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

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Chapter 1.

Introduction

General picture: ecosystem degradation

About one third of the earth’s land surface is covered by drylands. Severe degradation of ecological systems in these lands has mainly been caused by human population increase, bad resource distribution and over-exploitation (Aronson et al. 2002). About 12,000,000 km$^2$ of drylands are damaged beyond the repair capacity of individual farmers (Whisenant et al. 1995).

Common symptoms of ecosystem degradation are eroded or nutrient-poor soils, unstable soil moisture, low primary production and low biodiversity. “Original” ecosystems are generally believed to have a high complexity and species diversity on the one hand, and high values for ecosystem functioning on the other (Bradshaw 2002). The debate on the validity of this assumption lies beside the scope of this thesis. Ecosystem functioning was perceived as the capacity of a system to persist despite natural environmental fluctuations, through the cycling of energy and nutrients, by Palmer et al. (1997). Aronson et al. (2002) had a more anthropocentric view of ecosystem functioning, perceiving this as the degree to which an ecosystem provides benefits to humans. However, proper ecological functioning according to both definitions includes a high water retention and soil conservation (De Groot 1992). Hence, it is essential from both a nature conservationist and an agricultural point of view to stop the degradation processes and restore natural vegetation to – at least – a state with an accepted level of biodiversity and ecosystem functions.

Another important nature conservation issue in the tropics are the fast-growing exotic tree species – mostly Pinus and Eucalyptus species –, widely planted for timber production and protection against erosion. These planted forest monocultures generally have a number of drawbacks in terms of ecological function, e.g., high water consumption and evaporation (Lugo 1997; Van der Hammen 1997). Application of mixtures of species might provide a better use of resources, if these species differ in shade tolerance, rooting depth, and crown structure (Menalled et al. 1998). Therefore, the possibilities to convert these exotics’ forests to natural vegetation have gained interest.

Most of the state-of-the-art knowledge on forest recovery in the tropics comes from the humid lowlands and humid montane areas. Dry montane areas are virtually unexplored in this respect.
Natural vegetation recovery and its barriers

After abandonment of an arable field, the course of changes in vegetation composition (the successional pathway) depends on a number of factors (Clements 1916). Firstly, a certain set of species might already be present at the site, either as a plant or in the soil seed bank (which is influenced by the nature of disturbance), and hence, this largely determines short-term development of species composition (De Villiers et al. 2002). Secondly, a number of species enter the site by propagules (with fluctuating rates). And thirdly, environmental requirements of seeds to germinate, and of plants to mature, persist and reproduce, are generally not met for all species present (or arriving) at the site. This is partly due to abiotic conditions, e.g., soil chemical and physical characteristics, (micro)climate, eventual fire incidence, etcetera. Biotic between-plant interactions relevant for succession were treated by Connell and Slatyer (1977), who introduced the concepts of succession facilitation, inhibition and tolerance for species turnover processes. As Pickett et al. (1987) pointed out, these concepts apply to the mechanism through which an individual species enters a stand, develops, and/or outcompetes one or more other species in the same stand. A plant could modify its local environment, and thus either improve conditions for succession by certain invading species (facilitation), or prevent those from doing so (inhibition). If the successive species is not facilitated nor inhibited by the pioneer, but merely succeeds because of a longer life span or otherwise better competitive abilities, it would be called tolerant in this model. Fourthly, animal seed predators, herbivores and pathogens could influence the above-mentioned processes in any phase of succession (Rodriguez et al. 2003; Backeus et al. 1994; Olff et al. 1997; Fuhlendorf & Smeins 1998).

