Ecotypic Variation and Genetic Diversity in Plants: Is There Right and Wrong?

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I. Introduction

There is much discussion among ecologists regarding the biological correctness of moving native plants of a given genetic constitution, or "genome," from one part of their range to another. It is generally believed that many plants have evolved over time to adapt to the prevailing climatic and edaphic conditions of their regions and microsites. Because of this belief, many ecologists favor using seeds or propagules of native plants that have been procured from within a specifically-defined range from the site to be planted. Other ecologists believe that most plants have a more plastic gene pool that allows them to adapt to a wide variety of conditions across great distances within a climatic region, and in some cases, across vast distances of varying "ecozones" (defined here as regions of similar climate and photoperiod).

During the process of native plant community restoration, we are all faced with this question at one time or another. In the interest of "doing the right thing" (if there is one), we need to sift through the available evidence to determine the impact that might occur by introducing new genetic material into a region where there is a pre-existing population of the species to be planted. The following summary is directed at presenting some of the known information on speciation, genetics, and ecotypes in an effort to clarify what little is known about this complex, confusing, and contentious topic.

II. Just the Facts, Man

What do we really know about plants, their genetics, speciation, and long-term adaptation to their environment? Not a heck of a lot. However, a few studies have been done on this topic, and some natural-occurring evidence is available from which we can draw certain conclusions.

First, let us review a few aspects of genetic theory. Speciation is thought to be a long-term process, wherein a given organism evolves and adapts to the conditions to which it is subjected. By understanding the ways in which organisms adapt their genetic composition to meet the demands of their environment, we might possibly gain a better understanding of what constitutes a true, "functional ecotype," and hence a "unique regional gene pool."

SPECIATION AND DEVELOPMENT OF ECOTYPES

The development of ecotypes within a species can be a function of many factors. First, there is the stimulus-response feedback loop, sometimes known as the "Adapt or Die" theory. Those plants that are best adapted to the local environmental conditions will outperform those that are not so well adapted. Over time, a local population of best-adapted individuals should, in theory, result from this brutal process.

GENETIC DRIFT

In certain situations, the process of "genetic drift" may occur, wherein certain "alleles" (trait-carrying genetic parcels) become more pronounced within a given population. This occurs typically in small populations, where there is a tendency toward increasing "homozygosity," (similar to inbreeding). Over time, certain traits, often beneficial ones, can be lost, or become "masked" by other genes. The end result is that a given population can assume a distinct and sometimes narrow gene pool simply as result of chance. An ecotype thus results, without any evolutionary significance or advantage.

LINKED GENES

There can be "linked genes," wherein a certain advantageous trait is associated with another trait of no evolutionary significance. The linked traits are reproduced together because one of them was beneficial. The second trait is along for the ride, and may provide no real advantage to the plant.

POLYPLOIDY

It is not uncommon in the plant world for a species to carry large amounts of "excess baggage" in the form of multiple gene sets, or multiple "ploidy." The plant may only need one half or one fourth of this genetic material for its growth and survival. There is a cost to the plant to maintain the excess genetic information. However, it is believed that the species, as individuals or as populations, can use this broader genome to adapt to changing conditions and, in essence, "evolve" by utilizing the most appropriate genetic material available in its "suitcase." Studies have shown that plants that occupy stressful, rapidly-changing environments often have multiple ploidy, sometimes up to eight times as much as "normal." (i.e. diploid organisms). This theoretically allows the plant to draw upon a broad range of genetic information to enable survival under changing conditions.

The potential disadvantage of polyploidy, however, is that all this excess baggage can be unwieldy. It has been theorized that this may actually inhibit natural selection, because of the presence of excess genetic material that can potentially mask beneficial genes. Nevertheless, it is believed that multiple ploidy allows plants a certain degree of increased genetic plasticity and adaptability.

