Towards recovery of native dry forest in the Colombian Andes: a plantation experiment for ecological restoration
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Chapter 3.

Successional position of dry Andean dwarf forest species as a basis for restoration trials


**Abstract**

The successional affinity of nine woody species was inferred from the structure, diversity and disturbance history of the vegetation where these occurred. This was done in order to obtain a basis for a restoration experiment, currently in execution, in the dry Andean dwarf forest zone on the edge of the high plain of Bogotá (Colombia), at 2600-2950 m.a.s.l. We laid out 101 relevées in grassland and shrubland types in different stages of recovery, and in relatively little disturbed endemic *Condalia thomassiana* dwarf forest. The disturbance history of sites over the last ~60 years was inferred from aerial photograph series (1941-1991). CCA and logistic regression were applied to relate species composition to diversity, environment and disturbance history. All species showed a preference for certain structural groups. Also, a clear relation between species occurrence and vegetation diversity was found. *Baccharis macrantha*, and *Dalea coerulaea* appeared relatively tolerant to grazing, while the remaining seven species reacted negatively. Soil clay content, base availability and organic carbon content was also an important factor for occurrence of each species. Invasion of grasslands by woody species is pioneered by *Baccharis macrantha* and followed by *Dodonaea viscosa*. *Dalea coerulaea* was predominantly found on truncated clayey soils, which will probably not support *Condalia* dwarf forest. The hypothesized classification of the nine planted species to either pioneers or late-successional was fine-tuned. This exploratory study will be of use in the set-up of future succession-based restoration experiments, and for converting exotics afforestations to natural vegetation.
Introduction

Dry forests are among the more threatened ecosystems in the tropics, due to the combination of dense human population and regeneration-hampering resource deficiency (Aronson et al. 2002). This is especially so in the semi-arid northern edge of the high plain of Bogotá in the Colombian Andes. Apart from some remnants, the native dry montane Condalia dwarf forest has virtually disappeared due to inadequate land use, leading to a common sight of extensive badlands (Araque 1976; Thouret & Rovera 1983). This dwarf forest type has a rather rich understory in terms of biodiversity and vegetation structure, which generally enhances local water infiltration and retention (McFarlane et al. 1993). Consequently, water supply in the area has become scarce, and agricultural conditions have been deteriorating. Plantations with exotics (mostly Acacia decurrens) have been established in the 1980s, nowadays showing a virtual lack of understory vegetation, and a poor recovery of ecosystem functions – soil temperature stabilization and evapotranspiration reduction – as compared to the native dwarf forest (Van der Hammen 1997; 1998).

The original dwarf forest is characterized by the recently described endemic Condalia thomasiana (Van der Hammen 1997; Fernández-Alonso 1997). Very little is known about the basic ecology of Condalia forest - and of dry montane forest in general - or its recovery after disturbance. In spite of this, restoration efforts are needed, and a start has been made with a succession-based plantation experiment in the area of this study. The Corporación Autónoma Regional de Cundinamarca (CAR), which manages the (renewable) natural resources in the region, has become interested in recovering natural forests in the semi-arid parts of the high plain of Bogotá. Currently, a succession-based restoration experiment is being executed in cooperation with the CAR, in which mixtures of nine woody native species were inserted in different vegetation types. The choice of these species – important in terms of local abundance – and the estimation of their successional affinity, was based on preliminary observations.

In the course of vegetation succession after disturbance, the sequence of different life forms is generally predictable (Bazzaz 1996). Concurrently, species diversity generally increases, although species numbers reportedly often show a decline when a stand approaches maturity, due to reduction of undergrowth diversity after canopy closing (Horn 1974). However, this diversity decline probably does not occur until after a very long period without disturbance, as shown for old fields in the Venezuelan Andes (Sarmiento et al. 2003). Since the Condalia dwarf forest remnants are small (mostly one or a few hectares), and traces of disturbance are found in most of these patches, it is not likely that this diversity decline is to be found in the area.
Successional affinities of planted woody species

Table 3.1. Initially hypothesized successional affinity of the “restoration species”.

