INVITED ARTICLE

Consequences of hydrochory in *Hibiscus*

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Abstract

Seed dispersal provides a template upon which the demographic processes of plant life cycles operate and, most importantly, seed dispersal determines the spatial distribution of genetic variation. Here, we review recent studies on seed dispersal by water (hydrochory) in species of *Hibiscus* to elucidate the potential ecological and evolutionary consequences of hydrochory at different spatiotemporal scales. We consider seed dispersal related processes that determine the distribution and dynamics of genetic variation, that is, the spatial shuffling effect of the seed bank that modifies genetic make-up within a population, the formation of a genetic reservoir within a metapopulation, and lineage dispersions and speciation that may produce patterns in plant phylogeography. Seed movement patterns within ecological time and space are likely to leave non-random patterns in long-term plant evolution and phylogeny.

Introduction

Seed dispersal is a critical determinant of plant distribution and demography. It provides the initial template for all the demographic processes of plant life cycles, including establishment, growth and survival (Nathan & Muller-Landau 2000; Wang & Smith 2002). The genetic structure of plant populations is shaped through these processes at different life stages, but is strongly constrained by the initial template formed by seed dispersal.

In this article, we consider our recent studies on hydrochory in species of *Hibiscus*, Malvaceae. In a series of studies, we evaluated the role of seed dispersal in determining the spatial distribution of genetic variation, and its ecological and evolutionary consequences. We also studied the consequences of hydrochory at different spatiotemporal scales, that is, dispersals within populations during a single season and among populations for decades, and rare long-distance migrations over hundreds and thousands of years and longer. The consequences of hydrochory appear at different levels, including the genetic make-up within a population, dynamics of a metapopulation, genetic differentiation between populations, and patterns in speciation.

The aim of this article is to draw the reader's attention to the unique consequences of hydrochory at specific spatiotemporal scales, and to discuss the ecological and evolutionary implications of seed dispersal over short and long distances and over various periods of time. Although the importance of long-distance seed dispersal in understanding the ecology and evolution of plants has been recognized, it is one of the most challenging fields to collect empirical data (Cain *et al*. 2000). We consider that hydrochory provides opportunities to study the role of dispersal both over long distances and over long periods of time because those events are likely to occur more frequently in hydrochory than in other dispersal modes.

The genus *Hibiscus* contains between 200 and more than 300 species, the majority of which occur in tropical and subtropical regions (van Borssum Waalkes 1966; Pfeil *et al*. 2002). Some species in the genus occur in open habitats near water, such as riverbanks and freshwater wetlands, while others occur in brackish tidal and coastal wetlands. Hydrochory has been frequently observed in

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Hibiscus species (Ridley 1930; Tomlinson 1986). The seeds of hydrochorous species float for periods of several months, thus, they have the potential to be dispersed over long distances (Nakanishi 1985, 1988).

We have studied two *Hibiscus* systems. The first one was *H. moscheutos* L. in temperate freshwater–brackish wetlands (Fig. 1a) and the second was *H. tiliaceus* L. and its derivative species in the subtropical and tropical Pacific (Fig. 1c,d). Seed buoyancy in *Hibiscus* is provided by air space within a thick water-impermeable seed coat (Fig. 1b). We studied patterns within and among populations using the former system, and in the latter we studied the speciation process in relation to the shift in seed dispersal modes.

Consequences within populations: Spatial shuffling effect

Hibiscus moscheutos is an herbaceous macrophyte native to the wetlands of eastern North America. In tidal and non-tidal wetlands, interactions between microtopography and hydrology determine the depth, timing and duration of flooding, the length of the dry or exposed period, and the pattern of salinity in estuarine environments. Because of the spatial discontinuity in physical environments, *H. moscheutos* usually occurs in physically isolated patches that are potentially connected by unidirectional flow in freshwater wetlands and bidirectional flows in tidal wetlands. In addition, water levels vary seasonally, with flows being typically higher in the winter in non-tidal freshwater wetlands because of increased precipitation and decreased evaporation and evapotranspiration. We studied hydrochory in *H. moscheutos* within and among populations in non-tidal freshwater and brackish tidal wetlands in Maryland (Kudoh & Whigham 1997, 2001; R. Shimamura *et al.*, unpubl. data, 1998).

