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Community succession along a chronosequence of vegetation restoration on sand dunes in Horqin Sandy Land

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Abstract

Species diversity influences plant community structure and function. This paper examines the patterns and dynamics of species diversity along a chronosequence of vegetation recovery on sand dunes in a semi-arid region to assess the probability of vegetation recovery via succession, and provides some implications for revegetation practices in this region. Species richness and diversity indices gradually increased with succession, except for a decline in the community of 18 years, which is attributed to the strong dominance of *Artemisia halodendron*. In each stage of the restoration process, there was a dominant species with particular life history traits which contribute to the dominance of this species. Species replacement and habitat changes were the main drivers of succession, while plant species and community succession drove the process of vegetation recovery. Results showed that restoration via succession holds promise for vegetation recovery and desertification control within protected, fenced enclosures.

Keywords: Dominance; Life form; Species attributes; Species replacement; Species richness; Sandy land; Vegetation restoration

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1. Introduction

Desertified lands are widespread throughout the world in arid and semi-arid zones (Dregne, 2002), many owing their condition to human over-exploitation such as mining, clear-cutting, over-grazing, etc. Thus, many countries have made great efforts to control desertification by planting and fencing to restore vegetation.

The process of vegetation restoration on desertified land can be viewed as succession. Species diversity is the critical property of plant communities and is of considerable significance in the study of succession, since variations in diversity are presumably correlated with the stability of various biotic and abiotic components of ecosystems (MacArthur, 1955; Leigh, 1965). Plant species diversity can be the driver of early succession in abandoned agricultural fields. The diversity of plant species present at certain stages of succession may affect the course of succession (Van der Putten et al., 2000). Biodiversity has become an important measure for the evaluation of ecosystems (Magurran, 1988), although the role of species diversity in ecosystem functioning is disputed (Schulze and Mooney, 1994; Patrick, 1997). Research on species diversity along successional gradients is necessary for understanding the mechanisms of recovery via succession on mobile sand dunes in severely degraded lands. Such knowledge is needed for combating desertification and enhancing the sustainability of agro-ecological systems.

So by examining patterns and dynamics of plant species diversity along a successional gradient in sand dunes, the objectives of this paper are (1) to describe succession characteristics during the process of vegetation restoration in a severely degraded sandy land, and (2) to provide useful lessons for practices of revegetation in semi-arid regions, especially in desertified sandy areas.

2. Material and methods

2.1. Study area

This study was conducted at the Naiman Desertification Research Station, operated by the Chinese Academy of Sciences. The area lies at 42°54′N and 120°41′E, at an elevation of 300 m, within Naiman Banner County, Inner Mongolia Autonomous Region, northeastern China. The study area is located in the central-southern part of an extensive region of sandy soils known as the Horqin Sandy Land.

The region is typical of a semi-arid agro-pastoral transition zone, with mean annual precipitation of approximately 366 mm, falling predominantly between June and August. Average temperature in July is 23.7 °C and in January is −12.7 °C. Average annual wind speed is $3.5\,\mathrm{m\,s^{-1}}$, with most of the windy days and wind storms occurring between March and May. Because of cultivation and over-grazing, as well as the windy climate and loose sandy soils, land degradation in this region has spread rapidly. The landscape is characterized by a mosaic of mobile sand dunes, semi-fixed dunes, stabilized dunes and lowland meadows (Zhao et al., 2000). The predominant native plants are grasses, forbs and shrubs such as *Cleistogenes squarrosa* (Trin.) Keng, *Setaria viridis* (L.) Beauv., *Salsola collina* Pall., *Corispermum elongatum* (Bge. ex Maxim.), *Bassia dasyphylla* (Fisch. ex Mey.), *Artemisia halodendron* (Turcz. ex Bess) and *Chenopodium glaucum* L.