<table>
<thead>
<tr>
<th>species</th>
<th>family</th>
<th>growth form</th>
<th>seed dispersal mechanism</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pioneer species</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Baccharis macrantha H.B.K</td>
<td>Asteraceae</td>
<td>shrub (- treelet)</td>
<td>anemochory</td>
</tr>
<tr>
<td>Dalea coerulea (L.f.) Schinz &amp; Thell.</td>
<td>Fabaceae</td>
<td>shrub (- treelet)</td>
<td>barochory?</td>
</tr>
<tr>
<td>Dodonaea viscosa Jacq.</td>
<td>Sapindaceae</td>
<td>shrub (- treelet)</td>
<td>anemochory</td>
</tr>
<tr>
<td><strong>Late-successional species</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Condalia thomasiana Fernandez-Alonso</td>
<td>Rhamnaceae</td>
<td>treelet</td>
<td>endozoochory</td>
</tr>
<tr>
<td>Croton bogotanus Cuatrec.</td>
<td>Euphorbiaceae</td>
<td>treelet</td>
<td>ballistic/autochory</td>
</tr>
<tr>
<td>Duranta mutisii L.f.</td>
<td>Verbenaceae</td>
<td>treelet</td>
<td>endozoochory</td>
</tr>
<tr>
<td>Hesperomeles goudotiana (Decne,) Killip</td>
<td>Rosaceae</td>
<td>treelet</td>
<td>endozoochory</td>
</tr>
<tr>
<td>Myrsine guianensis (Aublet) Kuntze</td>
<td>Myrsinaceae</td>
<td>treelet</td>
<td>endozoochory</td>
</tr>
<tr>
<td>Xylosma spiculifera (Tul.) Triana &amp; Planch.</td>
<td>Flacourtia</td>
<td>treelet</td>
<td>endozoochory</td>
</tr>
</tbody>
</table>

The purpose of our study was to infer the successional position of these nine woody species (to be called “restoration species” hereafter) from vegetation structure, vegetation diversity, soil parameters, and disturbance history. The following general assumptions were made to investigate the behaviour of the restoration species: (1) pioneer species occur and rejuvenate mostly in relatively low and open vegetation, while late-successional species are found in higher, denser vegetation; (2) pioneer species occur in less diverse vegetation than late-successional species; (3) pioneer species are found at disturbed sites, while late-successional species mostly occur in relatively little disturbed vegetation. Based on preliminary observations, we expected the three shrubs (or treelets) Baccharis macrantha, Dodonaea viscosa and Dalea coerulea to behave as pioneers, and six as late-successional species: Condalia thomasiana, Croton bogotanus, Duranta mutisii, Hesperomeles goudotiana, Myrsine guianensis and Xylosma spiculifera (Table 3.1). We made vegetation relevées to obtain the data on vegetation structure and diversity. We applied sequential aerial photograph interpretation to infer the disturbance history of the relevée sites. Species response to the explanatory factor was investigated separately for each species, and in the context of the vegetation where they were found.

**Methods**

**Study area**

The fieldwork area is at the edge of the high plain of Bogotá, in the Eastern Cordillera of Colombia (Figure 3.1). It concerns a part of the valley of the Checua River, a tributary of the Bogotá River (5° 07' N, 73° 50' W), with an elevation between 2550 and 2950 m above sea level.
The zone has a semi-arid climate; receiving about 700 mm of annual rainfall, generally concentrated in two short periods. With an evapotranspiration of about 1050 mm, the annual deficit is around 350 mm (Claro-Rizo 1995). The mean annual temperature is around 13°C (Van der Hammen 1998).

The area is characterized by Cretaceous sandstone hills. Northward, the pediment material is strongly weathered Tertiary kaolinitic clay. The entire area was originally covered by a volcanic ash cap of 20 cm (summits) up to 70 cm thick (pediments). Erosion crevices of several meters deep are a common sight, exposing either sandstone or kaolinitic clay.

Most sites show a natric B soil horizon primarily containing clay, organic material, and sodium (Carrera et al. 1968). This illuviation horizon underlies a strongly leached E horizon, which in extreme conditions (on pediments) has formed a hardpan. An A horizon has hardly developed in the pediments, but in the higher - and more humid - parts of the study area, this horizon is often found. The slopes mostly expose sandstone, with soils mostly formed by colluvial deposits.