Although spontaneous succession has been successful at some sites (Hodacova & Prach 2003; Prach et al. 2001), restoring native vegetation without any interference has proven to be an unsatisfactory option for many disturbed sites. Secondary succession (i.e., succession after a (period of) disturbance) is often too slow or even arrested (Parrotta et al. 1997b), or takes a non-desired course (Sarmiento 1997; Gibson & Brown 1992). Natural vegetation succession is often hampered by abiotic or biotic barriers that persist over a larger time scale than that of short- and medium-term ecological and human needs (Nepstad et al. 1991; Raynal & Bazzaz 1973). After removal of a shade-providing canopy, a combination of high irradiance and more wind impact causes increased soil temperatures and decreased local soil humidity, and strong fluctuations of these two factors (Nepstad et al. 1990). This is especially so in areas with a marked dry season. Simultaneously, soil chemical conditions (e.g., nutrient availability) may impoverish, dependent on previous land use and current vegetation cover. Among others, the above-mentioned factors are probably the most relevant ones for (semi-)arid areas.

Biotic limitations to forest recovery are mostly a lack of seed dispersal: many forest species have been shown to disperse their seeds over a few tens of meters only.
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(Sarmiento 1997; Cubiña & Aide 2001; Nepstad et al. 1990; Vieira et al. 1994; Aide & Cavelier 1994; Aide et al. 1995). On top of that, seedlings often face competition for light, water and nutrients with exotic pasture grasses or other noxious weeds (Cabin et al. 2002; Hooper et al. 2002; Posada et al. 2000).

Restoration and rehabilitation: concepts and goals

The term restoration has been defined, distinguished from rehabilitation and reallocation, and split into restoration sensu stricto and sensu lato by various authors (Le Houérou 2000; Aronson et al. 1993). Recently, the Society for Ecological Restoration (SER 2004) stated: “Ecological restoration is the process of assisting the recovery of an eco-system that has been degraded, damaged, or destroyed.” For alteration efforts directly aiming at the reassembly of a predefined historic ecosystem with a certain set of species, the term “restoration sensu stricto” was suggested by Aronson et al. (1993). A mere halt to degradation and a redirection of a disturbed ecosystem towards a system comparable to the “original” one, i.e., an effort relying on subsequent natural recovery (soil formation processes, vegetation succession), would be called “restoration sensu lato” by Aronson et al. (1993), although this resembles much the above-stated recent definition by the SER. Rehabilitation is primarily focused on repairing ecosystem functions, thus enhancing productivity for human benefits. Reallocation refers to reassigning a use to a site that has no relation to the “original” ecosystem, and normally requires permanent management (Aronson et al. 1993).

Conceptual models aiming at summarizing processes of ecosystem degradation and (assisted) recovery highlighted the importance of thresholds of irreversibility (Aronson et al. 2002; Aronson et al. 1993; Hobbs & Norton 1996). A degrading ecosystem passing such a threshold would – even after elimination of the factors responsible for the degradation – not be able to return to the “original” undamaged stage. Interventions aiming at correcting the changes that caused the passing of the threshold would then be necessary, e.g., soil organic matter restocking or other site preparations (Aronson et al. 1993).

One could ask whether or not accelerated succession will achieve the same biodiversity levels as natural succession. Skeptics might argue that many species have complex relationships with other species in the successional pathway and that without the presence of these related species they will not establish. Dependent on the degree of ecosystem (or landscape) degradation, populations of rare or desired species might not be able to colonize or spread within an artificially restored system. Optimists may counter that establishment of species is above all dependent on suitable environmental conditions, which can be established by a limited number of “accelerator” species. It remains
open how long this will take, and the difference between the skeptics and the optimists might largely be one between “purists” and “pragmatics”.

In northern countries, concern for wildlife protection and “heritage landscapes” has become popular, at least among citizens. However, “ecological restoration”, in a pure ecological and species-conservationist (northern) sense has less political appeal in developing countries, where rehabilitation in order to improve production, watershed conservation and erosion control are considered more relevant. Man being the main cause of ecosystem deterioration around the world, any efforts to conserve or restore biodiversity should – especially in the tropics – be compatible with local livelihood needs. Hence, restoration practices should not seek to establish “living museums”, thus expressed by Aronson et al. (1993). Instead, strategies fulfilling human needs in terms of forest products (fuel-, pulp- and timberwood, fruits etc.) and enhanced ecological functions (mainly soil and water conservation), are likely to be more successful in developing rural countries (Montagnini 2001).

