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TOWARDS RECOVERY OF NATIVE DRY FOREST IN THE COLOMBIAN ANDES

A plantation experiment for
ecological restoration

Jeroen Groenendijk



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COLOMBIAN ANDES**

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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 km² 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

(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 re-allocation, 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.*

2003). 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 lebbek*, 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; Carriere *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.

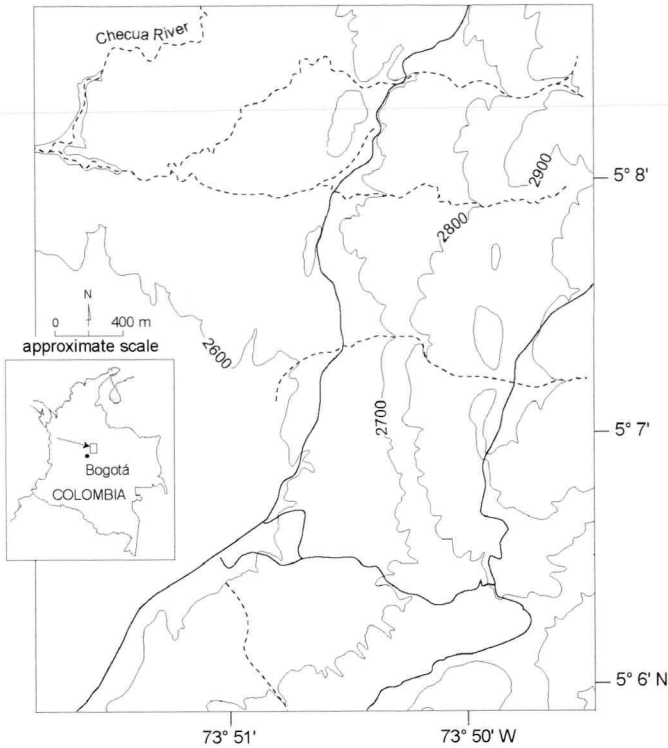


Figure 1.1. Map of the study area. Bold lines indicate roads, and dotted lines indicate streams, which are dry nearly all year round.

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.

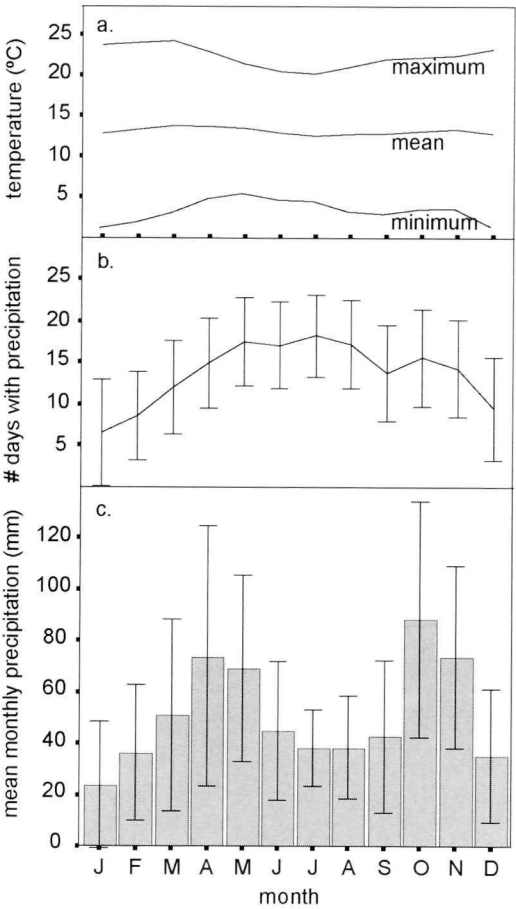


Figure 1.2. Climatic patterns during the course of the year, as measured by the Checua climate station near the fieldwork area at 2650 m.a.s.l., between 1963 and 2003. a.) Monthly mean, maximum, and minimum temperatures; b.) Number of days with precipitation, with errorbars indicating 1 S.D.; c.) Mean 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* – *Condaliatum*, 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 Bogotá 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).

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.

Chapter 2.