One of the unique consequences of hydrochory is a spatial shuffling effect of genetic lineages. Previous studies have shown that long-distance dispersal is frequent in hydrochorous species (Murray 1987; van den Broek *et al.* 2005). However, few studies have addressed the question of how hydrochory results in changes in the spatial structure of genetic lineages among seeds. Seed movement over long periods of time is another rather unique consequence of hydrochory (Nilsson *et al.* 2002; van den Broek *et al.* 2005) as seeds may float for longer than several weeks, resulting in an increased probability that seeds will be spatially shuffled.

R. Shimamura *et al.* (unpubl. data, 1998) studied the effect of hydrochory by comparing the genetic structure of the seed bank in *H. moscheutos* patches before and after water dispersal. They found that hydrochory resulted in
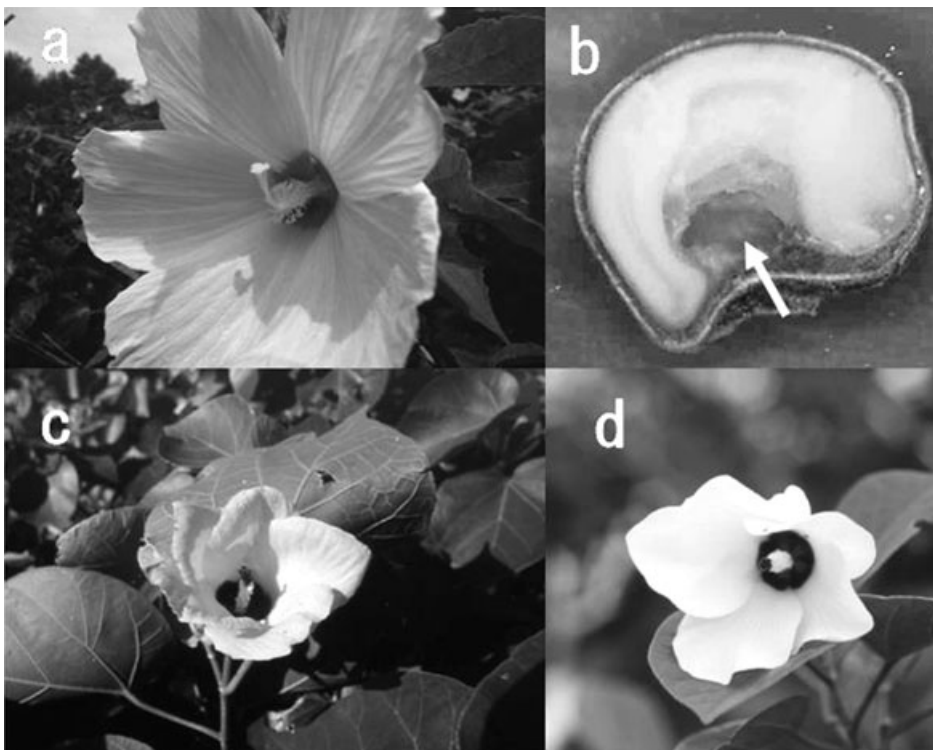

Fig. 1 Photographs showing *Hibiscus* species used in a series of studies, (a) *Hibiscus moscheutos*, (c) *Hibiscus tiliaceus* and (d) *Hibiscus glaber*, and (b) a dissectional photograph showing an air space (shown by an arrow) inside the water-impermeable seed coat of a *H. moscheutos* seed. *Hibiscus moscheutos* is native to freshwater and brackish wetlands of eastern North America. *Hibiscus tiliaceus* is common to coastal habitats across the subtropical and tropical regions of the Pacific, Indian and Atlantic Oceans. *Hibiscus glaber* is an endemic to the Bonin (Ogasawara) Islands, the oldest oceanic islands in the northwestern Pacific. Seeds of *H. moscheutos* and *H. tiliaceus* are buoyant, while those of *H. glaber* have lost their buoyancy.

significant differences in the genetic structure of the seed bank, especially in tidal wetlands. Seeds of *H. moscheutos* are initially dispersed by gravity and then secondarily by water during flooding events, mostly in the late autumn, winter and early spring. They sampled seeds from soils in autumn and the following spring, and determined the allozyme variation at three sites with contrasting flooding regimes. In two sites in brackish marshes, water fluctuations were frequent and hydrochory resulted in changes in the spatial heterogeneity of alleles. In a site in a freshwater marsh, water fluctuation was moderate and seed movements during flooding did not alter levels of spatial heterogeneity.