The dry montane dwarf forest considered in this paper was described as *Xylosmo – Condalietaum*, or “Condalia forest”, by Van der Hammen (1997). It reaches heights up to
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six meters, and has a highly diverse understory of herbs, mosses and lichens, both terrestrial and epiphytic. The secondary vegetation in this area shows an affinity with various semi-arid scrub- and grassland types described from the high plain of Bogotá (Vink & Wijninga 1987), and possibly with the Andean scrub (matorral andino) described by Balslev and Øllgaard (2002). The Condalia forest, however, is not found elsewhere, and shows only a slight resemblance to the Xylosma-Duranta-Vallea forests as described by Cleef and Hooghiemstra (1984).

Since pre-Columbian times, the area has been affected by forest cutting, agriculture, and cattle grazing (Van der Hammen 1998), which has favored exotic rural herbs like Hypochoeris radicata, Anthoxantbum odoratum, and Pennisetum clandestinum. As far as known, fire has not played a role in the area over the last decades. Recently, the intensity of agricultural land use in the area has reduced, and reforestation with Acacia decurrens by the CAR started.

Fieldwork

A total of 101 relevées were made between October 1999 and April 2001, following Braun-Blanquet (Mueller-Dombois & Ellenberg 1974). We aimed at including a maximal variation in vegetation diversity and structure, and at attaining a fair spatial spread (Figure 3.1). Severely eroded sites, rocky substrates and planted vegetation were avoided. Plot size was 10 x 10 m (85 plots), or 10 x 15 m (16 plots).

In each relevee, the cover percentage of all vascular plant species was estimated, and the vegetation structure was described by estimating the average height and cover of low herbs (< 10 cm), high herbs (≥ 10 cm), low shrubs, (< 1.5 m), high shrubs (≥ 1.5 m), and treelets. For each of the restoration species, cover was estimated separately of saplings, low shrubs, high shrubs, and treelets. A bulk sample was taken of the upper five centimeters of mineral soil, consisting of five subsamples (from the four corners and the center) of the relevee.

Vouchers of collected plants were deposited at the herbarium of the Instituto de Ciencias Naturales, Bogotá, Colombia (COL). We followed the species nomenclature of the w³TROPICOS database (MOBOT 2003).

Soil sample analyses

Soil analyses were carried out in the soil laboratory of the Geographical Institute “Agustín Codazzi” (IGAC) in Bogotá, Colombia. Samples were air-dried until constant weight. Texture was determined by means of a hydrometer (“bouyoucos”). Available K, Na, Ca, and Mg were extracted with NH₄OAc (pH = 7), and quantified by atomic adsorption spectrophotometry. Contents of available Ca, Mg, K, and Na were summed to obtain total available bases (TB). Organic C was oxidized by K₂Cr₂O₇ in acid medium (Walkley-Black method) and measured by titration with Fe(NH₄)₂(SO₄)₂. Cation exchange capacity (CEC) was measured in 1N NH₄OAc (pH = 7).
Chapter 3

Disturbance history derived from sequential aerial photographs

Each relevee was located on a series of black-and-white, panchromatic aerial photographs of the region taken in 1941, 1958, 1974, and 1991. The time period covered is about 60 years, including the data gathered during the field work in 1999-2001. The scales of the photographs varied from 1:10 000 to 1:20 000.

On the photographs, we assessed woody canopy cover and height, presence of erosion and signs of disturbance (e.g., cutting or grazing) in an area of about 30 x 30 m, directly surrounding each of the vegetation relevees. This led to eight units, presented here in order of increasing structural development: 1) grassland; 2) grassland with scattered low shrubs (<5% woody cover); 3) shrub patches on eroded land; 4) low shrubland with (grazed) gaps; 5) low shrubland; 6) high shrubland with (grazed) gaps; 7) high shrubland; 8) dwarf forest. We attempted to express the trend in unit transitions of each relevee site by creating the nominal dummy variables development (increased woody cover and height), degradation (decreased woody cover and height), instability (both development and degradation took place), and stability (no changes).