Vegetation patterns in a semi-arid dwarf forest zone: prospects for succession of abandoned pastures and scrubs

J.P. Groenendijk and A.M. Cleef, accepted for publication in *Phytocoenologia*

Abstract

A study on vegetation patterns in a semi-arid zone of the high plain of Bogotá (Colombia), at 2600-2950 m.a.s.l., is presented, as a basis for a restoration experiment in the dry Andean dwarf forest zone. We aimed at explaining successional pathways by means of environment and disturbance history data. We laid out 101 relevés in grassland and shrubland types in different stages of recovery, and in relatively little disturbed endemic *Condalia thomasiana* dwarf forest. CCA was applied to relate species composition to environment, disturbance history and to the spatial configuration of the relevés. Abiotic factors mostly related to species composition were soil nutrient richness and soil organic matter content. Invasion of grasslands by woody species is pioneered by *Baccharis macrantha* and *Dodonaea viscosa*. *Dalea coerulea* was the predominant woody species on truncated clayey soils, which will probably not support *Condalia* dwarf forest. This exploratory study will be of use in the set-up of future succession-based restoration experiments.

Introduction

Deforestation in the northern Andes is a major threat to all types of forest. Presently, most remnants of natural montane forest in this area are humid forests. Dry Andean forests are particularly threatened because the semi-arid areas are often densely populated, and have a long history of land use (Murphy & Lugo 1986). The population of the high plain of Bogotá depends heavily on the surrounding mountain ranges for their drinking water. Parts of the aquifers originate in semi-arid areas, where inadequate land use has drastically reduced the cover of water retaining natural vegetation; extensive badlands are a common sight (Araque 1976; Thouret & Rovera 1983). Plantations with exotics (e.g., *Acacia decurrens*) have been established in the 1980s, virtually devoid of understory vegetation, and showing a poor recovery of ecosystem functions – soil temperature and evapotranspiration reduction – as compared to the native dwarf forest (Van der Hammen 1997, 1998).

Remnants of dry montane dwarf forest were found in the semi-arid northern edge of the high plain of Bogotá, in the Eastern Cordillera of the Colombian Andes. Van der Hammen (1997) described this forest as *Xylosmo – Condaliatum*, or “*Condalia* forest”. One of the characteristic treelets, *Condalia thomasi* (Rhamnaceae), is a recently discovered endemic of this particular zone (Fernández-Alonso 1997). The *Condalia* forest reaches heights up to five meters, and has a highly diverse and dense understory of herbs, mosses and lichens, both terrestrial and epiphytic, with a high capacity of moisture retention.

Very little is known about the basic ecology of dry equatorial montane forest, or its recovery after disturbance. In spite of this, restoration efforts are needed, and the Corporación Autónoma Regional de Cundinamarca (CAR), which manages the (renewable) natural resources in the region, is now interested in this study. A start has been made with a succession-based plantation experiment in the area, involving application of mixtures of locally occurring species in different vegetation types in the study area, in cooperation with the CAR.

The area has suffered from many kinds of disturbance. Cutting, grazing and agriculture have been practiced since pre-Columbian times (Van der Hammen 1998; Marchant *et al.* 2004; Vélez *et al.* 2003), and have had a great impact on vegetation patterns and development (Adler *et al.* 2001; Backeus *et al.* 1994; Girardideiro *et al.* 1994; Hadar *et al.* 1999; Motzkin *et al.* 1999). Extensive grazing has favored the introduction of invasive herbs like *Hypochoeris radicata*, *Anthoxanthum odoratum*, and *Pennisetum clandestinum*. Disturbance history assessment has been used extensively in vegetation studies; however, the aim was mostly to assess changes in the cover of vegetation types (Kadmon & Harari-Kremer 1999; Verheyen *et al.* 1999). We used the individual disturbance history

over the last ~60 years of each vegetation relevee point as a means to explain the present-day species composition.

The purpose of our study was to describe the vegetation types of the surroundings of the Hacienda Susata, and to infer successional pathways from environmental variables and disturbance history. We assumed that vegetation development can be expressed in terms of structural development and diversity. In the present study, we chose not to consider heavily eroded sites, which would need engineering practices before any vegetation development could take place, and to limit our efforts to existing grasslands, scrubs and dwarf forest.

Methods

Study area

The fieldwork area is at the edge of the high plain of Bogotá, an intramontane basin in the Eastern Cordillera of Colombia (Figure 2.1). It concerns a part of the valley of the Checua River, an affluent of the Bogotá River, situated within the community of Suesca, Cundinamarca (5° 07' N, 73° 50' W). The height above sea level of the study area is between 2550 and 2950 m.

