DEVELOPMENT OF GENETIC DIVERSITY IN ATRIPLEX[1]

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Abstract: Polyploid plant taxa are usually low in genetic diversity and, consequently, are of limited value in revegetation of disturbed lands. This deficiency can be remedied in polyploid selections of Atriplex (saltbush) by using products of interspecific hybrids derived from parents having the same chromosome number and by using seed mixes derived from several contrasting ecotypes of the same species, all with the same chromosome number.

Additional Key Words: Polyploids; Hybrids; Reclamation; Die-off.

Introduction

The most conspicuous requirement for continued success of plant taxa in nature is genetic diversity. Species that are rich in genetic diversity "ride-out" environmental fluctuations; those that are uniform, face elimination.

In our efforts to reclaim disturbed sites we must therefore never use "pure-bred" introductions. This is particularly true for reclamation of mine spoils because the spoils are not only new and different but they are rapidly changing. Consequently a taxon, (particularly a genetically uniform taxon), that may appear to be a successful performer today, could be a complete failure later on.

The hazard accompanying low genetic flexibility is often seen in the valleys of the Great Basin of western United States where genetically uniform polyploid species experience extensive, sudden, "die-off." Many of these western valleys were covered with water as recently as 13,000 y.a. (Benson et al., 1990) and as the waters receded, vast new unoccupied landscapes became exposed which, in many respects, although on a much larger scale, resembled unoccupied, new mine-spoils. Because the valleys in the Great Basin have no drainage outlets, the lakes disappeared solely by evaporation and therefore left behind highly saline soils in the valley-bottoms. Since such soils are usually accomodated best by plants in the family Chenopodiaceae, Chenopods now dominate vast acreages throughout much of the Great Basin. Sarcobatus Nees, (Greasewood), Ceratoides Gagnebin, (winter-fat), Grayia H & A, (hop-sage), Kochia Roth, (gray molly), and Atriplex L., (saltbush) are the principal genera represented. Each of these, except Atriplex, contains only one or two species and are present throughout the Great Basin as genetically uniform monocultures or near monocultures. In contrast, the genus Atriplex contains numerous species and varieties, and hybridization, introgression, and polyploidization are common. As a consequence, some Atriplex immigrants in the Great Basin are severely genetically uniform, others are genetically rich.

On occasion, entire populations of Atriplex and other Chenopods that are genetically uniform, collapse. A striking example of this occurred in a population of A. confertifolia (Torr. & Frem.) Wats. (shadscale) in Rush Valley, Tooele Co., Utah. In this valley, shadscale plants above the high water level of Lake Bonneville are all diploid (2x=18) and show an abundance of genetic variation. Some are early-flowering, some late, some have broad leaves, some narrow, some have an erect, robust habit, some have a small, depauperate habit. At lower

[1]Paper presented at the 1995 National Meeting of the American Society for Surface Mining and Reclamation, Gillette, Wyoming, June 5-8, 1995.

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Proceedings America Society of Mining and Reclamation, 1995 pp 762-765
DOI: 10.21000/JASMR95010762
https://doi.org/10.21000/JASMR95010762

elevations, the shadscale populations are tetraploid, apparently derived from the nearby diploids. They are conspicuously uniform and extant. In 1990, after several earlier, yearly visits to these areas, every plant in the tetraploid population was found dead. Several plants in the diploid population had also succumbed that year but most of them were alive and healthy. Obviously some environmental assault had killed every plant in the tetraploid population, but only a few in the diploid population. Since each plant in the polyploid population had "exactly" the same genotype, whatever it was that killed one of them, killed all. Diploid populations, on the other hand, having the advantage of abundant genetic diversity showed very little die-back.

Genetic diversity, so important for success in nature, is equally important for plants used for reclamation of mine spoils. Homozygous selections in seed-mixes should be rigorously avoided and every possible avenue for including genetic variation, exploited. Within-species diversity is far more important than between-species diversity. Rich ecosystems will have both, but because all diversity ultimately stems from the presence of within-species diversity, sacrifice of between-species diversity is far less serious than limiting within-species genetic flexibility.

Methods

At the BHP coal mines in northwestern New Mexico, two methods have been used to introduce genetic flexibility into polyploid accessions of Atriplex used in revegetation of the mine spoils:

1. Selection of superior forms derived from products of interspecific hybridization.
2. Pooling of collections of diverse ecotypes of species of Atriplex, all having the same chromosome number.

Both methods appear to be effective.

Results and Discussion

1. Selection from products of interspecific hybridization.

Interspecific hybridization between perennial species of Atriplex is unusually common in nature in western United States and is easily accomplished experimentally. Being dioecious, hybrids between species of Atriplex can be obtained experimentally simply by dusting pollen from males of one species onto isolated females of another species. In nature this is commonly accomplished by wind-pollination.

Because of its widespread distribution and absence of strong reproductive barriers, Atriplex canescens (Pursh) Nutt. is the most promiscuous of all Atriplex species. Occurring in nature, or experimentally produced, hybrids are now available of A. canescens with A. confertifolia, A. corrugata Watson, A. cuneata Nelson, A. falcata Standley, A. gardneri Standley, A. obovata Moquin, A. polycarpa (Torrey) Watson and A. tridentata Kuntze. Some of these hybrids are highly sterile; some are fully fertile. Also, some interspecific hybrids, from the same parental species, have higher fertility than others. This is probably largely so because each of these species is represented by more than one chromosome race. When the chromosome number of the two parents is the same, high fertility may result whereas if they have different chromosome numbers, the hybrids will, expectedly, be highly sterile.

