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REPRODUCTIVE BIOLOGY AND PLANT SPECIES SELECTION FOR HABITAT RESTORATION IN THE VENEZUELAN GRAN SABANA PLATEAU

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SUMMARY

Plant species selection for the restoration of borrow pits in the Venezuelan Gran Sabana Plateau was based in plant species having high reproductive performance. The reproductive traits used are: 1- high and continuous seed production, 2- breeding system that promotes self-pollination and low expression of deleterious characters, 3- floral morphology allowing a large diversity of visitors, 4- a generalist biotic pollination system or wind pollination, and 5- abiotic dispersal syndrome of diaspores and/or capacity for colonization and eventual immigration. Plant life form is considered as a complementary character. After evaluations of 14 characters (scale from 0 to 1 for each character), 45 of 157 plant species were selected having a score >65%. The highest score for woody species (69.75%) was lower than that in herbaceous species (81.12%). The highest scores of herbaceous species were for Perama galioides *(Rubiaceae),* Aristida torta*,* A. recurvata*,* Panicum cyanescens, Andropogon selloanus *(Poaceae) and* Rhynchospora caracasana *(Cyperaceae), and the highest scores of woody species were for* Gongylolepis benthamiana *and* Chromolaena laevigata *(Asteraceae). Reproductive score (selected/non-selected species), natural distribution (disturbed/undisturbed distribution), and colonization of borrow pit (colonizing/non-colonizing species) interact significantly in the three factor dependence analysis (χ^2= 6.1; df= 1; P= 0.013519), indicating dependence of these variables on the colonization process. The combination of high reproductive score (70-81%), natural distribution on disturbed areas and capacity for spontaneous colonization of borrow pits is the best combination of traits for herbaceous species, other characters of which must be evaluated to design management and restoration plans for degraded areas.*

One of the greatest problems during the last decades has been the progressive anthropogenic disturbance of natural habitats. Many environmental agencies direct economic resources to stop non-reversible environmental damage and to promote spontaneous restoration. In many cases, programs of environmental management are designed for multiple purposes but privilege the use of woody species (forestation), while shrubs and herbaceous species are less commonly considered for habitat restoration. The main reason is that spontaneous colonization of degraded areas by herbaceous species commonly occurs at the beginning of natural succession. However, in deeply disturbed areas where the soil has been removed, non-vegetated areas remain (Rosales *et al.*, 1997). These disturbed areas are frequently planted with exotic species to avoid soil erosion. Bradshaw (1987) pointed out, however, that restoration of degraded areas would more likely be successful if native species were used. The current widespread interest in native herbs is due, in part, to the recent availability of plant material as well as recognition of the role of native herbal species in the restoration of biological diversity and the conservation of endangered species and habitats (Knapp and Rice, 1996). Restoration of plant communities structurally and functionally similar to those that pre-dated the site degradation could be accomplished if plant species from the same area were used in the restoration programs. Native species can be more appropriate than exotics because they are better adapted to local environmental conditions and seed and other propagules are locally available (Montagnini, 2001).

In the Gran Sabana Plateau, Venezuela, disturbed areas along the roads have remained without vigorous vegetation for 8 years since soil disturbance (Cuenca and Lovera, 1992; Lovera and Cuenca, 1996) and only a few native species have colonized these areas (Rosales *et al.*, 1997). They represent lands where soil horizons have been partially or completely removed. These areas are known as borrow pits; in some cases erosion has generated large gravel pits with deep furrows (Rosales *et al.*, 1997). Borrow pits differ from other disturbed areas in the Gran Sabana Plateau because after soil has been removed plant coloni-

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zation does not occur spontaneously under natural conditions in a short time. One of the most common exotic species used to avoid soil erosion in Venezuela is *Brachiaria decumbens* (Poaceae), which is sown in borrow pits (disturbed areas) close to roads (Cuenca and Lovera, 1992). This herbaceous species was sown 6 years ago without success in the Gran Sabana Plateau (Cuenca and Lovera, 1992). In these areas, the abundance of *B. decumbens* declines in the years following sowing, and some native species may colonize the area; however, the process is very slow (Gisela Cuenca, personal communication). In this context, the goal for restoration must be understood as a general strategy to overcome the various barriers to natural recovery. In addition to autochthonous species in habitat restoration, plant species selection has to be based on their adaptability to difficult site conditions, their probable biotic and abiotic influence on site conditions, and their future reproductive capacities, among other variables.

Reproductive biology is one of the most important aspects that should be considered in plant species selection for habitat restoration. The attributes should ensure high seed production, low mortality risk, and sustainability of the colonizing population (Bawa *et al.*, 1989). For example, weeds have reproductive and ecological traits that enhance their capacity to invade highly disturbed areas (Baker, 1974). The knowledge of plant species phenology, pollination, mating system and seed dispersal can refine our capacity to manage natural and disturbed areas for conservation and restoration. Selection of autochthonous plant species for restoration of degraded areas in the high basin of the Caroní River, Venezuela, was based on reproductive attributes which enhance biological success in marginal conditions. This is associated with life history of colonizing plants (Bazzaz, 1986).

The purpose of this study was to select native plant species with a high reproductive potential. In other words, this research intends to find plant species from herbaceous and shrubby communities in the high basin of the Caroní River in the Gran Sabana Plateau that have the combination of reproductive traits that allow them a high reproductive output. These traits are: 1- high and continuous seed production, 2- a breeding system that promotes self-pollination, 3- a floral morphology that allows a large diversity of floral visitors, 4- a generalist biotic pollination system or wind pollination, and 5- seed dispersal syndromes of diaspores with the capacity to colonize distant areas. In addition, the predictive value of reproductive attributes was tested for native colonizing plant species growing spontaneously on the borrow pits.