The zone receives about 700 mm of annual rainfall, generally concentrated in two short rainy periods. Evapotranspiration approximates 1050 mm annually, leading to a deficit of about 350 mm (Claro-Rizo 1995). The mean annual temperature is around 13°C (Van der Hammen 1998), which is below the minimum of the temperature range of "tropical dry forest" as set by Murphy & Lugo (1986).

The area has a hilly terrain morphology. Most of the hills are built up by sandstones belonging to the Guadalupe Formation (Cretaceous). 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 sites show a natric B horizon primarily containing clay, organic material, and sodium. 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. However, in the higher parts of the hills, where more humid conditions prevail, this horizon is often found. Slope deposits and fine alluvial caps have caused local variations in soil properties.

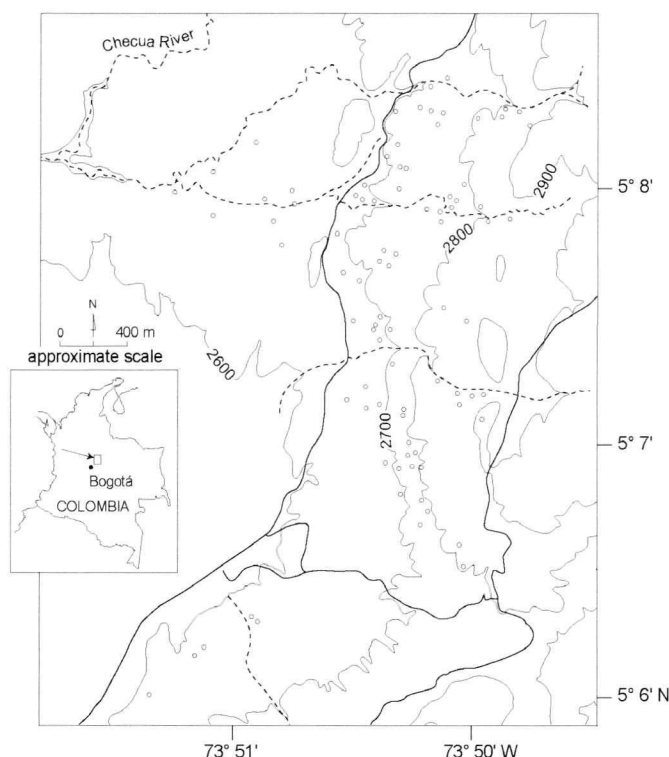


Figure 2.1. Locations of the vegetation relevees in the study area, indicated by circles.

Since pre-Columbian times, the area has been affected by forest cutting, agriculture, and cattle grazing. With the growing population pressure in the 20th century, grazing and cultivation of oat and lentils increased. Recently, the intensity of agricultural land use in the area has reduced, and parts of the area were reforested with *Acacia decurrens* by the Corporación Autónoma Regional de Cundinamarca.

Relevees

A total of 101 relevees were made between October 1999 and April 2001, following Braun-Blanquet (Mueller-Dombois & Ellenberg 1974). Selecting the relevee sites, we aimed at including a maximal variation in vegetation diversity and structure, avoiding planted vegetation and rocky substrates. Eighty-five of these had dimensions of 10 x 10 m, while the remaining 16 were rectangles of 10 x 15 m. The relevees of 10 x 15 m had no significantly different numbers of species than the ones of 10 x 10 m (*t*-test, $p=0.641$). 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 treelets, high shrubs, low shrubs, high herbs, low herbs, bryophytes, and lichens.

Vouchers were deposited at the herbarium of the Instituto de Ciencias Naturales, Bogotá, Colombia (COL).

In each relevee the following geographical data were taken: GPS position, elevation a.s.l., inclination, and exposure. Also, 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.

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 NH_4OAc (pH=7), and quantified by atomic adsorption spectrophotometry. Total available bases (TB) was calculated as the sum of available Ca, Mg, K, and Na concentrations. Organic C was oxidized by $\text{K}_2\text{Cr}_2\text{O}_7$ in acid medium (Walkley-Black method) and measured by titration with ferrous ammonium sulfate. Cation exchange capacity (CEC) was measured in 1N ammonium acetate at pH 7. Base saturation was calculated as the ratio total bases/CEC, expressed in percentages.