Among the best performers at the BHP mines in New Mexico that have been derived from hybrid ancestry, are those from hexaploid (6x) Atriplex canescens crossed with hexaploid (6x) A. obovata and tetraploid (4x) A. canescens crossed with tetraploid (4x) A. cuneata.

The hexaploid A. obovata x A. canescens hybrids are fertile, vigorous, long-lived (at least 15 years) and produce similarly vigorous, fertile segregating progeny. Because A. obovata and A. canescens differ genetically in numerous characteristics, the phenotypic diversity among the segregants is extensive. The most conspicuous segregating attributes are expressed in plant stature, leaf dimensions, branching patterns, flowering periods, and fruiting-bract characteristics. Less conspicuous but equally important are the numerous physiological differences that govern adaptations to environmental stresses such as drought, cold, pathogens, and herbivory. The most significant attribute that signifies promising success of these segregating selections is their capacity to reseed. In experimental plots established at the BHP Navajo Mine in northwestern New Mexico, numerous seedlings have become established around some of the older parental plants, and three-year-old plants derived from seeds collected from these volunteers, are richly diverse phenotypically, and are highly fertile.

Outplanting with seeds from selections of A. obovata x A. canescens onto mine spoils at three different sites, have all shown favorable establishment and performance.

Interspecific hybrids from tetraploid (4x) A. canescens x tetraploid A. cuneata also show high promise for use in revegetation because of their display of rich genetic diversity.

Other promising hybrid derivatives include Atriplex cuneata x A. corrugata, A. cuneata x A. confertifolia and A. obovata x A. confertifolia. A. canescens x A. polycarpa hybrids and hybrid derivatives show unusually high drought tolerance but are not sufficiently cold tolerant to accomodate northern New Mexico winters. Incorporation of cold-tolerance with drought-tolerance is being attempted by hybridizing A. polycarpa with A. canescens (A. aptera Nels.) from northern latitudes. The F_1 hybrids are fertile but have not yet been assessed for their capacity to produce viable, fertile, drought and cold tolerant segregants.

2. Pooling of diverse, within-species ecotypes.

Genetic uniformity in polyploids usually stems from their ancestry. Most polyploids are derived from a very narrow gene pool, sometimes from a single individual. In agriculture, such uniformity is usually desirable and is sought, so that yields, and the results of horticultural practices, can be predicted. Consequently most polyploid crops such as wheat (tetraploids and hexaploids), cotton (tetraploid), potatoes (tetraploid), and Alfalfa (tetraploid), are highly uniform, and desirably so. However, in nature, as well as sometimes in Agriculture, such uniformity invites eventual disaster. Any significant modification of the environment may prove to be extensively detrimental.

The disastrous collapse of the potato crop in Ireland in 1845 and 1846, resulting in the horrible famine that resulted in the death of over a million people (Wood, 1953) who depended on potatoes for food and the repeated destruction of wheat by wheat-rust fungi in North America (Martin and Salmon, 1953) illustrate the hazard of uniform polyploid genotypes.

Occasionally, in nature, exceptions to genetic uniformity in polyploid populations are found. One such instance was found a few years ago in northeastern White Pine county, NV, where a highly heterogeneous population of hexaploid (6x) Atriplex falcata var anomala (Jones) Stutz & Sanderson occupies a sizeable area (ca 6 ha^2) in Antelope valley. Each plant in this large population is phenotypically unique, fertility is high, and segregation abundant among seedlings derived from seed collected from individual plants. After much pondering and extensive study, it was determined that this genetically rich hexaploid population was derived from intermingling of two contrasting hexaploid populations of this species. Both of these parental populations are hexaploid, hybrids and hybrid products are fertile and, because the parents differ in several characteristics, segregating progeny are phenotypically diverse. Consequently this population is performing genetically like a segregating hybrid swarm derived from diploid parentage.

Since this escape from uniformity by polyploid species is so easily, albeit apparently rarely, accomplished, attempts have been made to use this procedure in preparing genetically rich polyploid selections for use in mine-spoil revegetation at the BHP mines. Mixtures of genetically rich polyploid species of Atriplex have been prepared at both the tetraploid (4x) and hexaploid levels and sown on reclaimed mine-spoil sites. The most promising tetraploid mixture that has been used thus far, is from ecotypes of Atriplex canescens (fourwing). Although A. canescens occurs in seven chromosome races throughout western United States (2x, 4x, 6x, 8x, 10x, 12x, 20x) (Sanderson and Stutz, 1994), tetraploids are the most common in northern latitudes. Consequently the major effort to develop genetically rich populations of A. canescens has centered around these tetraploids. Seed has been collected from several known tetraploid populations throughout the Intermountain West and pooled to provide a genetically rich mixture. Plants derived from these diverse seed-sources will, expectedly, provide a wide array of genetic diversity in the revegetation plots and when they intercross, can provide, in subsequent years, an ever richer segregating polyploid genetic swarm. Because of their abundant diversity, they should be able to accommodate almost any environmental assault that may arise.

Collections of other tetraploid species of Atriplex have also been included in the tetraploid seed-mix to provide similar opportunities for them to succeed and also to permit opportunities for interspecific hybridization and subsequent genetic introgression which can thereby enhance the production of genetic diversity even further.

The hexaploid (6x) selections used in preparing genetically rich populations include diverse ecotypes of hexaploid A. canescens, A. obovata, A. confertifolia, and A. falcata.

By utilizing products of interspecific hybridization and by pooling seed obtained from diverse within-species ecotypes all of the same chromosome number, sufficient genetic diversity can be introduced into revegetation trials to essentially guarantee long-term reclamation success.

Acknowledgments

Appreciation is extended to Stewart Sanderson for abundant technical assistance, particularly in providing many of the chromosome counts. Funding for these studies was provided by BHP minerals and Brigham Young University.

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