Previous studies have demonstrated that the spatial pattern of seed-fall and seedling emergence are not always closely correlated, suggesting that many seeds experience secondary seed dispersal prior to germination (Jordano & Herrera 1995; Bohning-Gaese *et al*. 1999; Tomita *et al*. 2002). Hampe (2004) reported that hydrochory extensively altered the spatial pattern of initial seed distributions formed by bird dispersals. Although few studies have compared the genetic structures of seed banks before and after secondary seed dispersals, several studies are worth mentioning here. In *Primula sieboldii*, a hydrochorous herb in riparian habitats, Kitamoto *et al*. (2005) found that spatial genetic structure of plant populations became absent at sites near streams. In other examples, artificial disturbances of soils have been shown to mix and destroy spatial genetic structures of seed banks (Bonnin *et al*. 2001; England *et al*. 2003).

It has been shown that the genetic structure of populations can be critical in the evolution of plant life history (Kalisz *et al*. 1999, 2001). We suggest that seed dispersal can be a component of the mating system by modifying the spatial distribution of genetically related individuals. Relatedness among neighboring plants often determines the levels of inbreeding (Griffin & Eckert 2003; Herlihy & Eckert 2004). Biparental inbreeding often increases with the number of genetically related individuals in neighboring plants (Snow *et al*. 1996; Degen *et al*. 2004). In populations with high biparental inbreeding, selective values for preventing geitonogomous pollinations are expected to be lowered because the relative advantages of interplant mating become weak. In our *H. moscheutos* system, spatiotemporal mixing of seeds by flooding is expected to reduce spatial aggregations of genetically related individuals and, consequently, lower the level of biparental inbreeding.

Kudoh and Whigham (1997) reported that *H. moscheutos* populations at the adult stage were genetically in Hardy–Weinberg equilibrium. A possible hypothesis for this is that the combination of hydrochory that weakens genetic structuring and the mating system that prevents geitonogamous pollination realizes random mating in *H. moscheutos* populations.

Consequences among populations: The formation of a genetic reservoir

Habitats near the water often experience natural disturbances caused by water increases resulting from flooding or high tide (Johansson & Nilsson 1993; Pollock *et al*. 1998), and these disturbances may cause frequent extinctions of local populations (Jakalaniemi *et al*. 2005). Plant species in wetlands, including seasonally flooded habitats, often have buoyant seeds with high mobility (Lopez 2001; Boedeltje *et al*. 2004; Jansson *et al*. 2005) and may form transient seed banks (van den Broek *et al*. 2005). Consequently, metapopulation structure becomes critical in determining how genetic diversity is maintained in hydrochorous species.

Kudoh and Whigham (1997) studied water seed dispersal among multiple populations of *H. moscheutos* by examining genetic structures and estimating gene flows. The levels of genetic differentiation indicated that the *H. moscheutos* populations are interconnected with each other by seed migration and form a metapopulation (Kudoh & Whigham 1997). The genetic structures were analyzed in relation to the background landscape, because seeds should go through landscapes to travel between populations. This type of approach in analyzing genetic structures has subsequently been called the landscape approach or landscape genetics (Sork *et al*. 1999; Manel *et al*. 2003).

Populations of *H. moscheutos* occur as physically isolated patches within wetlands. However, they are connected by water flow that allows seeds to travel between the physically isolated populations. In brackish wetlands, some populations occurred close to the tidal streams, while others occurred near the upland boundary in areas that were only connected to the tidal stream during periods of very high tides (e.g. spring tides or storm tides). We found that *H. moscheutos* patches in the two areas differed in connectivity through seed dispersal. Patches near the tidal stream had no significant genetic differentiation, while patches adjacent to the uplands were isolated genetically from other populations.