Study Areas

Plant species were selected from seven communities in the high basin of the Caroní River of the Gran Sabana Plateau, Canaima National Park, Bolívar State, Venezuela (Figure 1). These plant communities included shrublands, savanna, broad-leaved meadow, and secondary vegetation (Table I). The annual average temperature is 20.6ºC and annual precipitation is 2428mm, abundant throughout the year, with maximum in August and minimum from January to March (Ramírez *et al.*, 1988). Additional details of soil, climate and vegetation of the area can be found in Ramírez *et al.* (1988), Dezzeo and Föster (1994) and Huber (1994).

The shrublands have a physiognomy and floristic composition typical of the white-sand associations in Guayana, dominated by herbs and shrubs, and small trees. The shrublands are surrounded by *Trachypogon* savanna and frequently associated with broad-leaved meadows. The savanna is a typical grassland community, where *T. plumosum* is the most abundant species. Broad-leaved meadows are dominated by Xyridaceae, Rapateaceae, and Eriocaulaceae, being *Stegolepis ptaritapuiense* (Rapateaceae) the most frequent species. Secondary vegetation is represented by the re-growth of a forest deeply disturbed by anthropogenic activity, and an area of savanna abandoned after agricultural practices (fallow).

Plant species were studied in their reproductive attributes for 23 months in 4 years (1993-1996). Epiphytes, vascular parasitic, and Lentibulariaceae were excluded from the analysis. Voucher specimens were identified and deposited in the Herbario Nacional de Venezuela (VEN) and in the Missouri Botanical Garden (MO).

Methods and the significance of character selection

Methods and criteria employed followed an initial proposal of plant species selection for degraded areas (Ramírez, 1997) that was modified, using 14 characters. These characters are associated with the reproductive success and plant species performance, and potentially involved in invasion success (Baker, 1974; Sutherland, 2004; Lloret *et al.*, 2005).

Character selection

The selection of characters was based on their relation to high reproductive output. Characters were similar or contrasting alternatives, not necessarily opposites. Character selection was made irrespective of the presence of correlations or association among characters; each character was selected by itself and only in some cases some correlation existed. A preliminary evaluation indicated that most of the characters were not related, and in those cases when correlation existed, the coefficients of determination were low (0.025 to 0.314). In this first approximation, characters were not differentially weighted. For discrete variables, two or more states of each character were considered. Character states were ranked from 1 to n according to their capacity to enhance and promote reproduction. Each value assigned was divided by the maximum obtained, resulting in relative proportions. For continuous variables, most of the expressions were direct estimates of reproductive output.

Arbitrarily, the cumulative count of approximately 9 points, 65% of the 14 maximum possible points, was considered as the minimum required for selecting a plant species for restoration. Plant species with a minimum of 65% of the points have many of the characters enhancing reproductive output, with approximately 2/3 of the total count. To assess the validity of this minimum value of 65% for plant species selection, a standard discriminant analysis was performed, using field records of colonizing plant species on borrow pits as a grouping variable and their reproductive attributes as

TABLE I
CHARACTERISTICS OF THE STUDY SITES

Locality	Type of Community	Coordinates	Elevation (m)
1- Mareman	Shrubland	5º44.49'N, 61º24.20'W	1,386
2- Liworiwo	Shrubland	5º36.88'N, 61º29.66'W	1,208
3- Guamu-pe	Shrubland	5º35.00'N, 61º43.00' W	1,350
4- 168 Km	Broad-leaved Meadow	5º38.55'N, 61º22.94'W	1,343
5- Parupa	Savanna	5º42.68'N, 61º31.30'W	1,302
6- Parupa	Secondary forest, untilled	5º44.42'N, 61º32.54'W	1,300
7- Parupa	Secondary savanna, fallow	5º44.42'N, 61º32.54'W	1,300

independent variables. The capacity of plant species to spontaneously colonize borrow pits was obtained from previous studies (Rosales *et al.*, 1997). Plant species from the seven communities were classified as invaders and non-invaders of borrow pits. Besides, plant species were classified by the areas where they grow naturally: disturbed areas and/or undisturbed areas. When plant species occurred in disturbed and undisturbed areas, they were computed for both conditions. The number of communities where plant species grow naturally and their presence in borrow pits were compared with one way ANOVA (Sokal and Rohlf, 1995). Values were square-root transformed before analysis.

The level of dependence among plant species selected (score >65%), those non-selected (score <65%), their natural distribution, and their capacity to naturally invade borrow pits was established using a log-linear analysis of frequency. The three factors were used initially, and then a two factor model (StatSoft, 2001) was used. When the log-linear analysis was significant, then residual frequencies (observed minus expected frequencies) were estimated for each cell of the two-factor comparison, and residuals were standardized and tested for significance. This analysis indicated which pair of variables deviated significantly from the expected values (Legendre and Legendre, 1993) and, therefore, had a larger contribution to the association.