2.2. Selected study sites

Six vegetation restoration sites selected for study have been enclosed by fencing, and thus have been undergoing succession, for various lengths of time: 3, 6, 10, 18, 30 and 45 years. These sites are of similar topography and soil type, and have not been grazed since enclosure. The initial conditions of all sites were mobile sand dunes with a gentle slope. Surface areas of the sites range from 10.2 to 21.6 ha, and distances between sites are 0.5–7.2 km. Considering biogeographical distribution patterns (Qian, 1999), if the distance between two sites is too great, they may be influenced by different regional species pools, and this can confound comparisons between sites. The short distance between selected study sites ensures that all sites are under the influence of the same regional seed pool. Similarly, if the difference in surface area between two patches is too great, the time required for species to disperse and fully inhabit each patch would be very different, affecting studies of succession. In general, the larger the area the more time is required for species to occupy a patch, and thus the slower community succession will proceed. The comparable area of all selected sites ensures that they have similar rates of species dispersal and occupation, and their small size allows for relatively rapid succession.

The study area is characterized by high patchiness and fragmentation, with various landscape elements such as farmland, mobile sand dunes, semi-fixed dunes and stabilized dunes interspersed. One type of landscape may be surrounded by other types, and there is no single landscape type with a disproportionately large area. This is possibly attributable to the generally rapid transitions between different types of landscape, which are determined by the regional climate, soil properties and anthropogenic factors such as over-grazing, cultivation, etc. For example, if anthropogenic disturbances are excluded, vegetation can quickly colonize the mobile sand dunes, and community succession will occur. Vegetation can develop to an excellent state and community function will progressively recover. But under intensive disturbance, vegetation can also be degraded quickly on the loose, dry and fragile soils. The six sites selected for study each comprise a single landscape type, and are surrounded by one or more different landscape types.

The study of succession is difficult because of the time scale on which it occurs (Hibbs, 1983). Direct observation through longitudinal studies is often impractical. Studying a chronosequence of different sites, as in this paper, relies on finding a suitable set of sites, ideally with similar and known initial conditions, and separated by short and uniform time intervals. The six sites selected for this study were simply the best set available, matching the ideal criteria as closely as was possible to achieve.

2.3. Sampling and data collection

In each of the six sites, 60 quadrats of $1\,m^2$ were investigated, with the abundance, height and cover of every species measured and recorded. Abundance was defined as individual density or stem density. Cover of every species was visually estimated as percent canopy cover, and height was measured with a ruler on those ramets (culms) which represented the majority of the total ramets of the species. Biomass was not measured because of the undesirability of the required destructive sampling.

2.4. Calculation of species diversity indices

An importance value and a dominance value were calculated for each species. The importance value, IV, as

$$\mathrm{IV} = \mathrm{RA} + \mathrm{RH} + \mathrm{RC},$$

where RA is the relative abundance, RH is the relative height and RC the relative cover of the species. RA, RH and RC were all represented as percent values.

Species dominance was calculated as

$$\mathrm{DV} = \frac{\mathrm{IV}}{3}.$$

Species diversity was measured by three α-diversity indices (Fang and Peng, 1997; Li, 2001): the Shannon–Wiener (SW) index, the Simpson ecological dominance index (SN) and the Peng–Wang evenness index (PW) (Peng, 1983). Also calculated were three widely used β-diversity indices (Fang and Peng, 1997; Li, 2001):

The Whittaker index (Whittaker, 1972)

$$\beta_{\mathrm{ws}} = \frac{\mathrm{ss}}{\mathrm{ma}} - 1,$$

where ss is the sum of recorded species number in samples A and B, and ma is the average species number of each sample.

The Bray–Curtis index (Bray and Curtis, 1957)

$$C_{\mathrm{N}} = \frac{2\mathrm{jN}}{\mathrm{aN} + \mathrm{bN}},$$

where aN and bN are number of individual plants in plots A and B, respectively, and jN is the sum of the lesser number of individual plants of each species in common in plot A (jNa) and plot B (jNb).

The Morisita–Horn index

$$C_{\mathrm{MH}} = \frac{2\sum \mathrm{an}_i \times \mathrm{bn}_i}{(\mathrm{da}+\mathrm{db}) \times \mathrm{aN} \times \mathrm{bN}},$$

where an_i and bn_i are number of individuals of species i in plot A and plot B, respectively, and

$$\mathrm{da} = \frac{\sum \mathrm{an}_i^2}{\mathrm{aN}^2}, \quad \mathrm{db} = \frac{\sum \mathrm{bn}_i^2}{\mathrm{bN}^2}.$$

Because of variation in individual plant size, the importance value or species dominance value is preferable to data on individual plant abundance, height or cover, so all calculations in this paper have been done using species dominance.