Aerial photograph interpretation

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. The following categories were defined from the sequential analysis of the disturbance history of each relevee site: 1) *no disturbance*: no signs of major disturbance during the period, woody canopy more or less preserved; 2) *permanently grazed*: pasture during the entire period; 3) *abandoned*: transition from pasture to a woody vegetation; 4) *cut*: removal of woody vegetation and conversion to pasture; 5) *eroded*: badlands with no apparent pasture or continuous vegetation. These categories were used as explanatory variables in further analyses (see next section).

Data processing

Shannon's diversity (H') was calculated for all relevees. The relevees were classified by means of TWINSpan (Hill 1977). The phytosociological interpretation of this classification will be published in the near future. Since we assumed woody species to be the basis of dwarf forest regeneration, emphasis was put on these species by assigning them a weight of 5.0, against 1.0 for herbaceous species. The species that occurred in only one plot were excluded from the classification and subsequent ordinations.

Vegetation patterns were examined by means of ordinations, performed with Canoco 4.0 (Ter Braak & Šmilauer 1999). A preliminar Detrended Correspondence Analysis revealed a gradient length of 4.0 SD, which suggests the use of ordination methods assuming unimodal species responses (Jongman *et al.* 1995). Subsequently, we carried out a Canonical Correspondence Analysis (CCA) on log-transformed species abundances in the relevees. Explanatory variables were the soil chemical and geographical data and the disturbance categories as derived from the aerial photographs. Soil chemical parameters, except pH, were log-transformed prior to the CCA. The number of explanatory variables was reduced with the aid of Canoco's forward selection option, until the VIF's were below 15 (Jongman *et al.* 1995).

Results

Vegetation classification

In the 101 relevees, 241 vascular plant species were recorded, belonging to 173 genera and 65 families. A checklist is provided in Appendix 1. The best represented families are Asteraceae and Poaceae, with 35 and 29 species respectively, followed by Orchidaceae, Polypodiaceae and Fabaceae. Nineteen pteridophyte species were found, belonging to seven families. From the classification by the TWINSpan software we recognized six vegetation types:

Type I: grasslands

Cover of woody species, if any, mostly below 5%. Co-dominant species mostly *Pennisetum clandestinum* and *Aristida laxa*; *Hypochoeris radicata* and other asteraceous herbs are common.

subtype Ia: piedmont *Microchloa* grasslands

Characterized by *Microchloa kunthii* and *Schkuhria pinnata*. Other commonly found herbs include *Eragrostis intermedia*, *Bouteloua simplex*, and *Zornia diphylla*. Found at the piedmont at around 2650 m.a.s.l.

subtype Ib: hill summit *Anthoxanthum* grasslands

Co-dominated by *Anthoxanthum odoratum*. Other common species are *Hypericum silenoides*, *Rhynchospora nervosa*, *Lachemilla aphanoides*. Found between 2800 and 2950 m.a.s.l.

Type II: low *Baccharis* – *Dodonaea* scrubs

Generally of a lower stature than Type I, with a woody cover of 5 – 20%, reaching heights between 50 and 250 cm. Co-dominated by *Baccharis macrantha* in the shrub layer. Frequent occurrence of *Myrsine guianensis*, but with cover values mostly below 2%.

subtype IIa: *Baccharis* – *Dodonaea* scrub

Baccharis macrantha and *Dodonaea viscosa* dominate the woody stratum, and are mostly accompanied by *Stevia lucida*. *Myrsine guianensis* is found frequently, but mostly represented by a few small individuals. Herb cover is high, mostly with *Cuphea serpyllifolia*, *Lycurus phalaroides*, *Aristida laxa*, and *Pennisetum clandestinum*.

subtype IIb: *Dalea* scrub

Species-poor type characterized by *Dalea coerulea* co-dominating with *Baccharis macrantha*. Relatively high cover of *Lantana boyacana* and *Pennisetum clandestinum*; otherwise low herbaceous cover.

Type III: high scrubs and dwarf forests

Woody vegetation with a high cover of shrubs and/or treelets (generally > 20%), characterized by presence of *Xylosma spiculifera*, *Myrsine guianensis*, *Tillandsia incarnata*.

subtype IIIa: *Myrsine* – *Dodonaea* scrub

More herbaceous cover than dwarf forest, mostly of the grasses *Lycurus phalaroides* and *Eragrostis tenuis*. The pioneer shrubs *Baccharis macrantha* and *Dodonaea viscosa* are more common than in dwarf forest, and have higher cover values. Canopy height 150 – 250 cm.

subtype IIIb: *Condalia* dwarf forest

Characterized by *Condalia thomasiana*, *Duranta mutisii*, *Miconia squamulosa*. Herb cover is relatively low; characteristic species are *Peperomia galioides*, and species of *Asplenium* and *Tillandsia*. Epiphytic lichens are conspicuous. Canopy height up to 5 m.

