seed removal would be less than seed input because the arrow arum seeds would not float from the stand because the cattail areas always have considerable standing dead litter (van der Valk and Davis 1978). Results of the germination tests (Table 5) suggest that some other factor may inhibit seed germination. McNaughton (1974) has suggested that cattail is allelopathic. Bonasera, Lynch, and Leck (In prep.) working in the Hamilton Marshes, found that litter and sediment extracts from the same cattail stand inhibited the germination of lettuce seeds. Their results also suggest that allelopathy may be operative, but further research is needed before any conclusions can be made.

Examination of the samples after the completion of the germination tests showed that there were no ungerminated arrow arum seeds present. The presence of arrow arum seedlings in the cattail stand in May (Table 5) could indicate that the samples may not have adequately censused the buried seed populations. However, it is more likely that the seedlings found in May were seeds that rafted into the area during high spring tides.

In summary, differences in the distribution of established plants may be due to many factors. Because asexual propagation is minimal, the factors that determine where arrow arum seeds can successfully become established seem to be most important. The lack of established plants along stream banks and in deeper areas of ponds suggest that water velocity and low light conditions are two important factors limiting seedling establishment. One major unanswered question, however, is why there were distinct differences between the sizes of buried seed populations and the size of the seedling populations within the high marsh habitat. Similar unexplained results have been reported for prairie glacial marshes (van der Valk and Davis 1978). It is obvious that before this discrepancy can be explained, we need considerably more knowledge of the conditions that influence *Peltandra* seedling establishment in the high marsh habitat.

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