TABLE II
QUALITATIVE CHARACTERS AND THEIR CORRESPONDING POINTS ASSIGNED IN A CONTINUOUS SCALE

Characters	Points (respective fraction)
Life Form	
Annual herbs	5 (1.00)
Perennial herbs	4 (0.80)
Lianas	3 (0.60)
Shrubs	2 (0.40)
Trees	1 (0.20)
Sexuality	
Hermaphrodite	5 (1.00)
Andromonoecious	4 (0.80)
Gynomonoecious	3 (0.60)
Monoecious	2 (0.40)
Dioecious	1 (0.20)
Herkogamy	
Non-herkogamous	3 (1.00)
Herkogamous	2 (0.67)
Dioecious*	1 (0.33)
Dichogamy	
Adichogamous	4 (1.00)
Protandrous	3 (0.75)
Protogynous	2 (0.50)
Dioecious*	1 (0.25)
Pollination Unit	
Flower-inflorescence	3 (1.00)
Inflorescence 2 (0.67)	
Flower	1 (0.33)
Floral type	
Amorphic	6 (1.00)
Haplamorphic	5 (0.83)
Actinomorphic	4 (0.67)
Dish to bowl	3 (0.50)
Stereomorphic	2 (0.33)
Zygomorphic	1 (0.16)
Pollination system	
Wind	4 (1.00)
Polyphilous	3 (0.75)
Oligophilous	2 (0.50)
Monophilous	1 (0.25)
Dispersal syndrome	
Wind and autochory	5 (1.00)
Granivorous	4 (0.80)
Epizoochorous	3 (0.60)
Birds and mammals	2 (0.40)
Birds	1 (0.20)

* Dioecious species were included in these categories to avoid empty cells in the score of the plant species (see text for details).

Plant characters examined

Life form

Plant species were classified as trees, shrubs, lianas, and herbs. Lianas were divided into woody and non-woody lianas or creepers, and herbs were categorized as annual or perennial. Points were assigned according to the species colonizing ability: more points for herbaceous, including non-woody lianas, than for woody species (Table II).

Phenology

Ripe fruit phenology was monitored in each community bimonthly, between 1993 and 1996. Data recorded during this period were pooled, and then the monthly presence of ripe fruit was established for each species. Plant species were characterized by the number of months producing ripe fruits, from a maximum of 12 months.

Plant sexuality

Information about plant sexuality comes from a previous study (Ramírez, 1993a), and other plant species were evaluated in this study. The points were assigned following the progressive separation of sexual organs, maximum rank to hermaphroditic and minimum rank to dioecious species (Table II).

Temporal variation in sex expression

Information about the temporal variation in sex expression, used to rank plant species, comes from a previous study (Ramírez, 1993a) and unpublished data. Maximum points were assigned to adichogamous species and in a decreasing order from protandry to protogyny (Table II). To avoid empty cells in the model, dioecious species were included in this category with the lowest points, because they have no self-pollination, and fruit and seed set depend on pollination activity.

Herkogamy

Information about herkogamy (the spatial separation of pollen presentation and pollen receptivity) comes from a previous study (Ramírez, 1993a) and unpublished data. Non-herkogamous species were assigned 3 points and 2 points were assigned to herkogamous species (Table II). In addition, dioecious species were included in this category with the lowest points for three reasons: 1- to avoid empty cells in the model, and 2- dioecious species may be considered as herkogamous (see Webb and Lloyd, 1986), and 3- in dioecious species self-pollination did not occur, and fruit and seed set depend on pollination activity.

Pollination unit

Information of pollination unit comes from a previous study (Ramírez, 2003). Pollination units were characterized according to flower arrangement in the inflorescence and pollinator behavior (Faegri and van der Pijl, 1979; Ramírez *et al.*, 1990). Points were assigned according to the probability to be visited by a large variety of pollinators or potential pollinators, and hence promote fruit and seed set. Plant species with flower-inflorescence and inflorescence as a pollination unit were assigned 3 and 2 points, respectively. Flower as pollination units were assigned 1 point because they may represent the most specialized pollination units (Ramírez, 2003).

Floral types

Information of floral types come from a previous study (Ramírez, 2003). A classification of blossom, flowers and inflorescences was used following the classification systems of Leppik (1969) and Faegri and van der Pijl (1979), modified according to Ramírez (2003). The progression from zygomorphic to amorphic blossom represents a series of decreasing complication and different levels of specialization.

Therefore, points were assigned progressively from the more specialized to less specialized floral types (Table II), which is correlated with the fruit set (Ramírez, 2003).

Pollination system

Information about pollination comes from a previous study (Ramírez, 1993a) and unpublished data. Plant species were categorized according to the character of visits received (slightly modified from Faegri and van der Pijl, 1979). Points were assigned following decreasing levels of specialization, from specialized (monophily) to less specialized (polyphily) pollination systems. Anemophilous species were assigned the highest points because of their independence from biotic vectors.

Seed dispersal

Information about dispersal syndromes comes from a previous study (López and Ramírez, 1989) and unpublished data. Dispersal syndromes were established according to the criteria of Dansereau and Lems (1957) and van der Pijl (1972). Points were assigned progressively from 1 to 5 following the level of dependency on specialized animals (Table II).

Reproductive efficiency

Information about reproductive efficiency comes from previous studies (Ramírez, 1993b; Raimúndez 2000) and unpublished data. Reproductive efficiency was established at four levels: 1- fruit set was determined by the proportion of hermaphrodite and/or female flowers per inflorescence that developed into mature fruits; 2- seed per ovule was determined by dividing the average number of seeds per fruit by the average number of ovules per flower; 3- seed abortion was determined directly in 50-100 mature fruits, and aborted seeds per fruit divided by the average number of seeds per fruit was used to determine the proportion of aborted seeds; 4- seed set or fecundity was defined as the proportion of well-developed seeds per ovule per inflorescence (Ramírez, 1992). In the case of seed per fruit, the value was obtained dividing the largest value of the number of seeds per fruit in all plant species considered by the number of seeds per fruit of each plant species, which resulted in a fraction from 0 to 1.

Results and Discussion

Plant reproductive characters and plant species selection

Of 157 plant species evaluated in 13 reproductive attributes and life forms, 45 (28%) species had more than 65% of cumulative points in the scale proposed, which included 41 herbaceous and three woody species (Table IV). The highest values were found in herbaceous species, which indicated that these plant species have reproductive attributes that could enhance colonization of degraded areas. However, the three woody species selected shared some reproductive attributes with the herbaceous species selected: hermaphroditism, adichogamy and wind dispersal. In addition, there were no plant species with the maximum of points (100%), which indicates the difficulty of getting specific trait combinations.