Species diversity compared between vegetation types

Species numbers differed markedly between the TWINSPAN groups, while Shannon's H' was, on average, similar between groups (Figure 2.2). The two grassland types and the *Dalea* scrubs revealed, on average, less than 30 species in the 10 x 10 m relevés. *Myrsine* – *Dodonaea* scrubs appeared to have a mean species number of around 50, against 42 for the *Condalia* dwarf forests. *Anthoxanthum* grasslands are the least diverse in terms of both species numbers and Shannon's H' . The remaining five vegetation types have strongly overlapping ranges of H' , with *Condalia* dwarf forests having the highest diversity.

Relations with environmental characteristics and disturbance history

The relations between species occurrences and abundances in the relevés and the environmental characteristics and disturbance history was examined by CCA. Figure 2.3 shows a triplot produced by the CCA, in which the six relevés groups derived from the TWINSPAN classification are fairly well separated over the first axis. Dwarf forest plots (subtype IIIb) are plotted on the left side of the diagram, correlated with high CEC,

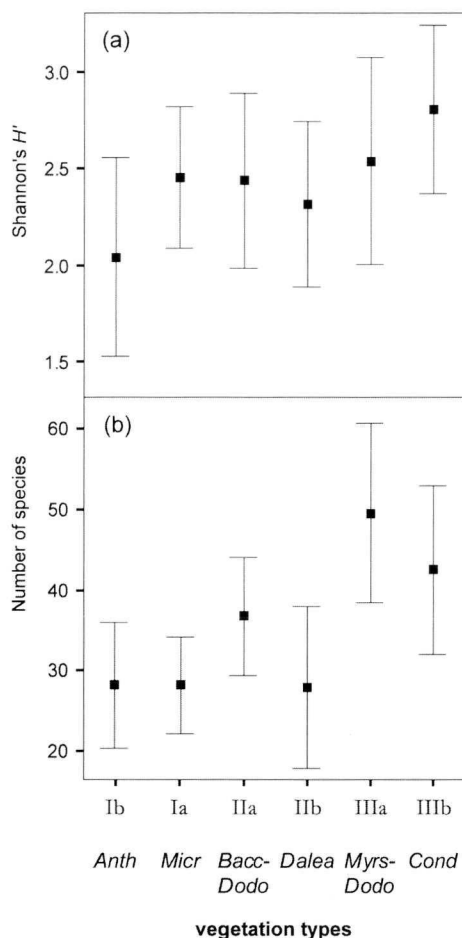


Figure 2.2. a) Average Shannon's diversity, and b) species numbers of the vegetation types. Error bars represent ± 1 SD.

organic C, inclination, K and Mg values. The two pasture subtypes (Ia and Ib) are on the positive end of the first axis, hence correlated with low available kation contents and organic C, and high pH. The shrub types IIa and IIIa were plotted in the center of the graph. The relevés belonging to Type IIb, the *Dalea coerulea* scrubs, were mostly found on the positive end of the second axis which corresponds to a high clay content. Thus, the first CCA axis represents a gradient of structural development, and the second axis a gradient of soil texture to which the *Dalea* scrubs clearly respond.

The categories of disturbance and land use over the last 60 years are also shown in Figure 2.3. Scrub and dwarf forest relevés have had a history without major disturbance over the last ~ 60 years, while the relevés that were abandoned within this period are more similar to the grasslands in terms of species composition. Eroded sites mostly supported *Dalea* scrubs.

