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

Groenendijk, J.P.

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General discussion

In this chapter, I will resume the results of chapters two to six and with that I intend to answer the research questions listed in the Introduction. Furthermore, I will discuss the implications of these results for the general views on barriers to natural forest regeneration and for practices of restoration and rehabilitation efforts. Extra emphasis was put on vegetation succession in the experimental plots.

Findings of this PhD research

Present vegetation patterns and successional prospects

The study area is the part of the Checua Valley probably least affected by erosion. Condalia dwarf forest has only been found on the Hacienda Susatá, an area of about 700 ha, in a relatively little disturbed state. The forest remnants, however, are very small and sparse. Outside the Hacienda Susatá, dwarf forest has been found but the understory was mostly severely disturbed. Human intervention, mainly livestock grazing, is the most important factor that has altered the landscape patterns in the study area over the last decades or even centuries (Van der Hammen 1998).

Based on a TWINSPAN classification we recognized two types of grasslands, three scrub types and a dwarf forest type (Chapter 2). A marked difference existed between pastures of low-altitude pediments and higher-altitude hill tops. The dry pastures of the pediments mostly have a low overall vegetation cover and a relatively high abundance of (annual) asteraceous herbs. The higher-altitude sub-humid pastures had a higher cover of *P. clandestinum*, *Anthoxanthum odoratum* and other graminoids. The latter pastures were found on relatively clay- and nutrient-rich soils as compared to the dry pastures. The exotic grasses, mainly *P. clandestinum*, might have a hampering effect on vegetation development towards a woody vegetation. Moreover, this grass species has shown to be able to invade *Baccharis* – *Dodonaea* stands and thus tolerates a certain degree of shading.

Most woody species invading the pastures are asteraceous shrubs (*Baccharis macrantha*, *Stevia lucida*, *Chromolaena levisii*). *B. macrantha* reaches a co-dominant status together with *Dodonaea viscosa* in pioneer scrubs. Occasionally, species typical of Condalia dwarf forests were found in these scrubs. In many of these cases, it apparently concerned remnant trees or shrubs, possibly indicating presence of a more extended dwarf forest in the past. These remnant individuals might have a stimulating effect on further development.
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of pioneer scrubs: they might act as perches for seed-dispersing animals and as local seed
sources (also for the associated understory herbs and epiphytes).

Dwarf forest stands were mostly found on strongly sloping and relatively rocky
sites, as compared to floristically similar pioneer- and late-successional scrubs. Probably,
farmers ignored these rocky slopes in their cutting activities for livestock grazing, such
that the relatively inaccessible parts were little disturbed.

The severely eroded parts of the study area where Tertiary clay has become
exposed mostly supported scrub stands dominated by Dalea coeruka and Baccharis macran-
thra. Understories were mostly species-poor, and overall vegetation cover was relatively
low. Since most species typical of late-successional scrubs and dwarf forests were not
encountered in the relevées on these soil types, it is most likely that succession in these
Dalea scrubs is arrested and will not develop towards Dodonaea – Myrsine – Condalia type
stands.

Successional affinity of common woody species

Successional affinity of the species used in the plantation experiments was as­
signed based on their life history characteristics (mainly occurrence of seedlings), struc­
ture and diversity of the vegetation patches, and occurrence in (formerly) grazed areas
(Chapter 3). Baccharis macrantha was found to be a true woody pioneer, while Dodonaea
viscosa – generally co-dominating pioneer scrubs with the former species – apparently
inclines to mid-successional affinity. Three species typical of mature Condalia dwarf for­
est, Hesperomeles goudotiana, Myrsine guianensis and Xylosma spiculifera, were found relatively
often in Baccharis – Dodonaea scrubs, also as juveniles, and were also considered mid-suc­
cessional species, although they never co-dominate in pioneer scrubs. The remaining
three dwarf forest species, Condalia thomastiana, Croton bogotanus, and Duranta mutisii, were
considered late-successional, and were only found in dwarf forests and occasionally in
high, dense Baccharis – Dodonaea scrubs.

The role of soil seed banks

The soil seed banks inventory showed that, in all of the main vegetation types in
the area, pioneer herbs dominated the seed stock (Chapter 4). In pastures, hardly any
seeds of late-successional woody species were found, and very sparsely so. Pioneer
shrubs did have a somewhat higher frequency in the soil seed banks of pastures. Hence,
local soil seed banks of the area gave poor prospects for autogenic recovery of dwarf
forests in the area. Yet, a stand of pioneer shrubs could develop from the soil seed bank,
and facilitate both the arrival of animal-dispersed propagules and the germination and
development of shade-tolerant dwarf forest species.

Preliminary censuses during a three-months’ period indicated that seed rain was
mostly composed of grasses and, especially in woody vegetation types, of plant species
directly neighbouring the seed traps (Van der Linden & Struik 2002). Although this
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census was not complete, it does suggest that seed sources of late-successional fleshy-fruited species are sparse, and seeds may be dispersed over very short distances only.