Reproductive traits in selected herbaceous species were similar in many cases. Similarity among herbaceous species stems from taxonomic affinity. Of the 41 herbaceous species, 21 were of the Cyperales order (11 Poaceae and 10 Cyperaceae), followed by eight Asteraceae, three Melastomataceae, and two Rubiaceae. The first group of 21 monocot species was anemophilous with amorphic floral traits, in many cases dispersed by granivourous or wind, one seeded fruits, and very different reproductive efficiency. The second group of herbaceous species differs from the first group in some attributes: zoophilous pollination, floral type, and many seeded per fruit, but also share some attributes with the first group: high reproductive efficiency and granivourous or wind dispersal.

Adichogamous and non-herkogamous species tend to be self-compatible and in many cases autogamous, because self-pollination is not avoided (Lloyd and Webb, 1986; Webb and Lloyd, 1986; Bertin and Newman, 1993). Adichogamy and non-herkogamy were found in many species (*Aristida torta*, *A. recurvata*, *Panicum cyanescens*, *Andropogon selloanus*, *Perama galioides*, *Ludwigia erecta*, *Polygala adenophora*, *Borreria capitata* and *Axonopus anceps*). Adichogamous species exhibit a lower frequency of cross-pollination compared to dichogamous species (Bertin and Newman, 1993) and non-herkogamy promotes self-deposition of pollen on the stigmas (Webb and Lloyd, 1986). Most of these plant species may be self-compatible. Self-fertilization in herbaceous species makes them successful weeds (Mulligan and Findlay, 1970). Self-compatibility has no deleterious consequences, and homozygosity may reduce genetic loads and increase seed set (Weins, 1984; Weins *et al.*, 1987); normally outbred species response to inbreeding depression than normally inbred species (Richards, 1986). During restoration, relatively isolated populations, self-compatible species, may have less chance of genetic erosion. Self-pollination and the patchy natural distribution of the species are both likely to contribute to the low level of gene flow, and can facilitate the divergence of populations over small spatial scales (Knapp and Rice, 1996). In addition, autogamous self-compatible species allow a single plant or a few individuals to establish populations (Anderson *et al.*, 1996).

Herbaceous species occurring in early seral stages frequently have anemochorous or epizoochorous dispersal syndromes (Opler *et al.*, 1980). The presence of wind dispersal syndrome in the herbaceous and woody species selected agrees with the expected results. In this context, abiotic or anemochorous species should be selected for habitat restoration. However, some herbaceous species selected had a granivourous dispersal syndrome. Seed dispersal by granivoures depends on birds (Ridley, 1930), mammals (Janzen, 1984) and/or ants (van der Pijl, 1972). In spite of the generalist character of plant species dispersed by granivoures, the dissemination of seeds may be limited in the absence of their dispersing animals. This situation may be pronounced in areas where soil has been removed and plant cover is absent, such as the borrow pits in the Gran Sabana Plateau.

Reproductive efficiency of herbaceous species was high for *A. torta*, *A. recurvata*, *P. cyanescens*, *Rhynchospora mexicana*, *P. galioides*, *L. erecta* and *P. adenophora*, intermediate for *Hypolytrum pulchrum* and *Rhynchospora rugosa*, and low for *T. plumosus*, *Echinolaena inflexa*, *A. anceps*, *Bulbostylis lanata* and *Lepidoploa ehretifolia*. In a similar way, woody species show high (*Chromolaena laevigata* and *Gongylolepis benthamiana)* and intermediate (*Mahurea exstipitata*) values of reproductive efficiency. The success of invasive plants appears to be related to high seed production, allowing the initial establishment of large numbers of individuals (Anderson *et al.*, 1996). In addition, ripe fruit phenology was longer for herbaceous than for woody species, and therefore reproductive efficiency is greater for herbaceous species. Extended reproductive activity increases the abundance of propagules and the probability of leaving offspring (Pianka, 1994). An organism can increase its reproductive output by breeding more often and breeding over a longer period of time (Pianka, 1994) and therefore, an active seed rain in the area, could improve establishment opportunities (Ramírez, 2002). This aspect has been demonstrated for alien plants on Mediterranean islands (Lloret *et al.*, 2005). Besides, some plant species selected may have low sexual reproductive efficiency. Some of these plant species may show a high asexual propagation capacity, by stolons (i.e. *H. pulchrum* and *E. inflexa*). Plant species with asexual reproduction can be considered for revegetation plans of degraded areas because of a lower number of biotic interactions (pollination and dispersal) for seed production, and, therefore, plans for habitat restoration could be more successful under the two alternative modes of reproduction. Vegetative growth may enhance stand formation after initial colonization (Baret *et al.*, 2005).

Plant species selection, natural distribution and colonization

Reproductive scores (comparing selected and non-selected species), natural distribution (comparing species occurring in disturbed and undisturbed sites) and colonization of borrow pits (colonizing and non-colonizing species) were significantly associated (χ^2= 6.1; df= 1; P= 0.013519), which indicates the interdependence of these variables in the process of plant colonization. In this sense, plant species distribution and habitat type where plant species grow naturally must be considered as an important criterion for plant species selection for habitat restoration. The presence of species in disturbed areas (Table IV) shows their natural colonizing ability. The condition of selected and non-selected species is significantly associated with their natural distribution of plant species (χ^2= 7.35; df= 1; P= 0.006688). Among selected species, 25 out of 44 plant species grow spontaneously in disturbed areas (Table III), which indicates their colonizing ability. However, plant species spontaneously colonizing borrow pits occur significantly ($F_{1,155}$= 12.3; P= 0.000592) in more communities (X= 4.1 ±2.4SD) than plant species that are non-colonizing in borrow pits (X= 2.5 ±1.4SD), which indicates that plant species with broad distributions are better colonizers. This may be considered as an important criterion for species selection and management plans for habitat restoration. Among plants with a broad distribution and/or specially those growing naturally in disturbed areas are herbaceous species as *P. galioides* (Rubiaceae), *P. cyanescens*, *T. plumosus*, *E. inflexa*, *A. anceps* (Poaceae), *H. pulchrum* and *R. rugosa* (Cyperaceae), shruby species such as *C. laevigata* (Asteraceae), and *M. exstipitata* (Clusiaceae).