Data processing

The set of explanatory variables on which the species occurrences were tested was obtained as follows. Each relevee was assigned to one of the following four vegetation structure types: grassland: < 5% woody cover; low shrubland: ≥ 5% cover of low (< 1.5 m) shrubs, and < 5% cover of higher woody plants; high shrubland: ≥ 5% cover of high (≥ 1.5 m) shrubs, and ≥ 10% overall woody cover; dwarf forest: ≥ 5% tree cover, and ≥ 30% overall woody cover. We decided not to use the aerial photograph vegetation units for the species response to vegetation structure because not all vegetation layers could be estimated from the photos.

We calculated Shannon's (1948) $H'$ to express the diversity of each of the relevees.

The period under grazing was inferred from the presence of grassland (aerial photograph unit 1 and 2). The middle between two subsequent aerial photograph years was assumed to be the transition moment of the state of a relevee site, from the former to the latter point in time. The duration of a state, in each relevee, was then calculated as the number of years between such a “middle year” before a state was first recorded, and the “middle year” after it was last recorded. The four dummies expressing trends in aerial photograph vegetation unit transitions, mentioned in the former paragraph, were also included.

Soil texture and chemical properties of each relevee were summarized by two respective Principal Components Analyses. The soil texture principal component ("PC soil texture") was extracted from percentages of clay, silt and sand, to be interpreted mainly as a gradient from sandy (negative end of PC) to clayey soils. Similarly, "PC soil
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chemistry" was obtained from log-transformed contents of soil K, Na, Mg, Ca, total bases, CEC, and organic C. High scores of the principal component express high contents of soil cations, CEC and organic C.

Response of each of the restoration species to the eight thus obtained explanatory variables was tested by multiple logistic regression (Legendre & Legendre 1998). We chose this method because it takes into account both presence and absence of species at certain sites. The model was as follows:

\[
p = \frac{1}{1 + e^{-z}}
\]

with \( z = b_0 + b_1 \cdot [\text{expl. var.1}] + ... + b_8 \cdot [\text{expl. var.8}] \)

where \( p \) is the probability of occurrence of a given species, \( b_0 \) is the intercept of the regression model, and \( b_1 - b_8 \) are the slopes of the explanatory variables.

No forward or backward selection was applied, so all variables were entered in the model. Of each explanatory variable \( x \), the parameters \( b_x \) of the model were tested for significance by Wald's statistic. All above-mentioned statistical analyses were performed with the SPSS 11.0 package (SPSS 2001).

In order to analyse species responses in the context of the vegetation in which they were found, Canonical Correspondance Analysis (with CANOCO 4.0, by Ter Braak and Šmilauer (1999)) was applied using the same explanatory variables mentioned above. The ordination was done with log-transformed abundances of all vascular plant species encountered in the relevees. Variance Inflation Factors (VIF's) did not exceed 2.5.

Results

In the 101 relevees, 230 vascular plant species were recorded, belonging to 174 genera and 64 families. A checklist is available upon request.

Vegetation structure related to restoration species occurrence

Figure 3.2 shows that \( B. macrantha \) occurred in more than 50% of the grassland relevees, and that it was the most common of the restoration species in low shrubland. Frequency decreased sharply from high shrubland to dwarf forest for both low and high shrubs. Saplings of \( B. macrantha \) were mostly found in grasslands. \( D. coerulca \), although showing an increase in frequency towards dwarf forest, was least often found in dwarf forest relevees as compared to the other species. \( D. viscosa \) shows a trend similar to that of \( B. macrantha \), but with its peak in high shrubland. Saplings were occasionally found, mostly in dwarf forests.
Figure 3.2. Fraction of occurrences of juveniles, low shrubs, high shrubs, trees and all stages lumped, in the four structural vegetation types, for each of the nine restoration species.

The six remaining species, *C. thomasiana*, *C. bogotanus*, *D. mutisii*, *H. goudotiana*, *M. guianensis*, and *X. spiculifera*, showed a steep increase of lumped frequency from grassland – where all except *H. goudotiana* were rare – to dwarf forest. *H. goudotiana*, *M. guianensis* and *X. spiculifera* were found in 25 to over 50% of the low shrubland releves. Especially *M. guianensis*, but also *C. bogotanus* and *X. spiculifera*, were represented with saplings mostly in high scrub and dwarf forest.