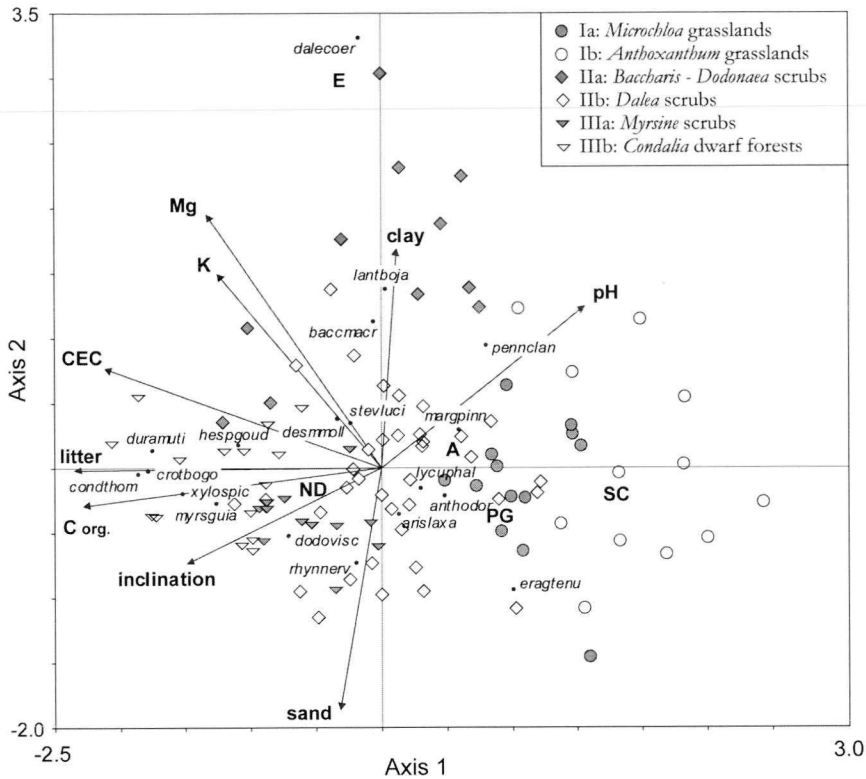


Figure 2.3. CCA scatter of sites based on species abundances. Symbols represent the TWIN-SPAN releve clusters, as indicated in the figure. Nominal variables are represented by abbreviations: A = abandoned; PG = permanently grazed; SC = shrubs cut; E = eroded; ND = no disturbance.

Discussion

Vegetation patterns

The secondary vegetation in this area shows an affinity with various scrub - and grassland types described from the high plain of Bogotá and adjacent dry parts of the Eastern Cordillera (Vink & Wijninga 1987; Fandiño Lozano 1996; Cortés-Sánchez *et al.* 1999), and possibly with the Andean scrub (*matorral andino*) as described by Balslev & 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 & Hooghiemstra (1984).

Species composition in the study area mostly react to gradients of nutrient richness and organic C content. These gradients coincide well with a vegetation structural

series: grasslands on nutrient- and OM-poor sites on the one end, and well-developed scrubs and dwarf forests on OM-rich sites with relatively high nutrient availability on the other. Moreover, substrate inclination is generally higher for scrubs, which probably has a historical explanation: sloping sites are generally less suited for agricultural practices, so the woody vegetation was less disturbed.

Many revegetation sites have developed structurally over the last 60 years. Locals informed that agricultural activity has decreased; many formerly cultivated sites appear not suitable anymore. We would probably need more detailed information on small-scale historical events like cutting, burning and grazing to be able to explain a larger part of the variation in present-day species composition. Since growth and development of species and communities is slow, a time span longer than 60 years would also be necessary.

Successional pathways

Species diversity was generally found to be higher in more structurally developed vegetation, with the exception of the *Dalea* scrubs. *Condalia* forests had a lower average species number, which could be attributed to canopy closure and a subsequent decrease of understory species richness (Horn 1974; Sarmiento *et al.* 2003).

The difference in species composition between the *Anthoxanthum* and *Microchloa* grassland types is explained largely by elevation, and hence by climatic conditions. *Microchloa* grassland occurs on lower elevated sites, on soils with hardly any formation of an A-horizon, occasionally topped with sandy alluvium. *Anthoxanthum* grasslands are found on higher elevations (over 2800 m), where the volcanic ash soils generally are intact. It is clear that no successional relation can be expected between these two grassland types.