3. Results

3.1. Species richness and dominance

Table 1 shows an overall increasing trend in species richness over time, but the rates of increase in various stages of succession were different. The number of species increased steadily from 7 in the initially established community on mobile sand dunes to 11 in the 6-year community, and then to 17 in the 10-year community. In a reverse trend, from 10 to 18 years the species number decreased from 17 to 14. However, this was immediately followed by a steep increase in species number from 14 to 28 (18–30 years), and then a weaker increase to 30 species from 30 to 45 years.

A common characteristic of species dominance was shared by all communities in the sequence. In each of the communities along the successional gradient, there was a predominant species which accounted for most of the community function. In the initially established community (3 years), *Agriophyllum squarrosum*, as a pioneer plant on shifting sand dunes, was the predominant species, accounting for nearly 70% of the total dominance. Then its dominance shrank rapidly to about 28% and again to $<1\%$ by year 10. *Setaria viridis* and *Agriophyllum squarrosum* were the co-dominants in the 6-year community, with about 30% and 28% dominance, respectively. Then *B. dasyphylla* became the predominant species in the 10-year community, with about 33% dominance, and *A. halodendron* in year 18 with 73% dominance, the highest in the whole sequence. *Salsola collina* was the dominant by year 30, with 21% dominance, the lowest in the sequence, and *C. squarrosa* was predominant in the 45-year community, with 24% dominance.

3.2. Changes in species diversity indices

The value of the SW index displayed a trend similar to that of species richness during succession, but with an exception from 30 to 45 years (Table 2). From 3 to 6 years, then to 10 years, SW increased steadily, but from 10 to 18 years there was a sharper decrease in the value of SW index than that in species richness. Then SW also showed a resurgence similar to that in species richness, but from 30 to 45 years SW decreased weakly while species richness increased somewhat.

Table 1
Patterns and dynamics of species composition of plant communities in the process of vegetation recovery (dominance %)

Species	Succession age (year)					
	3	6	10	18	30	45
Agriophyllum squarrosum (L.) Moq.	68.08	28.02	0.69	0	0	0
Setaria viridis (L.) Beauv.	16.91	30.81	12.92	3.72	10.50	8.24
Bassia dasyphylla (Fisch. et Mey.) D. Kuntze	9.06	18.31	32.91	4.83	6.26	0.96
Salsola collina Pall.	3.39	5.55	16.42	4.09	21.01	6.39
Corispermum elongatum Bge. ex Maxim.	0.19	1.23	4.45	3.19	4.83	2.98
Cynanchum thesioides (Freyn) K. Schum.	1.43	0	5.07	1.39	3.41	0.15
Artemisia halodendron Turcz. ex Bess.	0.94	3.76	7.54	73.60	13.41	0
Digitaria ciliaris (Rotz.) Koeler	0	2.42	4.12	0.49	0.61	0.49
Ixeris chinensis (Thunb.) Nakai subsp. Graminifolia (Ledeb.) Kitag.	0	3.34	2.69	1.44	2.65	0
Eragrostis pilosa (L.) Beauv.	0	0	0.39	0.26	3.41	10.42
Aristida adscensionis L.	0	0	1.13	0.98	11.74	9.68
Chloris virgata Swartz	0	0	0	0	0.71	12.26
Cenchrus calyculatus Cavan.	0	0	2.12	0	0	0
Lespedeza davurica (Laxam.) Schindl.	0	0.80	2.17	1.94	0.78	2.90
Melissitus ruthenicus (L.) C. W. Chang	0	0	1.68	0	2.64	0.43
Messerschmidia rosmarinifolia Willd. ex Roem. et Schult.	0	4.08	1.83	0	0	0
Euphorbia humifusa Willd.	0	0	1.89	0.46	6.47	0.22
Pennisetum centrasiaticum Tzvel.	0	0	0	0.40	1.29	1.26
Leymus secalinus (Georgi) Tzvel.	0	0	0	3.20	0.42	0.04
Euphorbia esula L.	0	0	0	0	0.23	0.11
Artemisia frigida Willd.	0	0	0	0	1.96	1.64
Gueldenstaedtia stenophylla Bge.	0	0	0	0	0.07	0
Phragmites australis (Cav.) Trin. ex Steudel Nomencl.	0	0	0	0	0.92	0.46
Thalictrum squarrosum Steph. ex Willd.	0	0	0	0	0.59	0.36
Kummerowia striata Willd.	0	0	0	0	0	0.06
Allium senescens L.	0	0	0	0	0.25	0.90
Carex durinscula C. A. Mey.	0	0	0	0	0	0.26
Lappula myosotis V. Nolf	0	0	0	0	0	0.64
Olgaea leucophylla Willd.	0	0	0	0	0.05	0.02
Cthinops gmelini Turcz.	0	0	0	0	0	0.02
Saposhnikovia divaricata (Turcz.) Schischk.	0	0	0	0	0.14	0.66
Potentilla bifurca L.	0	0	0	0	0	0.75
Tribulus terrestris L.	0	1.67	0	0	0.06	3.99
Chenopodium glaucum L.	0	0	0	0	0.69	6.85
Artemisia scoparia Waldst. et Kit.	0	0	1.97	0	0.88	2.85
Cleistogenes squarrosa (Trin.) Keng	0	0	0	0	4.03	24.03
Total number of species	7	11	17	14	28	30