The $\chi^2$-test for independence of each of the restoration species from the four vegetation structure types resulted in a significant difference for all species except *D. coerulea*, which had a marginally significant dependence (Table 3.2).

Correlations between explanatory variables

Apart from some obvious correlations between dummy variables, correlations were mostly not very strong (Table 3.3). Grazing period appeared negatively correlated with Shannon's $H'$, and with base and organic C content (PC soil chemistry). Soil clay content (PC soil texture) was positively correlated with base and organic C content.
Table 3.2. Results of the $\chi^2$-test for independence of total (lumped) occurrences of the species in the four structural vegetation types.

<table>
<thead>
<tr>
<th>Species</th>
<th>$\chi^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baccharis macrantha</td>
<td>11.96</td>
<td>0.008</td>
</tr>
<tr>
<td>Dalea coerulea</td>
<td>7.33</td>
<td>0.062</td>
</tr>
<tr>
<td>Dodonaea viscosa</td>
<td>23.76</td>
<td>0.000</td>
</tr>
<tr>
<td>Condalia thomasi ana</td>
<td>32.33</td>
<td>0.000</td>
</tr>
<tr>
<td>Croton bogotanus</td>
<td>21.64</td>
<td>0.000</td>
</tr>
<tr>
<td>Duranta mutisii</td>
<td>33.83</td>
<td>0.000</td>
</tr>
<tr>
<td>Hesperomeles goudotiana</td>
<td>11.33</td>
<td>0.010</td>
</tr>
<tr>
<td>Myrsine guianensis</td>
<td>46.59</td>
<td>0.000</td>
</tr>
<tr>
<td>Xylosma spiculifera</td>
<td>25.43</td>
<td>0.000</td>
</tr>
</tbody>
</table>

Table 3.3. Spearman’s coefficients of rank correlation between explanatory variables used in logistic regression and CCA. The interpretation of the two principal components (PC) is given between brackets. Note that the column of $H'$ and the row of instability (containing empty cells only) were omitted.

<table>
<thead>
<tr>
<th>Variables</th>
<th>PC soil texture</th>
<th>PC soil chemistry</th>
<th>grazing period</th>
<th>development</th>
<th>degradation</th>
<th>stability</th>
<th>unstability</th>
</tr>
</thead>
<tbody>
<tr>
<td>$H'$</td>
<td>-0.152</td>
<td>0.086</td>
<td>-0.331</td>
<td>0.224</td>
<td>-0.060</td>
<td>-0.248</td>
<td>0.040</td>
</tr>
<tr>
<td>PC soil texture (clayey soils)</td>
<td>0.368</td>
<td>0.005</td>
<td>-0.052</td>
<td>0.023</td>
<td>-0.064</td>
<td>0.095</td>
<td></td>
</tr>
<tr>
<td>PC soil chemistry (high nutr. &amp; org. C)</td>
<td>-0.384</td>
<td>0.163</td>
<td>-0.021</td>
<td>-0.113</td>
<td>-0.045</td>
<td></td>
<td></td>
</tr>
<tr>
<td>grazing period</td>
<td>-0.088</td>
<td>0.114</td>
<td>0.032</td>
<td>-0.008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>development</td>
<td>-0.200</td>
<td>-0.391</td>
<td>-0.507</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>degradation</td>
<td>-0.168</td>
<td>-0.218</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stability</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-0.427</td>
<td></td>
</tr>
</tbody>
</table>

Logistic regression: diversity, environment and disturbance history

The multiple logistic regressions revealed that, in general, soil properties – both texture and chemical characteristics – and grazing period determined occurrence of the nine species (Table 3.4). Baccharis macrantha and Dalea coerulea responded positively to clayey soils (PC soil texture), and Condalia thomasi ana, Croton bogotanus and Duranta mutisii negatively so. A high soil base availability and organic C content (PC soil chemistry) enhanced the probability of presence of C. thomasi ana, C. bogotanus, M. guianensis and X. spiculifera, and marginally so for D. coerulea. Only C. thomasi ana showed a significant positive response to Shannon’s $H'$. Six species showed a significantly negative association with grazing period: D. viscosa, C. thomasi ana, D. mutisii, H. goudotiana, M. guianensis, and
Table 3.4. Results of the multiple logistic regression of each of the restoration species on the explanatory variables (first column). For the two Principal Components (PC), the interpretation of the positive end is given between brackets. Values are \( p \)-values of the parameter corresponding to each explanatory factor in the logistic model. "+" and "-" indicate positive and negative response, respectively, of the species to an explanatory factor.