ACTUAL CASE STUDY

A study of switchgrass (Panicum virgatum) throughout the Midwest showed that the species occurred across the region with widely variable sets of chromosome numbers (ploidy). They occurred in sets of 18, 27, 36 and 54, with these variants often growing in close proximity to one another. (Note: This research has been superseded using more powerful chromosome identification techniques. The exact chromosome numbers in this study are no longer considered to be accurate. However, the existence of these various multi-ploidy races of Switchgrass is not in question, only the exact chromosome counts.)

The authors concluded that this genetic diversity within the populations in various regions gave them strong adaptive capacities: "The range of cytological variation and the resultant complex breeding structure of local populations, particularly those in the central and southern portions of the study area, suggest a genetic mechanism enabling the extensive distribution of Panicum virgatum over a diversity of habitats." (Cytogeography of Panicum virgatum in Central North America, by Calvin McMillan and John Weiler, American Journal of Botany Vol 46, Oct. 1959, pages 590-593)

THE CENTRAL QUESTION: WHAT IS THE TRUE ADAPTABILITY OF PLANTS?

In the case of plants, the major factors in adaptability include:
Climate
Soils
Interactions with other plants and animals

CLIMATE

Climate is central to most plants' existence. They must respond to factors such as daylength, rainfall, maximum and minimum temperatures, relative humidity, and wind velocity. Climates tend to occur on regional scales, often involving a multi-state area, although microclimates can be critical in a plant's habitat preferences.

Studies of prairie grasses that were cross-transplanted from Texas to North Dakota showed there was a significant variation in response of the grasses to daylength. Grasses of southern accessions were unable to flower and produce viable seed when moved too far north. Northern ecotypes, when moved south, grew tall and leggy and became more susceptible to disease. (The Role of Ecotypic Variation in the Distribution of the Central Grassland of North America by Calvin McMillan, Ecological Monographs, Vol. 29, No. 4, Oct. 1959, pages 285-308).

EMPIRICAL DATA FACTOID!

The general rule of thumb in the native grass seed business is to move a species no more than two degrees latitude north or south of its point of origin. This is based upon the accumulated experience of people who have been establishing native grasses in the Midwest over the past 50 years.

SOILS

Soils may be an important factor in ecotypes. Soil may be as important, or even more important, than distance in determining the adaptability of a certain "ecotype" to a given planting site. Some species have very specific soil requirments, while others are capable of successfully occupying a wide variety of soils with differing textures, nutrients status, and pH. It would be expected that the more adaptable species would by their very nature be less susceptible to genetic disruption due to introduction of genes from other populations.

ACTUAL CASE

The native grass, Little Bluestem (Andropogon scoparius or Schizachyrium scoparium), has been documented to occur naturally in central Wisconsin in one site on dry sand , and in wet clay at another location only a few miles away. In addition to their differences in habitat selection, the plants exhibit phenotypic color variation in their leaves. If indeed there is ecotypic variation between these two populations of the same species, it is most likely occurring as a function of habitat, rather than as a function of physical distance. Thus, restorationists who wish to ensure "genetic correctness" of ecotypes are faced with a quandary. Should the criteria for an ecotype be based upon distance alone, or are other factors equally, if not more important? It may very well be that in some cases there is more genetic variation between two populations a few miles away from one another on widely varying soils than there might be between two populations growing on similar soils that are hundreds of miles apart!

ACTUAL CASE STUDY:

Investigations of common cattail (Typha latifolia) have shown that there is essentially no variation in the genetic composition of this species across North America. This means that there are no ecotypes of Typha latifolia, and it is endowed with such an incredibly adaptable and successful set of genes (or somehow immutable genes) that it has not had the need or opportunity to develop ecotypes.

GENETIC PLASTICITY

Genetic Plasticity is of critical importance in determining whether or not a plant will survive and prosper in a location that is distant from its most recent point of origin. Some plants appear to be extremely plastic: just look at the many weeds that we all contend with on a regular basis! Most of our weeds came to the New World from Eurasia, and spread rapidly into disturbed habitats created by agriculture. Other "non-weedy" plants seed to grow extremely well in a variety of situations: day lilies, hostas, iris, and a host of other perennials. Many naturalized plants from other parts of the world do just fine here. Some seem to have no obstacles to their success!