One of the characters occurring in most of the woody and herbaceous species selected was the low number of seeds per fruit, which seems to be primarily related with the taxonomic affinity of plant species (Poaceae, Cyperaceae, and Asteraceae). In the present study, the floristic evaluation of plant species growing in borrow pits in the Gran Sabana Plateau showed that many of the plant species had a low seed number per fruit, as was also shown by Rosales *et al.* (1997). This result is opposite to the general trend, where plant invasiveness is determined by high seed production (Naylor, 1984; Rejmánek and Richardson, 1996; Morgan *et al.*, 2002; Murray *et al.*, 2002). Low seed numbers per fruit may be selected in invading or colonizing species because of their reproductive significance. Low numbers of seeds per fruit may be related to the high efficiency in seed/ovule ratio (Uma Shaanker *et al.*, 1988; Ramírez, 1992), and the advantage associated with the low pollen requirement and low competition among seeds (Nakamura, 1988; Uma Shaanker *et al.*, 1988).

A large number of biotic interrelations may be considered a restrictive factor in colonization. The production and dissemination of seeds may be limited in the absence of their dispersing animals. Colonizing species found in degraded lands of the same geographic area studied, mainly showed abiotic reproduction modes, and the number of biotic interrelations was limited to one, when it occurred (Rosales *et al.*, 1997). Under such circumstances, plant species with a low number of biotic interrelations can be considered as the most appropriate species to be used in the first stages of habitat restoration. The most important plant reproductive attributes for habitat colonization were ripe fruit phenology, adichogamy-non-herchogamy, anemophily or polyphily pollination, high reproductive efficiency, and abiotic or unspecialized seed dispersal. Moreover, the best choice for habitat restoration are those plant species with high scores, natural distribution on disturbed areas and natural invasion of borrow pits, such as *A. torta*, *A. recurvata* (Poaceae), *B. capitata* (Rubiaceae), *H. pulchrum*, *Rhynchospora barbata* (Cyperaceae) and *E. inflexa* (Poaceae).

Further studies must be considered before implementing management plans for habitat restoration in the Gran Sabana Plateau. Plant species selected by reproductive traits have to be examined for their recruitment capacity. The relationship between selected and non-selected species and natural colonization of borrow pits (Table III) was statistically significant (χ^2= 11.04; df= 1; P= 0.000891). Residual analyses showed that plant species selected (>65% of points) invaded borrow pits spontaneously. Spontaneous colonization of borrow pits can be considered as a measure of recruitment capacity. The results of discriminant analysis indicate that 66.7% (12 out of 18) of plant species colonizing borrow pits spontaneously are also classified as colonizing species according to reproductive attributes. Moreover, the reproductive attributes allow statistical discrimination of borrow pit colonizing and non-colonizing species (Squared Mahalanobis distance of 1.85; $F_{14,142}$= 1.83; P= 0.038272). These results show that the reproductive attributes used in this study have a high predictive value in plant species selection for habitat restoration. For restoration purposes, plant species must establish themselves under harsh conditions and improve soil and other features of the environment for subsequent species. Reproductive biology as proposed in this study provides the basis of reproductive success in degraded areas. However, initial introduction of many plant species may be constrained by their obligate mycorrhizal association (Cuenca and Lovera, 1992; Lovera and Cuenca, 1996; Rosales *et al.*, 1997; Cuenca *et al.*, 2002) and the low percentage of germination in some herbaceous species (*E. inflexa* and *A. anceps*) studied by Cuenca *et al.* (2003). Initial habitat restoration depends on plant species recruitment success; then,

TABLE III
FREQUENCY DISTRIBUTION OF SELECTED AND NON-SELECTED PLANT SPECIES RELATIVE TO NATURAL DISTRIBUTION IN THE AREA AND THE INVASION CAPACITY ON BORROW PITS

Plant species	Score: ≥ 65% (Selected) N(%)	Score: < 65% (Non-selected) N(%)	Total N(%)
Natural distribution			
Disturbed areas	25 (33.8)	49 (66.2)	74 (47.1)
Undisturbed areas	19 (22.9)	64 (77.1)	83 (52.9)
Natural invasion			
Colonizing borrow pits	11 (61.1)*	7 (38.9)	18 (11.5)
Non-colonizing borrow pits	33 (23.7)	106 (76.3)	139 (88.5)
Total	44 (28.0)	113 (72.0)	157 (100)

N(%): Observed frequency and percentage. * Significant of residual analysis at P<0.05.