Restoration and rehabilitation: methods and experiences

There are numerous ways to artificially influence an ecosystem or its successional processes. In this thesis, I will focus on situations where ecosystem degradation has not yet passed through thresholds only to be undone by drastic reparations of the abiotic settings. Hence, cases of pollution, severe erosion, floodings etcetera, are considered outside the scope of this thesis. The choice of restoration or rehabilitation methods depends (apart from the desired characteristics of the ecosystem) largely on the degree of site degradation, and can be aimed at halting disturbance, restoring soil properties, and promoting establishment of desired organisms. It is widely assumed that ecosystem development towards a higher complexity and species diversity also causes – probably with some positive feedback mechanisms – an increase in ecosystem functioning (Bradshaw 1987, 2002), although the debate on this topic has not stopped (Cameron 2002). Hence, the methods used for either rehabilitation or restoration are often similar. Below, I will discuss (not exhaustively) a few methods to enhance establishment of desired plant species.

A catalytic effect of exotic tree plantations for natural regeneration, mostly by mitigating soil temperature and humidity fluctuations, has been shown by many authors (Yirdaw 2001; Fimbel & Fimbel 1996; Geldenhuys 1997; Parrotta 1992, 1993, 1995). However, whether such a plantation is catalytic or not depends on management (disturbance), planted species (possible allelopathic effects), distance to natural forest (seed supply), site degradation (soil properties), and grazing, and consequently there are many sites where regeneration is hampered (Van der Hammen 1998; Cortés et al. 1990; Hofstede et al. 1998; 2002; Cavelier & Santos 1999; Cavelier & Tobler 1998; Van Wesenbeeck et al.
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In Sri Lanka, underplanting of native seedlings in Pinus caribaea forests was more successful when the pine canopy was thinned (Ashton et al. 1998). Hence, as stated in the second paragraph of this chapter, I tend to regard exotic species plantations as an ecological problem rather than a solution to it.

In the 1990's, the term “framework species” was introduced for fast-growing tree species with abilities to outshade weeds and attract seed-dispersing animals, and hence most suited for restoration projects (Goosem & Tucker 1995). Plantation is generally executed in one single session, but a method of “staggered plantation” has been proposed by Knowles and Parrotta (1995): plantation of exposure-tolerant species is carried out in a first phase, and after establishment of a canopy with some accepted degree of closure, the plantation is enriched with shade-tolerant species. As in the previous paragraph, choice of species is fully pragmatic, and hence, exotic species are not excluded beforehand.

Experience with plantation of native species is still relatively sparse, although many experiments have been initiated. Most of these are in the humid tropics (Carpenter et al. 2004; Hooper et al. 2002; Parrotta & Knowles 1999; Leopold et al. 2001). Some studies on native species plantation highlighted the importance of weed control (Cabin et al. 2002; Hooper et al. 2002). Understory succession was least arrested in a mixed native species plantation as compared to adjacent exotic species plantations in the Brazilian Amazon (Parrotta & Knowles 1999). However, in a plantation with native Alnus acuminata in the Central Cordillera of the Colombian Andes, understory diversity was markedly lower than in adjacent secondary forest of the same age (Murcia 1997). Plantation of Albizia lebbeck, a nitrogen-fixing leguminous naturalized species, greatly enhanced recruitment by forest species as compared to adjacent pastures in Puerto Rico (Parrotta 1993). The importance of shrubs in facilitation of succession, especially in Mediterranean-climate areas, has been stressed by Castro et al. (2002; 2004).