Performance of planted seedlings in open secondary vegetation

Planted seedlings of pioneer species performed best in dry pastures (Chapter 5). The canopies were about one meter high, with a cover of 10 – 20%. In shrublands, survival of these species was lower. Survival percentages of the species of the late-successional mixture did not differ across vegetation types. Growth rates were poor for all late-successional species: the upper buds of many species died off, after which resprouting occurred from a lower bud. Cover percentages did not increase for any of the latter species. The stones and fertilizer treatments had positive effects on survival, growth, or both, for a number of species.

Succession in the experimental plots

As explained in Chapter 5, successional changes in the plots were few and could not be attributed to any effect of the planted seedlings. In order to place the temporal changes in plant species composition in the plantation plots in the perspective of the desired end point of restoration, I carried out an additional Detrended Correspondence Analysis over the species abundances of the matrix vegetation in the experimental plantation plots in dry pastures, sub-humid pastures, and shrubland (excluding the planted seedlings), and also those of the dwarf forest relevees (data used for Chapters 2 and 3). In this analysis, the experimental plots were represented by their species composition in 2000 and that in 2004. Since no differences were found between the plots with plantation of seedlings and the control plots (Chapter 5), I made no distinction between them for this analysis. The dwarf forest relevees were included in order to examine whether the floristic changes are in the "desired" direction (i.e., whether succession actually proceeds towards dwarf forest), and to have some idea of the floristic distances yet to be overcome. Figure 7.1 shows an ordination diagram of this DCA, revealing that the first DCA axis represents a development gradient from pastures on the left side to dwarf forests on the right side, the scrubs in the middle next to the dwarf forests. The arrows represent the average direction and magnitude over all individual plots per vegetation type, from the situation in 2000 to that in 2004. The sub-humid plots showed the strongest shift, along the second DCA axis in the negative direction, with a small component in the positive direction of the first axis. Dry pastures and shrublands showed only a minor shift to the right along the first DCA axis. Both pasture types are obviously still far from similar to the woody vegetation types.
Figure 7.1. Ordination diagram of a DCA carried out on species abundances in the vegetation of the experimental plots (excluding the planted seedlings), and of dwarf forest vegetation relevées. For the experimental plots, the situation of 2000 and that of 2004 were included. Samples are indicated by symbols (see legend). Species are indicated by an "x", with truncated names (see Appendix 2.1). Arrows represent the average change of the plots in the two-dimensional ordinal space, by their angle and length, over each of the three vegetation types.

The diagram allows some general remarks on floristic changes in the experimental plots. Dry pastures had a decrease in cover of annuals like Microchloa kunthii and Schkuhria pinnata, and an increase of the perennial graminoids Cyperus aggregatus and Piptochaetium panicoides. In sub-humid pastures, the exotic weedy herbs Pennisetum clandestinum, Hypochaeris radicata and Anthoxantum odoratum declined in favour of the subshrub Margyricarpus pinnatus, and the graminoids Bulbostylis asperula and Aristida laxa.

Performance of planted seedlings in Acacia forest understories

The pioneer shrubs B. macrantha and D. viscosa performed badly in Acacia understories: their overall mortality was high (Chapter 6). Apart from H. goudotiana, the mid- and late-successional dwarf forest treelets all performed well in these planted forests, at least in terms of survival. Growth rates were spectacularly high for C. bogotanus in the plots with the highest elevation (and humidity): many individuals were over three meters high at the time of the latest census. The remaining dwarf forest species did not grow more rapidly than in pastures or low scrubs.
Can natural succession be accelerated by plantation of native woody species?

As stated in Chapter 5, successional changes were probably not linked to any canopy closure of the planted seedlings assembly, but merely to a cattle exclosure effect. The only response that was statistically detected was an increase of total herb cover in the plots planted with a pioneer mixture. However, I expect that, in the coming years, stronger changes will occur in the plantation plots as compared to the unplanted control plots, at least in pastures. Currently, the canopies have reached a cover of up to 20% only and moreover, this cover was achieved only recently. Environmental characteristics might just have started to change, and facilitating conditions might not have been very strong to date. We need monitoring data of microclimate to measure a possible relation between air humidity and species turnover rates.

The only measured effect of the planted canopy on the matrix vegetation was found in pasture plots with plantation of pioneer shrubs: a larger increase of herb cover was found than in the control plots. It means that conditions for herbs were more favourable in these plantation plots. If this is the case, the probability of successful establishment of other plant species in the future might be enhanced. This might be interpreted as an onset of accelerated succession, although species turnover was not found to be higher.