Kudoh and Whigham (2001) further analyzed the genetic composition of *H. moscheutos* seeds that were floating in the tidal stream. They found that the genetic make-up of floating seeds was similar to those of populations along tidal streams, demonstrating that seeds were widely dispersed throughout the tidal stream over distances of several hundred meters.

The two studies suggested an interesting structure of the *H. moscheutos* metapopulation, and its role in preserving genetic diversity within the system. There was a genetically united core population along the tidal stream with hydrochory being responsible for the maintenance of a single genetically panmictic population. This core population works as a genetic reservoir, because it turned out that a rare allele, *Est-c*, was kept in this core population. This finding is reasonable if extensive seed dispersal by water unites multiple populations and makes the effective population size great enough to prevent the loss of alleles by random genetic drift.

River systems are also known to be important corridors of plant dispersion (Schneider & Sharitz 1988; Nilsson *et al*. 1991; Johansson & Nilsson 1993; Merritt & Wohl 2002). Fragmentation of natural water flows, however, has become common because of water regulation by human activities, and this fragmentation can affect surrounding vegetations (Jansson *et al*. 2003). In this line of arguments, our results suggested that fragmentation of water systems may destroy the function of a metapopulation of hydrochorous plant species. Therefore, even in cases without changes at the level of species make-up of wetland/riparian vegetation, river fragmentation will alter the seed flow and structure of metapopulations (Jansson *et al*. 2005). Genetic analysis of hydrochorous species will become increasingly important to understand how natural and altered landscapes determine the structure of plant metapopulations (Lundqvist & Andersson 2001; Imbert & Lefevre 2003).

Phylogeographic consequences: Lineage dispersions and speciation

Seed dispersal is an ecological phenomenon that determines where offspring of certain lineages exist in the next generations. Because isolation of lineages is a major cause of speciation, seed dispersal has long-term consequences that may create specific patterns in plant phylogeography. The long-term consequence of hydrochory is often observed in island biogeography (Carlquist 1974). Because all ancestors of island species should have crossed ocean, hydrochory is known to be a major dispersal mode for ancestral populations of island flora.

In the north-western Pacific, three *Hibiscus* species occur that belong to section *Azanza*, that is, *Hibiscus tiliaceus*, *Hibiscus hamabo* Siebold et Zucc. and *Hibiscus glaber* Matsum. ex Nakai. *Hibiscus tiliaceus* is common to subtropical and tropical regions across the Pacific, Indian and Atlantic Oceans (Fryxell 2001; Takayama *et al*. 2002),

and its geographic and local distribution is largely determined by seed dispersal by ocean currents. The species occurs on most islands in the region irrespective of their origins (i.e. oceanic and continental) and the wide distribution is obviously realized by long-floating buoyant seeds (Nakanishi 1988). In contrast to its wide geographic distribution, its local occurrence is often restricted to coastal habitats (Tomlinson 1986), where they typically occur as a series of physically isolated and variously sized local populations that are connected by seawater (Kudoh & Kachi 1997). The reported pattern in genetic variation, large intrapopulation genetic diversity with high estimated gene flow between adjacent populations, suggests that local populations form a metapopulation connected by seed dispersal through water (Tang *et al*. 2003).

Hibiscus hamabo occurs in coastal habitats in the warm temperate regions of the north-western Pacific and it is known to possess long-floating buoyant seeds (Nakanishi 1985). *Hibiscus glaber* is an endemic to the Bonin (Ogasawara) Islands, the oldest oceanic islands in the north-western Pacific. Reflecting the long geographic isolation from the continental area, the Bonin flora includes a large number of endemic species, but most species have closely related counterparts on continental areas. Seeds of *H. glaber* do not float on sea water (H. Kudoh *et al*., unpubl. data, 1999). The loss of seed buoyancy and its endemism to the Bonin Islands suggested that two events occurred in the speciation of *H. glaber*. First, it was most likely derived from an ancestral population with buoyant seeds and, second, the speciation should have occurred in the Bonin Islands. It is most reasonable to consider that *H. glaber* has derived from one of the lineages of *H. tiliaceus.*

We have been examining possible isolation mechanisms that resulted in the evolution of *H. glaber* in an island system where it co-occurs with *H. tiliaceus* (Takayama *et al*. 2005). The analysis of chloroplast DNA sequences revealed that *H. glaber* shares the most common ancestor with one of the widespread lineages of *H. tiliaceus* that are absent from the Bonin Islands (Takayama *et al*. 2005). The results suggested multiple migrations of this group of plants to the Bonin Islands.