<table>
<thead>
<tr>
<th>Species</th>
<th>H'</th>
<th>soil PCs</th>
<th>grazing period</th>
<th>development</th>
<th>degradation</th>
<th>stability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baccharis marantha</td>
<td>0.161 -</td>
<td>0.041 +</td>
<td>0.786 +</td>
<td>0.173 -</td>
<td>0.261 +</td>
<td>0.904 +</td>
</tr>
<tr>
<td>Dalea coerulea</td>
<td>0.478 +</td>
<td>0.005 +</td>
<td>0.065 +</td>
<td>0.783 -</td>
<td>0.874 +</td>
<td>0.806 +</td>
</tr>
<tr>
<td>Dodonaea viscosa</td>
<td>0.673 -</td>
<td>0.310 -</td>
<td>0.193 -</td>
<td>0.000 -</td>
<td>0.161 -</td>
<td>0.541 +</td>
</tr>
<tr>
<td>Condalia thomasiana</td>
<td>0.016 +</td>
<td>0.000 -</td>
<td>0.007 +</td>
<td>0.022 -</td>
<td>0.951 -</td>
<td>0.330 -</td>
</tr>
<tr>
<td>Croton bogotanus</td>
<td>0.070 +</td>
<td>0.026 -</td>
<td>0.019 +</td>
<td>0.378 -</td>
<td>0.344 +</td>
<td>0.624 +</td>
</tr>
<tr>
<td>Duranta multiflora</td>
<td>0.264 +</td>
<td>0.049 -</td>
<td>0.438 +</td>
<td>0.050 -</td>
<td>0.068 -</td>
<td>0.243 -</td>
</tr>
<tr>
<td>Hesperomeles</td>
<td>0.290 +</td>
<td>0.248 +</td>
<td>0.598 +</td>
<td>0.009 -</td>
<td>0.130 -</td>
<td>0.402 -</td>
</tr>
<tr>
<td>Myrsine guianensis</td>
<td>0.132 +</td>
<td>0.101 -</td>
<td>0.040 +</td>
<td>0.000 -</td>
<td>0.090 -</td>
<td>0.920 +</td>
</tr>
<tr>
<td>Xylosma spiculifera</td>
<td>0.512 +</td>
<td>0.286 -</td>
<td>0.045 +</td>
<td>0.002 -</td>
<td>0.420 -</td>
<td>0.175 -</td>
</tr>
</tbody>
</table>

The fourth nominal variable, "unstability", does not appear in the table because of collinearity with the first three of the dummy set.

Canonical ordination: diversity, environment and disturbance history in vegetation context

The eigenvalues of the first and second CCA axis were 0.339 and 0.126, respectively. Figure 3.3 shows that Dalea coerulea was clearly separated from the other eight species, responding most strongly to clayey soils (PC soil texture) and high base availability and organic C content (PC soil chemistry). Baccharis marantha showed a similar, but far less explicit, response, and appeared to be relatively tolerant to long grazing periods. Dodonaea viscosa, Condalia thomasiana, Croton bogotanus, Duranta multiflora, Hesperomeles goudotiana, Myrsine guianensis, and Xylosma spiculifera responded positively to H', negatively to grazing period, and were grouped around the development centroid. The latter six of these group, forming the initially assumed "late-successional species" group (Table 3.1), reacted more positively to the "PC soil chemistry" variable.