The canonical ordinations showed clear floristic transitions between grasslands and scrubs. However, it remains questionable whether these grasslands will develop along this development sequence, even if grazing would be precluded. Regeneration of native vegetation is known to be thwarted by exotic perennial grasses (Cabin *et al.* 2000). *Pennisetum clandestinum* – belonging to this group – has been sown in pasture lands, and is commonly found in grasslands, but also in *Baccharis-Dodonaea*-scrubs, and even in dwarf forests. Most probably, this species invaded these already existant vegetations. D'Antonio *et al.* (1998), studying seasonally dry woodland on Hawaii, showed that *Dodonaea viscosa* grew faster after removal of alien invasive perennial grasses, probably as an effect of increasing light availability and N-pools. We expect *P. clandestinum* and *Anthoxanthum odoratum*, reaching covers up to 95% and 55%, respectively, to have a large inhibitory effect on recruitment by (woody) species. Posada *et al.* (2000) found that grazing favoured woody species recruitment in *P. clandestinum* pastures. Hence, *Baccharis macrantha* is probably capable of invading even under grazing pressure; if this would decrease, a *B. macrantha* scrub vegetation could develop. Still, *P. clandestinum* would persist for a long time. In a mixed *Alnus incana* plantation in the vicinity of our study area, *P. clandestinum* has per-

sisted over almost 13 years and even climbed tree trunks in search for light and space (pers. obs. 2004).

Anthoxanthum grassland, *Baccharis-Dodonaea* scrub, *Dodonaea-Myrsine* scrub and *Condalia* dwarf forest are mostly separated along the first CCA axis, which is mostly related to soil nutrient availability, organic matter content, and disturbance history. Nutrient richness and OM content of the soil probably largely increased in the course of the development of the vegetation. We suggest that the *Dodonaea-Rhynchospora* scrub, the *Myrsine-Dodonaea* scrub, and the *Condalia* dwarf forest form a successional series. If propagule supply, seed banks, and exotic grasses pose no limits, *Dodonaea-Rhynchospora* shrubs can probably develop into *Myrsine-Dodonaea* scrub and dwarf forest. The stronger inclination of dwarf forest sites is probably a consequence of farmers preferring less sloping areas for agricultural use. Dwarf forests were cut on the more accessible parts of the study area, and therefore, potential dwarf forest growth sites are probably more diverse than can be inferred from our data.

However, many *Baccharis* – *Dodonaea* scrub patches have not developed structurally, in spite of the apparent absence of disturbance. Succession and structural development are taking place with very low speed. This could be due to seed dispersal limitation, or soil characteristics may impede recruitment of certain species. These scrubs often occur on gravelly slopes mostly with shallow soils, and hence soil temperatures might fluctuate strongly, making the site unsuited for many species.

Dalea scrubs were mainly found on truncated soils where old weathered clay caps are exposed. No other woody vegetation types were found on these soils, from which we concluded that *Dalea* scrubs will not develop into *Condalia* dwarf forests.

Acknowledgments

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Appendix 2.1. Species list of all relevees. Values are percentages of the relevees of each vegetation type in which the corresponding species was found.

	<i>Micr</i> grassl. Ia	<i>Antb</i> grassl. Ib	<i>Bacc-</i> <i>Dodo</i> IIa	<i>Dalea</i> scrub IIb	<i>Myrs-</i> <i>Dodo</i> IIIa	dwarf forest IIIb	total occ.
PTERIDOPHYTA							
Aspleniaceae							
<i>Asplenium dissectum</i> Sw.	0.0	0.0	16.2	9.1	25.0	68.8	21
<i>Asplenium harpeodes</i> Kunze	0.0	0.0	10.8	0.0	8.3	56.3	14
<i>Asplenium sessilifolium</i> Desv.	0.0	0.0	0.0	0.0	0.0	6.3	1
Ophioglossaceae							
<i>Ophioglossum nudicaule</i> L.f.	16.7	30.8	2.7	0.0	0.0	0.0	7
Polypodiaceae							
<i>Niphidium crassifolium</i> (L.) Lellinger	0.0	0.0	2.7	0.0	16.7	37.5	9
<i>Pecluma camptophyllaria</i> (Feë) M.G. Prince	0.0	0.0	10.8	0.0	0.0	43.8	11
<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.	0.0	0.0	27.0	18.2	41.7	56.3	26
<i>Polypodium lasiopus</i> Klotzsch	0.0	0.0	2.7	0.0	0.0	0.0	1
<i>Polypodium pycnocarpum</i> (Rosenst.) Tryon &	0.0	0.0	2.7	0.0	8.3	31.3	7
<i>Polypodium thyssanolepis</i> A. Braun ex Klotzsch	0.0	0.0	5.4	0.0	8.3	0.0	3
<i>Polypodium thyssanolepis</i> x <i>Pleopeltis macrocarpa</i>	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Polypodium triseriale</i> Sw.	0.0	0.0	2.7	0.0	0.0	0.0	1
Polypodiaceae indet.	0.0	0.0	2.7	0.0	8.3	12.5	4
Pteridaceae							
<i>Cheilanthes bonariensis</i> (Willd.) Proctor	8.3	0.0	27.0	0.0	41.7	6.3	17
<i>Cheilanthes lendigera</i> (Cav.) Sw.	0.0	0.0	2.7	0.0	0.0	6.3	2
<i>Cheilanthes myriophylla</i> Desv.	0.0	0.0	43.2	18.2	16.7	31.3	25
<i>Pellea ternifolia</i> (Cav.) Link	8.3	23.1	59.5	27.3	66.7	25.0	41
<i>Pityrogramma calomelanos</i> (L.) Link	0.0	0.0	0.0	0.0	0.0	6.3	1
Dryopteridaceae							
<i>Elaphoglossum</i> sp.	0.0	0.0	0.0	0.0	0.0	6.3	1
Selaginellaceae							
<i>Selaginella sellowii</i> Hieron.	66.7	30.8	70.3	27.3	66.7	43.8	56
Woodsiaceae							
<i>Woodsia mollis</i> (Kaulf.) J.Sm.	0.0	0.0	2.7	0.0	0.0	0.0	1
ANGIOSPERMAE							
Acanthaceae							
<i>Stenandrium dulce</i> (Cav.) Nees	16.7	15.4	18.9	18.2	8.3	0.0	14
Agavaceae							
<i>Agave</i> sp.	0.0	0.0	2.7	0.0	16.7	12.5	5
Aizoaceae							
<i>Aptenia cordifolia</i> (L.f.) Schwantes	0.0	0.0	0.0	0.0	0.0	6.3	1