As mentioned in the Introduction, barriers to natural forest regeneration often include strongly fluctuating soil temperatures and humidity. This is especially true for the Condalia dwarf forest zone: total precipitation is low, its distribution is unreliable, and soils are often strongly eroded. Because of the harsh climatic and edaphic conditions in (semi-)arid areas, facilitation is probably more important in vegetation succession in such areas than in humid areas. For example, in semi-arid Mediterranean regions, seedlings planted under the canopy of shrubs generally had a higher survival and growth rate than those planted in open fields (Castro et al. 2002). However, the net (either beneficial or detrimental) effect of a shrub on a planted or naturally established seedling actually is the balance between facilitation and enhanced competition. Facilitation can be caused by, for example, a microclimate-improving crown or by soil structure improving roots. Competition might exist for water- and nutrient uptake, or for light. Hence, a shrub with, for example, a slender canopy and a dense and widely extended root system offers few benefits to and will compete strongly with a nearby seedling, and would thus be an inhibitor in stead of a facilitator. Indeed, in experiments in the Spanish Sierra Nevada mountains some nurse shrub species merely decreased performance of planted seedlings (Gomez-Aparicio et al. 2004).

Apart from these environmental effects, understory development in the study area was limited by propagule supply. The time scale in which a "substantial" turnover will take place thus depends on site characteristics (climate, soil, etcetera) and species traits (reproductive characteristics, life history, germination demands, etcetera). Prolonged monitoring of the experimental plots is therefore needed to obtain an idea of the
development of Condalia dwarf forest from pastures and from scrubs, either with or without plantation of seedlings. To date, the bulk of the publications addressing plantation of native species for restoration practices have focused on performance of the planted seedlings. To my knowledge, no monitoring data are yet available of pasture development after plantation of woody species, apart from those presented in Chapter 5 of this thesis.

Recommendations for restoration and rehabilitation efforts

Further research on seedling performance

The differences in performance between pioneer species on the one hand, and late-successional species on the other, might be explained by differences in strategies for nutrient uptake and photosynthesis. Rooting strategies can be expected to differ between species. Although generalizations are very hard to make, it appears that late-successional species are generally more easily affected by desiccation (by declining photosynthetic rates) than pioneers (Bazzaz 1979). One might expect that pioneer species take up nutrients relatively easily when the concentration of soluble nutrients is low as compared to late-successional species, but this remains to be investigated for the species of the dwarf forest region, and probably for the plant species of most other successional seres worldwide. Also, pioneers might be limited by other nutrients than late-successional species. Analysis of nutrient concentrations, mainly N and P, in leaf tissue of planted seedlings from different growing sites (comparing fertilized and non-fertilized ones) could give insights in whether N or P is limiting performance of the restoration species.

More detailed comparisons of local photosynthetic active radiation (PAR) with performance could give a better insight in light demand and shade tolerance of the planted species.

Further succession-based restoration experiments

Seed dispersal limitation could be overcome by supplying seeds of desired species. Sowing experiments could be carried out for dwarf forest species in scrub types with different overstorey and understory cover, in order to define a "threshold-scrub type" in which development of dwarf forest species could be successful.

Based on the idea that Baccharis macrantha – Dodonaea viscosa scrubs are an essential stage to be passed in the course of vegetation succession towards Condalia dwarf forest, further plantation experiments in the study area should include these two species. In one single plantation effort, seedlings of pioneer shrub and mid/late-successional treetlet species could be planted. I expect the pioneer shrubs to form a relatively closed canopy within five years or so, after which the dwarf forest species could start growing. Inserting the late-successional species after establishment of a pioneer shrub canopy – "enrichment planting" as used by Knowles and Parrotta (1995) – would permit the choice of suited spots (under
shrub crowns), but this would be much more laborious: one should avoid damage to the vegetation.

For conversion of *Acacia* forest into “natural” woody vegetation, underplanting of *Condalia* dwarf forest species could give promising results. More experiments are needed to determine after what period of time the *Acacia* canopy should be thinned or cleared, and to assess the effects of this activity on growth rate of the underplanted species and vegetation succession. Since *A. decurrens* is able to sprout from roots, the complete eradication might be laborious and should be done repeatedly.

In spite of the bad reputation of exotic tree species in plantation efforts – which I do not dispute for *Acacia decurrens* in monocultures – we should perhaps not completely exclude them as candidates in plantation efforts to force an initial jump-start in succession. One could support the pragmatic view that it might be better to quickly establish a setting in which natural vegetation could develop, in stead of being a “purist”, only willing to apply native elements at the cost of speed. In this pragmatic view, *A. decurrens* might be applied in the initial phase of catalytic scrub establishment, in a mixture with *B. macrantha, D. viscosa* and some mid- and late-successional dwarf forest species. Since *A. decurrens* is the fastest canopy expander and possibly an N-fixer, the plantation might profit from this. Monitoring and management would be needed to control the *Acacias* and thin or remove them at a certain stage.