Discussion

Successional position of "restoration species"

We expected pioneer species to occur mostly in open, low, species-poor, and disturbed vegetation, as opposed to late-successional species. The data presented in this
Successional affinities of planted woody species

1. development
2. degradation
3. stability
4. unstability

Dale coer
PC soil texture
(clay)

Bacc macr
PC soil chemistry
(high nutr./Corg)

Hesp goud

Xylo spic

Myrsguia fond thorn

Mt Dura muti

Crot bogo

1. Xylo spic

Myrsguia fond thorn

Mt Dura muti

H' Crot bogo

-1.5

-1.0

-0.5

0.0

0.5

1.0

1.5

2.0

Figure 3.3. CCA ordination diagram displaying the nine restoration species and explanatory variables. Species are indicated by dots, with truncated names. Centroids of the nominal disturbance history variables were plotted as numbers, as indicated above-left.

Paper permitted us to fine-tune the initial hypotheses regarding successional affinities of the restoration species, as summarized in Table 3.5.

In comparison to the other restoration species, B. macrantha was mostly found in scrubs and grassland, with a low diversity in terms of Shannon’s H'. It appeared relatively tolerant to grazing, in spite of the apparent absence of any browsing-inhibiting morphological trait, probably because of a high wind-dispersed seed production and recruitment. Moreover, B. macrantha was often present on sites with a dense cover of weedy exotic grasses, mostly Pennisetum clandestinum. It was commonly found on many growing sites, in spite of its apparent preference for somewhat clayey soils. We concluded that B. macrantha is a typical woody pioneer.

Dodonaea viscosa was also relatively important in low and high shrubland, and less in dwarf forest. However, it was found in intermediately diverse vegetation. D. viscosa is a subcosmopolitan species, known from all over the (sub)tropics (Liu & Noshiro 2003). Fossil pollen of Dodonaea was found in cores from the high plain of Bogotá, together with disturbance indicators (Van Geel & Van der Hammen 1973; Mommersteeg 1998), which corroborates its pioneer-like behaviour. However, monospecific shrub stands of D. viscosa are hardly found, contrarily to B. macrantha. We conclude that D. viscosa tends towards a mid-successional affinity. Since treelets of both B. macrantha and D. viscosa were frequently found in dwarf forests, these species might be regarded as “facilitators” in terms of (Connell & Slatyer 1977), that apparently persist for a long time.
Table 3.5. Summary of successional affinities as indicated by their preferences for vegetation structure and diversity, tolerance to grazing, and environmental restrictions.

<table>
<thead>
<tr>
<th>successional affinity</th>
<th>species</th>
<th>structure</th>
<th>diversity</th>
<th>grazing period</th>
<th>environmental preferences</th>
</tr>
</thead>
<tbody>
<tr>
<td>pioneer</td>
<td><em>Baccharis macrantha</em></td>
<td>grassl. – high scrub</td>
<td>low</td>
<td>tolerant</td>
<td>clayey soils</td>
</tr>
<tr>
<td>pioneer-mid</td>
<td><em>Dodonaea viscosa</em></td>
<td>scrub-dwarf forest</td>
<td>intermediate</td>
<td>negative</td>
<td></td>
</tr>
<tr>
<td>mid-late</td>
<td><em>Myrsine guianensis</em>, <em>Hesperomeles goudotiana</em>, <em>Xylosma spicatifera</em></td>
<td>scrub-dwarf forest</td>
<td>interm.-high</td>
<td>negative</td>
<td>OM/nutr. rich</td>
</tr>
<tr>
<td>late</td>
<td><em>Condalia thomasiana</em>, <em>Croton bogotanus</em>, <em>Duranta mutisii</em></td>
<td>dwarf forest</td>
<td>high</td>
<td>negative</td>
<td>OM/nutr. rich</td>
</tr>
<tr>
<td>outlier</td>
<td><em>Dalea coerula</em></td>
<td>scrub(-dwarf forest)</td>
<td>low</td>
<td>tolerant</td>
<td>eroded clayey soils</td>
</tr>
</tbody>
</table>

Although *Dalea coerula* shows a response to vegetation diversity and grazing period similar to that of *B. macrantha* and *D. viscosa*, it appears to be an outlier as compared to the other eight species. In all four structural vegetation types, it was relatively infrequent. The species is typically found on truncated clayey soils, and is mostly not co-occurring with any of the other restoration species.