Table 2
Patterns and dynamics of species diversity in the process of vegetation restoration

Succession age (year)	3	6	10	18	30	45
α-Diversity						
Shannon–Wiener index (SW)	1.0112	1.8092	2.1572	1.1761	2.5951	2.5265
Ecological dominance (SN)	0.4966	0.2074	0.1691	0.5456	0.0947	0.1046
Community evenness (PW)	0.5198	0.7546	0.7609	0.4459	0.7800	0.7439
β-Diversity between successive communities in the process of succession						
Whittaker index (β_{WS})		0.3333	0.2857	0.1613	0.3333	0.1379
Bray–Curtis index (C_N)		0.5852	0.5022	0.3034	0.3586	0.4436
Morisita–Horn index (C_{MH})		0.7300	0.6012	0.1608	0.3625	0.4741

Table 3
Patterns and dynamics of plant life-form composition along the sequence of succession

Succession age (year)	Species number	Therophytes			Perennials		
		Species number	Percent (%)	Dominance (%)	Species number	Percent (%)	Dominance (%)
3	7	6	85.71	99.06	1	14.29	0.94
6	11	8	72.73	95.44	3	27.27	4.56
10	17	13	76.47	85.92	4	23.53	14.09
18	14	9	64.29	19.43	5	35.71	80.57
30	28	18	64.29	71.65	10	35.71	28.35
45	30	21	70.00	68.09	9	30.00	31.91

Along the whole succession sequence, the value of community evenness (PW) varied congruently with changes in SW, while the value of ecological dominance (SN) shifted in the reverse manner.

The three β-diversity indices changed with similar tendencies except for the Whittaker index from 30 to 45 years, which deviated from the Bray–Curtis index (C_N) and Morisita–Horn index (C_{WH}) by decreasing rather than increasing. From 3 to 18 years, β-diversity showed a decreasing trend and reached its lowest point at 18 years. After that, it changed in an increasing trend from 18 to 30 years, and from 30 to 45 years with the exception just mentioned.

3.3. Life-form composition

Plants were grouped into two life forms: therophytes (annuals and the few biennials) and perennials. The number of species of both therophytes and perennials increased with succession except that the number of therophytes decreased in the 18-year community (Table 3). In the early stages of succession (from 3 to 18 years), dominance of therophytes decreased slowly, while that of perennials increased, until

Table 4
Patterns and dynamics of plant family composition

Succession age (year)	Species number	Families number	Chenopodiaceae			Compositae			Gramineae			Leguminosae		
			Ns	Pn (%)	Ds (%)	Ns	Pn (%)	Ds (%)	Ns	Pn (%)	Ds (%)	Ns	Pn (%)	Ds (%)
3	7	4	4	57.14	80.71	1	14.29	0.94	1	14.29	16.91	0	0	0
6	11	6	4	36.36	53.12	2	18.18	7.09	2	18.18	33.24	1	9.09	0.80
10	17	7	4	23.53	54.47	3	17.65	9.51	5	29.41	20.29	2	11.76	3.85
18	14	6	3	21.43	12.12	2	14.29	75.04	5	35.71	8.56	1	7.14	1.94
30	28	10	4	14.29	32.79	4	14.29	18.90	8	28.57	33.02	3	10.71	3.48
45	30	12	4	13.33	17.19	3	10.00	4.50	9	30.00	66.38	2	6.67	0.43

Ns: number of species; Pn: percent of Ns; Ds: dominance of species.