It would appear that many native plants also have great genetic plasticities within their genomes. Much more research is required to determine the limits of each species and its ecotypes. There is no doubt that each species will be unique in its genetic behavior and its ecotypic variation. Therefore, each species must be handled on an individual basis with regard to understanding its genetics and the implications for gene transfer among populations.

III. "Natural" Plant Distribution: How Plants Move Around

People seldom think of plants as mobile entities. We never see them move from place to place. However, as populations, plants can move gradually, or surprisingly rapidly, across a state, a country, or a continent.

The big question is "How much adaptation occurs during the process of plant migration from one area to another?" Is it a rapid process of sorting out, or a slow, lengthy series of adaptations? Are species that are distributed across wide ranges significantly different from one another genetically, and if so, by how much? Are any such differences sufficient to make a difference in their adaptability from location to location?

METHODS OF PLANT DISTRIBUTION

Methods of plant distribution are central to understanding their population genetics and the possibility for rapid movement of genetic information across large distances. The major modes of seed distribution are:

1) Wind
2) Water
3) Animal
4) Seed Ejection Systems (plant catapults)

The above distribution vectors are listed in order of maximum potential distance that can be achieved. Obviously, wind-carried seeds can travel hundreds of miles per day. Twenty four hours on a twenty mile an hour breeze can move a seed from Chicago to Pittsburgh in a day. Wind-distributed species tend to have broad ranges across an ecozone. The migration of new genetic information into these populations from far afield is a common occurrence, and would be expected to prevent the formation of significantly inbred or strongly ecotypic populations.

Due to the prevailing westerly winds in North America, there is generally a west to east movement of genetic material in the form of seeds and pollen (in wind-pollinated species such as grasses and many trees). Thus, there is an historical precedent for a westerly influence on the genetic constitution of the flora to the east, across the continent.

Water can also distribute seeds across long distances. The cardinal flower (Lobelia cardinalis) is "designed" so that the seedheads fall into water and the seeds are then carried long distances downstream. Many seeds have flotation mechanisms that allow them to be carried across oceans to new homes. Living plant parts can also be carried long distances in rivers, streams, and oceans.

Animals can carry seed in their fur, on their feet, and in their digestive system. It is interesting that White Pine (Pinus strobus) is distributed across northeastern North America. The next nearest location for this tree is in the mountains of Central America. How many birds migrate annually between these two destinations? Could these animals and this plant's distribution somehow be linked?

Newly-created wetlands constructed in what were formerly upland situations are often readily colonized by a surprising variety of plant species shortly after filling with water. Waterfowl are known to carry seeds and plant propagules from wetland to wetland, often across great distances.

Large, heavy seeds tend to be distributed slowly across the landscape. A survey of forbs native to North America indicates that many large-seeded herbaceous plants tend to have more limited distributions than their more nimble, wind-travelling counterparts. These large, non-mobile species would be expected to have a higher probability of developing local populations with ecotypic characteristics, simply due to their being more readily cut off from gene influx from other populations.

Many people today believe that humans should have no part in plant distribution, and that to move plants into ranges where they do not presently occur is "unnatural." This concept apparently did not seem unnatural to our predecessors here in North America. Native Americans moved plants readily to serve their needs. In Wisconsin, we find Canada plum (Prunus canadensis) and Cream Gentian (Gentiana flavida) associated with historic Indian encampments. The Pecan tree (Carya illinoensis) is distributed throughout the south central U.S. However, there are isolated populations north of its main range, mostly along the Upper Mississippi River and even up along the Wisconsin River. It is rather doubtful that the seeds floated upstream all that way. The conclusion is almost inescapable that this highly nutritious and easily stored food was purposely planted by Native Americans for food.

IV. What's So Bad About Moving Ecotypes Around?

The main argument against moving plants from one location to another is that their genes will "pollute" the local plant material. If indeed a local population has evolved to adapt to the specific conditions of an area, and plants of different provenance are brought into contact with them, the bastard offspring of this union are assumed to be maladapted to the area and the local population will be weakened.