The most plausible scenario is as follows. The earlier immigrants of *H. tiliaceus* to the Bonin Islands had adapted to inland habitats and evolved into *H. glaber*. The mechanisms that resulted in the formation of the new species were geographic isolation and the loss of seed buoyancy, the latter restricting the distribution of *H. glaber* to the Bonin Islands. More recent migrations of *H. tiliaceus* have resulted in the present pattern of co-occurrence of *H. glaber* and *H. tiliaceus.* The scenario just presented corresponds with what is known about island

geography of the north-western Pacific. The Bonin Islands are far older than other islands in the area, having their origin in the Pleistocene and 1.8–3.2 million years' history of island biota (Ito 1998; Takayama *et al.* 2005).

The *H. glaber* example clearly shows how ecological specialization of seed dispersal could create a distinct phylogenetic pattern. Takayama *et al.* (2005) further reported that changes in seed dispersal modes resulted in contrasting genetic structures between species. The majority of haplotypes of *H. tiliaceus* are widely distributed across the Pacific islands and their geographic ranges overlap each other. In *H. glaber*, each haplotype turns out to be localized into its own particular area within the islands. A pattern explicable as consequences of the shift in the seed dispersal mode of *H. glaber* to gravitational seed dispersal.

Even for hydrochorous seeds, dispersal over extremely long distances greater than 1000 km is rare. This rarity, however, provides geographic isolation that allows the descendants of the successful immigrant to diverge into new species. We expect that decreasing seed dispersal ability will evolve in these derived species, because long-distance seed dispersal will have no adaptive value in the isolated habitats. This may create the phylogenetic patterns that long-distance seed dispersers form the main stem of a phylogenetic tree that often bears derived branches of locally adapted short dispersers. Similar phylogenetic patterns have been recognized in Hawaiian plants (Price & Wagner 2004).

Cause or consequence?

Our studies of seed dispersal in *Hibiscus* clearly demonstrate that hydrochory influences the dynamics of populations at a range of spatial and temporal scales. Our research has not, however, answered important questions about the evolutionary forces that are responsible for the long-term seed buoyancy of hydrochorous species that have such an important impact on dispersal and subsequent population genetics.

As far as our study system is concerned, we suggest the primary importance of selection at a metapopulation scale. Wetland and coastal habitats are expected to experience frequent disturbances by inundation or drought because the habitats are located in a relatively narrow boundary between water and landmass. In such places, the longevity of local populations is expected to be short and lineages are likely to be maintained through seed exchanges that work as risk spreading.

The importance of spatial shuffling in maintaining hydrochory is to be tested in future studies. The issue is related to how seed dispersal and pollen dispersal (or breeding system) interact with each other in their evolutionary processes. Artificial shuffling of plant positions has been shown to largely alter plant mating patterns (Griffin & Eckert 2003).

Speciation following one-way, long-distance seed dispersal is a consequence rather than a cause of hydrochory. This is suggested by the fact that the seed characters for long-distance dispersal are often lost from island populations after their arrival (Carlquist 1974; Cody & Overton 1996). In our example, even for wide-spread species such as *H. tiliaceus*, natural selection acting at metapopulation and local population scales would be important to maintain hydrochory.

As observed in the hydrochory of *Hibiscus*, the consequences of seed dispersal may appear at diverse spatiotemporal scales. In particular, it is important to recognize that seed movement patterns within ecological time and space are likely to leave non-random patterns in long-term plant evolution and phylogeny. Future studies need to correlate the short-term consequences of seed dispersal with the long-term consequences. This task is especially challenging because seed dispersal patterns are determined not only by seed characteristics, but also by the background landscape. The rate of seed movements itself is an evolving character that changes dramatically under different landscape contexts, including those altered by human activities.

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