TABLE IV

PLANT SPECIES, FAMILY, DISTRIBUTION, LIFE FORM, NUMBER AND PERCENTAGE OF POINTS ACCUMULATED FOR 157 SPECIES STUDIED

Plant species	Family[1]	Locality[2]	Life form[3]	Score	%[4]
Perama galioides	RUB	1-2-3-4-5-6-7	AH	11.36	81.12
Aristida torta **	POAC	5-6	PH	11.19	79.94
Aristida recurvata **	POAC	4-5-7	PH	11.02	78.72
Panicum cyanescens	POAC	1-4-5-6-7	PH	11.01	78.67
Andropogon selloanus	POAC	5	AH	10.90	77.88
Rhynchospora caracasana	CYP	1-2-3-5	PH	10.67	76.24
Rhynchospora mexicana	CYP	5	PH	10.61	75.77
Borreria capitata **	RUB	3-5-6	PH	10.61	75.77
Rhynchospora velutina	CYP	5	AH	10.43	74.51
Hypolitrum pulchrum * **	CYP	1-4-5-6-7	PH	10.28	73.44
Ludwigia erecta	ONAG	6	AH	10.27	73.37
Mesosetum sp.	POAC	4	AH	10.20	72.83
Rhynchospora rugosa	CYP	5-6-7	PH	10.18	72.70
Ludwigia sp.	ONAG	6	AH	10.15	72.48
Polygala adenophora	POLYG	5	PH	10.14	72.46
Axonopus anceps	POAC	1-2-3-4-5-6-7	PH	10.07	71.92
Rhynchospora barbata **	CYP	1-2-3-4-5-6-7	PH	10.05	71.77
Echinolaena inflexa **	POAC	1-2-3-4-5-6-7	PH	9.82	70.15
Bulbostylis lanata	CYP	1-5-7	PH	9.82	70.13
Gongylolepis benthamiana var. *pubescens*	AST	1-2-3	SH	9.76	69.75
Chromolaena laevigata	AST	1-3-5:6-7	SH	9.76	69.73
Irlbachia nemorosa	GENT	1-3-4	AH	9.76	69.70
Panicum micranthum **	POAC	5-6	PH	9.60	68.55
Xyris fallax	XYR	4	PH	9.59	68.49
Desmoscelis villosa	MELAST	5	AH	9.56	68.27
Lepidoploa ehretifolia	AST	5	PH	9.50	67.87
Syngonanthus xeranthemoides	ERIOC	1-2-3-4	PH	9.50	67.87
Leiothrix flavescens	ERIOC	4	PH	9.47	67.68
Brachiaria decumbens **	POAC	6-7	PH	9.38	67.00
Mahurea exstipitata	CLUS	6	TR	9.38	66.99
Trachypogon plumosum * **	POAC	1-2-3-4-5-6-7	PH	9.35	66.81
Calea cardonae	AST	2-4-6	PH	9.35	66.79
Comolia microphylla *	MELAST	2-3-4-6	PH	9.32	66.57
Brocchinia reducta	BROM	1-2-3-4	PH	9.32	66.57
Calea nana	AST	5	PH	9.28	66.26
Mikania micrantha	AST	6	LI	9.25	66.10
Paspalum lanciflorum **	POAC	1-4-5-7	AH	9.24	65.99
Rhynchospora pilosa	CYP	1-2-3-4-5	PH	9.16	65.45
Bulbostylis paradoxa	CYP	5	PH	9.16	65.43
Scleria distans	CYP	5	PH	9.15	65.38
Calea alchioides	AST	6	PH	9.15	65.35
Cyrilla racemiflora	CYR	1-2-3-4	PH	9.14	65.30
Irlbachia purpurascens	GENT	1-5-6	AH	9.14	65.26
Mikania psilostachya	AST	3-6	LI	9.13	65.21
Sipanea galioides	RUB	1-3-4-5-6	PH	9.07	64.79
Xyris roraimae	XYR	4	PH	9.06	64.70
Macairea lasiophylla	MELAST	1-4-5	AH	9.01	64.34
Raddiella esembeckii	POAC	5-6	PH	9.01	64.33
Vernonia bolivarensis	AST	3	AH	9.00	64.28
Calea divaricata	AST	1	PH	8.98	64.15
Nietneria paniculata	LIL	1-4	AH	8.96	64.02
Baccharis leptocephala	AST	5-6-7	PH	8.96	63.97
Siphanthera cordifolia	MELAST	1-2-3-4-5-6-7	AH	8.93	63.78
Xyris setigera Oliver	XYR	1-2-3-4-5	PH	8.91	63.63
Bulbostylis conifera * **	CYP	5	PH	8.88	63.45
Stomatochaeta condensata	AST	1-2-3-4	PH	8.88	63.43
Calea lucidivenia * **	AST	3	PH	8.86	63.25
Pagameopsis garryoides	RUB	3	PH	8.82	62.97
Buchnera pallustris	SCROPH	1-2-4-5-6	PH	8.80	62.86
Stegolepis angustata	RAP	1-2-3-4	PH	8.75	62.53
Stegolepis ptaritapuiensis	RAP	2-3-4	PH	8.73	62.38
Rhynchospora globosa	CYP	1-4-5	PH	8.69	62.06
Xyris involucrata	XYR	3-4-6	PH	8.62	61.60
Xyris uleana	XYR	2-4	PH	8.62	61.60
Remijia densiflora ssp. *stenopetala*	RUB	2-3	SH	8.60	61.40
Psycotria sp.	RUB	1-2-6	PH	8.57	61.20
Lagenocarpus rigidus * **	CYP	1-2-3-4-5-6-7	PH	8.53	60.94
Albolboda acaulis	XYR	1-2-3-4	PH	8.53	60.91
Xyris bicephala	XYR	3-4	PH	8.41	60.05
Roupala montana	PROT	1	TR	8.40	59.97
Erythroxylum citrifolium	ERYTH	6	SH	8.37	59.76
Bonnetia sessilis	THEAC	1-2-3-4	SH	8.35	59.64
Austroeupatorium inulaefolium	AST	6-7	SH	8.35	59.63
Albolboda machrostachya var. *robusta*	XYR	4	PH	8.35	59.61
Coutoubea reflexa	GENT	1-4-5	PH	8.34	59.59
Declieuxia fruticosa var. *fruticosa*	RUB	1-3-5-6-7	PH	8.32	59.40