In the event that a larger population of a species is established using plants from a distant source, a phenomenon known as "genetic swamping" might occur. In such an instance, pollen from the interlopers will be accepted by the local girls, as they breed unsuspectingly and indiscriminately with the new kids on the block.

The question then arises: Is this bad? The answer: A resounding Maybe.

If a unique local ecotype does indeed occur, should it not be preserved in the interest of biodiversity? If it functions as a uniquely adapted ecotype, should it be allowed to be "polluted" by other genomes? Will it indeed be affected in a negative fashion by this injection of outside genetic material? Or will the strong plants continue to survive, and the weak ones fall by the wayside as they do everywhere else?

In an interesting example, a very rare and endangered plant, the Lakeside Daisy (Hymenoxys acaulis), was rescued from possible extinction by mixing two distant populations. One population occurred on the south shore of Lake Michigan, and the other was on the south shore of Lake Erie. The Lake Michigan population was not producing viable seed. In desperation, plants from one population were transplanted to the other. Lo and behold, the fruits of these labors resulted in viable seed. Apparently the Lake Michigan population was inbred to the point of being unable to breedwithin itself. Outcrossing with the distant Lake Erie population was apparently the only way to preserve the Lake Michigan population (see Relationship of Breeding System to Rarity in the Lakeside Daisy (Hymenoxys acaulis var. glabra) by Marcella M. DeMauro, Conservation Biology, 1993 Volume 7, No. 3, pages 542-550).

Indeed the philosophers are correct when they state that the only constant in life is change. So it is with plant societies as it is with human societies. It would seem a bit parochial and overly-indulgent of the status quo to operate under the premise that no migration or introduction of new genes should be allowed into a plant population. This is antithetical to the natural systems of plant distribution that have been in place for eons.

However, there are those who would say that if we must err, let us err on the side of safety. Let's not take a chance and then find out too late that we were wrong, and that there is indeed a negative effect associated with exposing local plant populations to outside genomes.

It would appear that the most appropriate policy regarding the mixing of native plant populations is that it is very much a matter of degree, and must be determined on a species by species basis. Highly variable species with narrow ranges of adaptation may be strongly influenced by the introduction of new and different genetic information. Other more genetically-constant species may experience little or no impact by the introduction of "foreign" plant material.

Ultimately, it must be determined what local populations are potentially placed "at risk" by the introduction of distinctly different ecotypes. For that matter, there may be separate and distinct "species" that are capable of hybridizing with other "species," but have been separated by various barriers over the years. With the introduction of one of these species into the domain of the other, it is possible that it could "corrupt" the home species through hybridization. In the case of local populations of rare species, this is a major concern and should be taken seriously.

V. In Conclusion

Clearly the sparse evidence presented above provides only the most meager starting point for reaching a conclusion on the matter of ecotypic variation and the impact of mixing plants from various distant provenances. There is no doubt that plants respond to their environment, and somehow over time attune themselves to their surroundings. A plant that originates from a distinctly different latitude or climatic ecozone will likely have some difficulty in becoming established when planted in a distant region. If it grows and flowers, does it present a possible threat to its distant cousins in the neighborhood? Even so, will Nature in her infinite wisdom winnow out the weak and assure the continued survival of the species?

Will the species be so weakened by the incursion of dysfunctional genetic material into its ranks that it is no longer strong enough to compete against other plant species, and ultimately lose the battle for survival in that location?

Or is the infusion of new and different genes into populations a potentially good thing? Can it help strengthen plant populations that have been separated and isolated, due to the destruction of habitat, and loss of former "gene migration corridors" that once kept it diverse and vibrant? Will outcrossing with other ecotypes actually give old populations new vigor, and increase their competitiveness and chances for survival?

The answer in all too many cases is: Nobody knows.

And as has been said so many times before, in so many ways: **In Ecology there is no Right or Wrong, merely Consequences.**