Grazing and trampling of weedy grasses by sparsely introduced cattle had a positive influence on germination site availability in pastures, and thus on recruitment by woody species, although the diversity of these was low (Posada et al. 2000). Of course, cattle density should be low, since a trade-off exists between the above-mentioned positive effect and the formation of “erosive ravines” by trampling (Sarmiento 1997). Artificial seed enrichment has successfully been applied in abandoned pastures by Posada et al. (2000) in the Colombian Andes. Perches (i.e., structures attracting seed-dispersing animals) have been suggested to greatly enhance local seed dispersal (Ferguson & Drake 1999; Carrière et al. 2002; Holl 1998).
Aims and research questions of this thesis

This thesis reports on the onset of a restoration experiment of late-successional dwarf forest in the Checua valley, based on the idea of vegetation succession accelerated by canopy closure of planted woody species. While executing this restoration attempt, I gained basic knowledge on habitat requirements of desired species, growing site characteristics of the desired vegetation type, and propagule dispersal abilities. The principal research questions addressed are:

- Which types of vegetation are present in the study area, and what pathways of (secondary) succession are likely to occur?
- Is seed dispersal a limiting factor for development of secondary scrub and dwarf forest?
- How do planted pioneer- and late-successional species perform in open secondary vegetation types?
- Can natural succession in pastures and scrubs be accelerated by plantation of native woody species?
- How do planted pioneer- and late-successional species perform in exotic *Acacia decurrens* forest?
- Does plantation of native species give prospects for conversion of exotics’ forests into native vegetation?

Study area

The fieldwork area is at the northern edge of the high plain of Bogotá, which is an intramontane basin in the Eastern Cordillera of Colombia (Figure 1.1). It concerns a part of the Checua River valley, affluent to the Bogotá River, situated within the municipality of Suesca, Cundinamarca. The altitude above sea level of the study area is between 2550 and 2950 m.

Although most of the high plain of Bogotá has a fairly humid climate, extensive parts of the northern fringe have a semi-arid climate with around 650 mm of annual precipitation. Evapotranspiration approximates 1050 mm annually, leading to a deficit of about 350 mm (Claro-Rizo 1995). The data of a climate station (CAR, unpublished data from 1962 - 2003) in the lower part of the Checua Valley show two relatively rainy periods (Figure 1.2b, c), although local farmers stated that, in recent years, those periods do not reliably occur in these months, or with the indicated intensity. This is illustrated by the high standard deviations of the monthly precipitation averages. The mean annual temperature is around 13° C (Van der Hammen 1998), and varies little during the year (Figure 1.2a). During dry periods, night frosts frequently occur.
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The area has a hilly terrain morphology. Most of the hills are built up by sandstones belonging to the Guadalupe Formation (Van der Hammen 1998). Northward, the pediment material probably is strongly weathered kaolinitic clay of the Balsillas Formation, of early Pliocene age (Helmens 1990). The entire area is covered by a volcanic ash cap, which varies in thickness from less than 20 cm (upper slopes and summits) to 70 cm (pediments). Due to erosion, the hills are intersected by crevices, up to several meters depth, exposing either sandstone or kaolinitic clay.

Soil formation in the ash layers has taken place under semi-arid conditions. Most soils are Alfisoles, showing a B horizon primarily containing clay and organic material. On the pediments, where climatic conditions are more extreme, the E horizon is strongly leached, and has locally formed a hardpan. An A horizon has hardly developed, and the B horizon is natric with a pH of 9-10. However, in the higher parts of the hills, where more humid conditions prevail, an A horizon is often found, and the B horizon is not natric. On slopes, colluvial deposits and fine alluvial caps have caused local variations in soil properties.