Passiflora auriculata	PASS	4-6-7	LI	8.31	59.36
Fimbristylis sp.	CYP	4	PH	8.27	59.08
Marcetia taxifolia * **	MELAST	1-2-3-4-5-6-7	SH	8.23	58.81
Metastelma hirtella	ASCL	1-5-6	LI	8.22	58.71
Sabicea velutina	RUB	1-5-6	LI	8.21	58.66
Solanum (sec. Maurella) sp.	SOL	6	AH	8.21	58.62
Centropogon cornutus	CAMP	6	PH	8.19	58.48
Dalbergia monetaria	FAB	6	TR	8.12	57.97
Microlicia benthamiana * **	MELAST	2-3-4	PH	8.10	57.87
Chamaecrista ramosa	CAES	2	PH	8.07	57.65
Thesium tepuiense	SANT	4	PH	8.03	57.39
Lindmania guianensis var. *vestita*	BROM	1-2-3-4	PH	8.02	57.27
Scleria cyperina * **	CYP	1-2-3-4-5-6-7	PH	8.01	57.25
Digomphia laurifolia	BIGN	1-2-3-4	SH	7.92	56.59
Vellozia tubiflora	VELL	2-5	PH	7.92	56.57
Mandevilla benthamii	APOC	1-2-3-4-5-6	PH	7.90	56.42
Ternstroemia pungens	THEAC	1-2-3	SH	7.89	56.33
Sauvagesia guianensis	OCHN	4	PH	7.84	55.99
Clidemia sericea	MELAST	1-5-6-7	PH	7.84	55.99
Ternstroemia crassifolia	THEAC	1-2-3	SH	7.81	55.81
Sisyrinchium vaginatum	IRID	6	PH	7.78	55.59
Chamaecrista devauxii var. *mollisima*	CAES	1-2-5	PH	7.78	55.55
Chalepophyllum guianense	RUB	1-2-3-4	SH	7.71	55.06
Miconia ciliata	MELAST	1-2-3-4-6	PH	7.70	54.99
Galactophora schomburgkiana	APOC	2-3	SH	7.68	54.86
Ochthocosmus longipedicellatus	IXON	1-2-4	SH	7.65	54.61
Passiflora sclerophylla	PASS	1-3-4	LI	7.64	54.60
Tibouchina fraterna	MELAST	1-2-3-4	SH	7.63	54.48
Ditassa tatei	ASCL	1-2-3	PH	7.59	54.18
Macairea pachyphylla	MELAST	3	SH	7.58	54.17
Bonyunia minor	LOG	1-2-5	SH	7.54	53.83
Miconia sp.	MELAST	6	SH	7.53	53.83
Miconia sp.	MELAST	6	TR	7.53	53.78
Tococa nitens	MELAST	1-2-3-6	PH	7.51	53.63
Chaetocarpus schomburgkianus	EUPH	1-6	TR	7.49	53.50
Trimezia fosteriana	IRID	3-4	PH	7.47	53.33
Securidaca paniculata	POLYG	6	LI	7.44	53.18
Hirtella scabra	CHRYS	2	SH	7.43	53.10
Humiria balsamifera	HUM	1-2-3-4	SH	7.42	52.99
Palicourea crocea	RUB	6	SH	7.41	52.92
Calliandra resupina	MIM	2	LI	7.40	52.88
Philodendron ptarianun var. *rugosum*	ARAC	1-2-3	PH	7.39	52.76
Brocchinia steyermarkii	BROM	4	PH	7.37	52.65
Ochthocosmus attenuatus	IXON	2	TR	7.33	52.36
Mandevilla leptophylla	APOC	5-6	LI	7.30	52.15
Solanum stramoniifolium	SOL	6-7	PH	7.21	51.49
Befaria sprucei	ERIC	1-2-3-6	SH	7.16	51.17
Poecilandra pumila	OCHN	2-4	SH	7.13	50.90
Elaeoluma schomburgkiana	SAPOT	1-2	TR	7.09	50.66
Notophora schomburgkii	ERIC	1-2-3	SH	7.03	50.25
Macairea parvifolia	MELAST	2-3	SH	7.03	50.20
Blepharodon ulei	ASCL	2-4	LI	7.02	50.15
Pagamea capitata	RUB	1-2	SH	6.98	49.86
Dycimbe fraterna **	CAES	2	SH	6.96	49.72
Ditassa bolivarensis	ASCL	5-6	LI	6.96	49.70
Clidemia pustulata	MELAST	1-5-6	SH	6.95	49.67
Blepharodon nitidus	ASCL	4-5-6	LI	6.95	49.62
Vaccinium euryanthum	ERIC	1-2-3	SH	6.94	49.60
Byrsonima verbascifolia	MALP	1-5-7	PH	6.93	49.50
Miconia phaeophylla	MELAST	1-3-6	TR	6.93	49.48
Poecilandra retusa	OCHN	1-2-3	SH	6.92	49.45
Vantanea minor	HUM	2	SH	6.90	49.29
Euphronia guianensis	EUPHR	1-2-3	TR	6.86	48.99
Byrsonima crassifolia	MALP	1-3-5-6	SH	6.84	48.83
Byrsonima concinna	MALP	1-6	SH	6.81	48.66
Vismia guianensis	CLUS	3-5-6	TR	6.80	48.56
Aegiphila integrifolia var. guianensis	VERB	6	SH	6.79	48.48
Ilex retusa	AQUIF	1-2-3	SH	6.53	46.64
Miconia sp.	MELAST	6	SH	6.50	46.46
Clusia grandiflora	CLUS	3-6	TR	6.50	46.41
Miconia ibaguensis	MELAST	6	SH	6.46	46.17
Heliamphora heterodoxa	SARR	3	PH	6.42	45.89
Clusia schomburgkiana	CLUS	1-6	TR	6.42	45.83
Psycotria barbiflora	RUB	6	SH	6.39	45.61
Ilex danielis	AQUIF	1-6	SH	6.39	45.61
Clusia pusilla ssp. pusilla	CLUS	1-3-4	SH	6.39	45.61
Abarema ferruginea	MIM	1	TR	6.28	44.89
Solanum campaniforme	SOL	5-6	SH	6.08	43.46
Clusia focklana	CLUS	1-2	TR	5.92	42.26
Ouratea gillejana	OCHN	1-2-3	SH	5.76	41.17
Myrsine coriaceae	MYRS	3-6	TR	5.29	37.76