18 years. In the 18-year community, dominance of therophytes reached a low of 19.4% and that of perennials reached a peak of 80.5%. Subsequently, a sharp increase in therophytes and a steep decline in perennials occurred. At the end of the succession sequence there were only small changes in both therophyte and perennial dominance.

3.4. *Plant composition by family*

The number of plant families exhibited a progressively increasing trend over time (Table 4), and the most important four families were Chenopodiaceae, Compositae, Gramineae and Leguminosae.

The number of species of Chenopodiaceae was stable along the succession sequence, while the number of Compositae and Leguminosae species fluctuated slightly, and that of Gramineae species steadily increased. The dominance of Chenopodiaceae plants was highest in the earliest stage of succession, and much greater than that of the other three families listed. Chenopodiaceae dominance declined from 80.7% in year 3 to a low of 12.1% in year 18, then showed a resurgence to 32.8% in the 30-year community before declining again to 17.2% in year 45. The other three families also showed non-monotonic changes in dominance values over the whole successional period, but all in different patterns (Table 4). Gramineae plants were dominant and controlled community function in the final stage of succession. Leguminosae plants fluctuated in dominance over succession, but always with a minor position in the community.

4. Discussion and conclusions

4.1. *Community succession in the process of vegetation restoration*

Species diversity has great influence on community structure and function. Changes in species diversity and species composition are the most conspicuous characteristics of succession (Hibbs, 1983). We have compared the species diversity and species composition of six plant communities which constitute a chronosequence of succession. Our results indicate that succession has driven the process of vegetation restoration in this seriously degraded sandy land.

β-Diversity of communities, which refers to the degree of species replacement with changes along an environmental gradient, is also known as species turnover rate, species replacement rate, or rate of biotic change (Pielou, 1975; Magurran, 1988). It can indicate the dissection of habitats on a site or habitat diversity of different sites. According to this, great changes took place in community or habitat from 10 to 18 years and from 18 to 30 years. In the former period, the most important change was the population increase of *A. halodendron*, and for the latter period it was the population decrease of *A. halodendron*.

In the first case, because of the population prosperity of *A. halodendron*, vegetation cover was enhanced greatly, thus the protection afforded to the soil surface by vegetation was also improved, and wind erosion was alleviated gradually until it was almost totally prevented in the end. At the same time, community habitat was altered in character from mobile sand dunes to semi-fixed dunes, and again into fixed sand dunes. Also, biomass accumulation resulting from the population increase of *A. halodendron* intensified soil water flux through transpiration, and soil aridity developed progressively (Cong et al., 1993). All these changes in community habitat resulted ultimately in the population decrease of *A. halodendron*, because *A. halodendron* is a sand plant, and its growth is promoted by sand burial on mobile dunes. With community habitat converted into fixed sand dunes, *A. halodendron* lost its former competitive advantages and could not regenerate effectively.

Therefore, in the second case, population decline of *A. halodendron* provided space for invasion of other species. The abrupt rise of species richness and diversity in this stage (30 years) could be regarded as an outcome of such processes as habitat shift and an increase in heterogeneity (Bazzaz, 1975). Also, the process of vegetation restoration was accompanied by other changes in habitat such as deposition of wind-blown materials, formation of soil crust, increase in soil organic matter and increase in soil fertility (Cong et al., 1993). These changes contributed to an increase in species diversity. Here, we see that the interdependence between vegetation development and changes in habitat was the main driver of succession.

4.2. Indicator plants in the process of vegetation restoration

A particular predominant species could be identified in each stage of the succession. What factors might account for this? We consider that this was closely related to three factors: plant life history traits, community habitat characteristics and interactions between species (e.g. exploitative or interference competition). Certain properties such as life form, seed dispersal, physiological attributes, etc. might tailor a species's fitness to a particular habitat, and the higher fitness would allow the species to colonize, grow and propagate in the site more successfully than other species, becoming dominant.