Figure 1.1. Map of the study area. Bold lines indicate roads, and dotted lines indicate streams, which are dry nearly all year round.
Figure 1.2. Climatic patterns during the course of the year, as measured by the Checua climate station near the fieldwork area at 2650 m.a.s.l., between 1963 and 2003. a.) Monthly mean, maximum, and minimum temperatures; b.) Number of days with precipitation, with errorbars indicating 1 S.D.; c.) Mean monthly precipitation, with errorbars indicating 1 S.D.
The study area is a mosaic landscape of grassland, scrubs, planted exotics' forest, and fragments of dwarf forest. Disturbances have been common and severe, and exotic grasses have large cover values. Most of the area is covered by pastures and planted *Acacia decurrens* forests, the steeper and more rocky slopes are covered with *Baccharis macrantha* – *Dodonaea viscosa* scrubs in different states of recovery. The dry andean dwarf forest was described as *Xylosmo – Condalietaum*, or “Condalia forest”, by Van der Hammen (1997). The Quaternary history of the dry vegetation in the study area is not known, and hence it is very difficult to define an "original" ecosystem for the area. However, the Condalia dwarf forest zone can be regarded as an enclave in both a climatical and a botanical point of view. One of the characteristic treelets, *Condalia thomasiana* (Rhamnaceae), is a recently discovered endemic of this particular zone (Fernández-Alonso 1997), and relatively many species, both herbaceous and woody, are not found elsewhere on the high plain of Bogotá and the surrounding mountains, and are typical of areas at a lower altitude above sea level (J.L. Fernández-Alonso, pers. comm.). Hence, I believe that many species typical of Condalia dwarf forest have a long history in the study area, and because of that can be regarded "native" or "original" to the area. Combining this with the assumedly high degree of ecological functioning, I think that the Condalia forest deserves the status of "original ecosystem", and hence serves as the "desired end point" for restoration efforts.

The high plain of Bogotá is one of the most populated and intensely cultivated regions in the Andes of Colombia. The increase of the human population, and hence of resource demands, have experienced a strong acceleration during the last decades (Van der Hammen 1998). For its drinking water supply it is heavily dependent on the surrounding mountain ranges, especially on the northern part, where the Bogota River originates. This is one of the important water suppliers for the high plain and the city of Bogotá. Due to inadequate land use a vegetation cover with a substantial water retention and soil covering abilities is almost completely absent (Van der Hammen 1998), and almost all water is being lost by superficial run-off. This has had a strongly degrading effect on the unprotected soils, and extensive badlands are a common sight (Araque 1976; Thouret & Rovera 1983). The effects on the high plain's water supply are severe as well, as the water flow is not evenly spread in time, but peaks tremendously after a heavy shower after which it drops to insubstantial levels. The sediment load of the Checua River, frequently reaches 60% of the volume (CAR 1996).

Plantations with exotics - mostly *Acacia decurrens* and *Pinus radiata* - have been established in the 1980s for soil conservation purposes; however, an understory vegetation has hardly developed, and ecosystem function recovery is poor, as compared to the native dwarf forest (Van der Hammen 1998, 1997). The picture of poor understory development was confirmed for other sites in the Andes of Colombia where *Pinus* species were planted (Van Wesenbeeck *et al.* 2003; Cavelier & Tobler 1998).
Chapter 1

**Thesis outline**

Basic knowledge on ecosystem composition, structure and vegetation succession was gathered in the early phases of the research, and the results of this research are presented in the second, third and fourth chapter. The results of the restoration experiment after four years are given in chapter 5 and 6.

Chapter 2 gives a short description of the most important types of vegetation found in the study area. Relations between species composition and vegetation structure, environmental factors, and disturbance history were made, which permitted to establish prospects for succession in the described vegetation types. Chapter 3 investigates the successional affinity of the nine woody species that were used in the restoration experiment, by means of an assessment of species relations with environment and disturbance history, and life history characteristics. Chapter 4 reports on soil seed banks of the vegetation types relevant to the successional processes leading to *Condalia* dwarf forest and to the restoration experiment. On the basis of the germinated seeds found in secondary and artificial planted vegetation types, I address the question whether recovery of mature dwarf forest could proceed without intervention, or if one should make artificial modifications to speed up succession.

The results of the plantation experiment in pastures and open scrubs are presented in Chapter 5. Both planted seedling performance and the influence of canopy formation on development of the matrix vegetation (*i.e.*, the non-planted vegetation) are treated here. Chapter 6 reports on a plantation experiment following a comparable methodology to that of the previous chapter, but executed in a planted *Acacia decurrens* forest. The results of Chapters 2 to 6 are evaluated in the General Discussion, followed by recommendations for succession-based restoration in the Checua Valley, and in a wider perspective.