The six species initially hypothesized to be late-successional (Table 3.1) showed a fairly consistent response to structure, diversity, disturbance and soil characteristics. They all mostly occurred in relatively developed and little disturbed dwarf forest. All of these species but *C. bogotanus* have fleshy fruits apparently designed for endozoochorous dispersal. Since fruit production in these species is mostly low (pers. obs.), and vertebrate diversity and abundance are low, successful seed dispersal events are probably rare. However, it is not known which animal species disperse the seeds of the fleshy-fruited late-successional species of the area.

Within this late-successional set, two groups can be identified. Firstly, *Condalia thomasiana*, *Croton bogotanus* and *Duranta mutisii* were clearly most frequent in dwarf forest, and were found in the most diverse releves. The response to grazing period was most strongly negative as compared to the other species. Similarly to *B. macrantha*, the possession of spines did not appear to be important for this apparent effect, but should probably be attributed to a seed dispersal limitation and bad germination conditions for the late-successional species in pastures. Thus, these three consistently behaving species were regarded as typically late-successional. In spite of being "characteristic" species of the dwarf forest, *Condalia thomasiana* was not always found in dwarf forest plots, which is probably due to the small size – 10 x 10 m – of the releves, and to the single relevee the description by Van der Hammen (1997) was based on.
Secondly, the remaining three species, *Hesperomeles goudotiana*, *Myrsine guianensis* and *Xylosma spiculifera* behaved similarly to the *C. thomasiana* group, but more moderately so. *M. guianensis* was more frequent in low and high (*Dodonaea*-dominated) secondary shrubland types – apparently rejuvenating well – and intermediately diverse relevees. A comparison can certainly be made between *Dodonaea viscosa* and *M. guianensis*.

In conclusion, an abandoned grassland is most probably invaded by *B. macrantha*. *D. viscosa* and *M. guianensis* are most probably the species most probable to invade an established *B. macrantha* scrub, followed by the remaining species *H. goudotiana*, *X. spiculifera*, *C. thomasiana*, *C. bogotanus*, and *D. mutisii*.

**Applications**

In ecological restoration, natural processes are attempted to be restored. A growing amount of literature is becoming available on ecosystem restoration by means of native species planting (Montagnini 2001; Parrotta et al. 1997a; e.g., Leopold et al. 2001). Even when species are not dispersal-limited, plantation could enhance regeneration by providing a closed canopy in a relatively short time, because the vulnerable state of seedlings is skipped.

The six late-successional species could establish in nutrient- and OM-rich soils. Probably, they require a certain amount of shade, although small individuals (< 0.5 m height) frequently were found in low, open shrublands. The late-successional species could be applied in restoration trials, but are most probably not suited for eroded sites, since they have a relatively high demand of nutrients, and growth of these species is slow. If *Condalia* dwarf forest is to be re-established, kaolinitic sites should be avoided. These eroded clayey sites could possibly be stabilized by plantation of *D. cornulea* and *B. macrantha*, although chances of failure are high due to further soil erosion.

Until about 20 years ago, rangeland managers mainly attempted to recover soils and water retention by rapid reforestation, which led to vast plantations of species of *Eucalyptus*, *Pinus*, and *Acacia* in the Neotropical mountains. Cavelier and Santos (1999) found that undergrowth development in planted forests was poor in terms of species richness. However, effects on undergrowth development and soil properties are, dependent on many factors (Hofstede et al. 2002), and therefore hard to generalize. Both natural resource managers and restoration ecologists have become interested in conversion of plantation forests to more natural woody vegetation types (Ashton et al. 1998, 1997; Chapman & Chapman 1996; Parker et al. 2001). Although some authors suggested that exotics forests could eventually change through a catalyzing effect of its canopy (Parrotta et al. 1997a; Ray & Brown 1995; Ashton et al. 1997), insertion of native woody species might accelerate regeneration: colonization by woody species is often limited by lack of seed bank (Senbeta et al. 2002), or by a thick litter layer (Van Wesenbeeck et al. 2003). The nine restoration species treated in this paper could play an important role in the
conversion of local *Acacia decurrens* or *Pinus patula* forests to native shrublands or dwarf forests.

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