For example, long observation in the region has shown that *Agriophyllum squarrosum* is, almost without exception, the pioneer plant initially colonizing mobile sand dunes and becoming predominant in that habitat. There are two difficulties for vegetation development on mobile sand dunes (Li et al., 1997): (1) the extremely barren soil limits plants growth, and (2) the unstable substrate (wind erosion) prevents the propagules of most plants from establishing on these sites. But because of its special properties *Agriophyllum squarrosum* can establish itself and grow readily in mobile sand dunes. Its small and flat seeds have the advantage of wide dispersal with resistance to wind erosion and good retention in the soil. After germination its embryo roots promptly and rapidly develops a deep root system to maintain the seedling in the soil against wind buffeting. *Agriophyllum squarrosum* is also adapted to barren, low-fertility soils and can grow vigorously on mobile sand dunes (Li et al., 1992; Nemoto and Lu, 1992).

After the initial *Agriophyllum squarrosum* community became established on mobile sand dunes, the mobility of the soil surface was reduced. *A. halodendron*, a semi-shrubby perennial plant, invaded into the community by seed, and began the process of propagation by vegetative growth. *A. halodendron* has slim, flexible shoots which can easily be buried by sand accumulation. After being buried, the plant can sprout numerous new shoots from the buried old shoot and also generate adventitious roots. Because of its fitness in the habitat of this stage, *A. halodendron* was seen to perform well in semi-fixed sand dunes.

Again attributable to vegetation development, community cover was further enhanced, community function was progressively restored and community habitat converted into fully fixed sand dunes. This was also accompanied by deposition of fine soil particles, formation of soil crust, accumulation of soil organic matter and increase in soil fertility (Cong et al., 1993). Under these conditions, a grass, *C. squarrosa*, and a number of forb species invaded into the 30-year community, with *Cleistogenes* growing into the dominant plant from 30 to 45 years with 24% dominance in the community. *C. squarrosa*, a xerophytic perennial grass with a strong root system distributed mainly in the 0–30 cm soil layer, is a dominant of the zonal vegetation type in this region. So we see a trend in which the successional communities on the study sites developed toward the typical zonal climax vegetation. Because of its xerophytic properties, *C. squarrosa* can maintain a stable population in arid conditions. Therefore, community stability was increased with succession. According to this, we predict that dominance of *C. squarrosa* will rise to a still higher level with further successional development on the study sites, and species diversity will decrease weakly. Therefore, the patterns and dynamics of indicator plant species observed along the succession gradient should be largely attributed to interactions between species and their environments.

4.3. Implications for vegetation restoration

We have observed a vegetation restoration process through plant community succession under the influence of a regional seed pool, and gained some understanding of the mechanisms of species replacement. Although succession is a well-worn topic (Clements, 1916; Pickett and McDonnell, 1989; Bazzaz, 1996; Lichter, 2000), the application of succession concepts to vegetation restoration holds promise (Young et al., 2001). Our results have shown that plant species attributes and community succession are drivers of the process of vegetation restoration, and this provides a testable model for the implementation of revegetation via succession. Generally, species richness and species diversity increased with longer succession time. Measured by both number of species and dominance value, Gramineae plants were predominant in the community with longest succession time. All these indicated that community function recovered to an excellent state, and that vegetation developed well through succession.

The Horqin Sandy Land, subject of our study, was once the most typical, representative steppe zone in northern China, and remained good pasture for royals' livestock through much of the Qing Dynasty (1616–1884) (Liu et al., 1996). However, the arid, windy climate and the loose sandy soil make the eco-environment very fragile in this region (Zhao et al., 1998). Because of a rapid increase in population, resulting in over-grazing by livestock (mainly sheep and horses) and cultivation of marginal land by local people, desertification has spread dramatically in this region in the last 50–100 years. For the urgent practice of vegetation restoration in this region, plant species replacement and community succession are the fundamental principles for effective revegetation. Enclosing areas to be revegetated is necessary. Only under protection from grazing and other disturbance can the ecological processes of species invasion, establishment, propagation and succession develop smoothly in a natural and progressive way.

Considering our observation that a particular species, accounting for most of the community function and promotion of vegetation restoration, is the dominant in a given successional stage, we recommend that supplemental seed sources of the appropriate dominant species be provided through artificial collection, and used according to site habitat characteristics and successional stage in order to expedite community succession and vegetation development.

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