[1] Family name abbreviation.
[2] Plant species distribution (see Table I).
[3] Life forms. TR: trees, SH: shrubs, LI: lianas, PH: perennial herbs, AH: annual herbs.
[4] Percentages are given as a relative value to the maximum score of 14 points.
* Plant species growing spontaneously in borrow pits (from Rosales *et al*., 1997)
** Plant species growing spontaneously in borrow pits (from Cuenca *et al*., unpublished).

germination and mycorrhizal-dependence information must be included in the plant species selection.

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BIOLOGÍA REPRODUCTIVA Y SELECCIÓN DE ESPECIES DE PLANTAS PARA RESTAURACIÓN DE HÁBITAT EN LA GRAN SABANA, VENEZUELA

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RESUMEN

El uso de características reproductivas en la selección de plantas para la restauración de áreas profundamente perturbadas (préstamos) en la Gran Sabana se basó en la selección de especies con una alta capacidad reproductiva utilizando las siguientes características reproductivas: 1- elevada y permanente producción de semillas, 2- sistema reproductivo que promueva autopolinización y baja expresión de caracteres deletéreos, 3- morfología floral que permita la polinización por una amplia diversidad de visitantes, 4- sistema de polinización generalista o polinización por el viento, y 5- síndromes de dispersión de diásporas abiótico y/o con capacidad de colonización y eventual inmigración. La forma de vida de las plantas fue considerada como un carácter complementario. El análisis de 14 caracteres (escala 0-1 para cada carácter) permitió seleccionar 45 de 157 especies de plantas con puntaje >65%. La mayor puntuación para especies leñosas (69,75%) fue menor que para especies herbáceas (81,12%). Las herbáceas con mayor puntuación fueron Perama galioides *(Rubiaceae),* Aristida torta*,* A. recurvata*,* Panicum cyanescens*,* Andropogon selloanus *(Poaceae) y* Rhynchospora caracasana *(Cyperaceae), y las leñosas con mayor puntuación fueron* Gongylolepis benthamiana *y* Chromolaena laevigata *(Asteraceae). La condición de selección reproductiva (seleccionadas/no seleccionadas), distribución natural (en áreas perturbada/no perturbadas), y colonización espontánea de préstamos (colonizadoras/no colonizadoras) interactúan significativamente en el análisis de dependencia (χ^2= 6,1; df= 1; P= 0,013519) indicando dependencia de estas variables en el proceso de colonización. La combinación de alto valor reproductivo (70-81%), distribución natural en áreas perturbadas y capacidad de colonizar los préstamos espontáneamente permite la mejor selección de especies herbáceas, que deben ser evaluadas en otros caracteres para diseñar planes de manejo y restauración de áreas degradadas.*

BIOLOGÍA REPRODUTIVA E SELEÇÃO DE ESPÉCIES DE PLANTAS PARA RESTAURAÇÃO DE HABITAT NA GRAN SABANA, VENEZUELA

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RESUMO

O uso de características reprodutivas na seleção de plantas para a restauração de áreas profundamente perturbadas (empréstimos) na Gran Sabana baseou-se na seleção de espécies com uma alta capacidade reprodutiva utilizando as seguintes características reprodutivas: 1- elevada e permanente produção de sementes, 2- sistema reprodutivo que promova autopolinização e baixa expressão de caracteres deletérios, 3- morfologia floral que permita a polinização por uma ampla diversidade de visitantes, 4- sistema de polinização generalista ou polinização pelo vento, e 5 - síndromes de dispersão de diásporas abiótico e/ou com capacidade de colonização e eventual imigração. A forma de vida das plantas foi considerada como um caráter complementário. A análise de 14 tipos de caráter (escala 0-1 para cada caráter) permitiu selecionar 45 de 157 espécies de plantas com pontuação >65%. A maior pontuação para espécies lenhosas (69,75%) foi menor que para espécies herbáceas (81,12%). As herbáceas com maior pontuação foram Perama galioides *(Rubiaceae),* Aristida torta*,* A. recurvata*,* Panicum cyanescens*,* Andropogon selloanus *(Poaceae) e* Rhynchospora caracasana *(Cyperaceae), e as lenhosas com maior pontuação foram* Gongylolepis benthamiana *e* Chromolaena laevigata *(Asteraceae). A condição de seleção reprodutiva (selecionadas/não selecionadas), distribuição natural (em áreas perturbada/não perturbadas), e colonização espontânea de empréstimos (colonizadoras/não colonizadoras) interatuam significativamente na análise de dependência (χ^2= 6,1; df= 1; P= 0,013519) indicando dependência destas variáveis no processo de colonização. A combinação de alto valor reprodutivo (70-81%), distribuição natural em áreas perturbadas e capacidade de colonizar os empréstimos espontaneamente permite a melhor seleção de espécies herbáceas, que devem ser avaliadas em outros tipos de caráter para desenhar planos de manejo e restauração de áreas degradadas.*