	<i>Micr grassl. Ia</i>	<i>Anth grassl. Ib</i>	<i>Bacc- Dodo IIa</i>	<i>Dalea scrub IIb</i>	<i>Myrs- Dodo IIIa</i>	<i>dwarf forest IIIb</i>	<i>total occ.</i>
Amaranthaceae							
<i>Alternanthera porrigens</i> var. <i>porrigens</i> (Jacq.)	0.0	0.0	2.7	0.0	0.0	6.3	2
<i>Iresine diffusa</i> Humb. & Bonpl. ex Willd.	0.0	0.0	2.7	9.1	16.7	31.3	9
Amaryllidaceae							
<i>Bomarea</i> cf. <i>floribunda</i> (H.B.K.) Herb.	0.0	0.0	0.0	0.0	0.0	12.5	2
Apiaceae							
<i>Cyclospermum leptophyllum</i> (Pers.) Sprague	8.3	23.1	18.9	18.2	16.7	18.8	18
<i>Daucus montanus</i> Humb. & Bonpl. ex Spreng.	0.0	0.0	0.0	9.1	16.7	12.5	5
Asclepiadaceae							
<i>Ditassa longiloba</i> Benth.	0.0	0.0	13.5	0.0	33.3	50.0	17
Asteraceae							
<i>Achyrocline bogotensis</i> (H.B.K.) DC.	0.0	38.5	59.5	18.2	66.7	18.8	40
<i>Alloispermum caracasum</i> (H.B.K.) H.Rob.	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Baccharis macrantha</i> H.B.K.	50.0	61.5	83.8	100.0	83.3	43.8	73
<i>Baccharis rupicola</i> H.B.K.	0.0	7.7	13.5	9.1	33.3	50.0	19
<i>Bidens pilosa</i> L.	8.3	23.1	0.0	0.0	0.0	0.0	4
<i>Bidens rubifolia</i> H.B.K.	0.0	0.0	0.0	0.0	25.0	56.3	12
<i>Bidens triplinervia</i> H.B.K.	58.3	92.3	54.1	27.3	33.3	6.3	47
<i>Chaptalia excelsa</i> (Pers.) Baker	75.0	69.2	64.9	18.2	33.3	0.0	48
<i>Chromolaena bullata</i> (Klatt) R.King & H.Rob.	0.0	0.0	0.0	0.0	41.7	25.0	9
<i>Chromolaena leivensis</i> (Hieron.) R.King & H.Rob.	75.0	30.8	94.6	81.8	100.0	62.5	79
<i>Conyza</i> sp.	0.0	0.0	2.7	0.0	0.0	0.0	1
<i>Conyza uliginosa</i> (Benth.) Cuatrec.	8.3	7.7	5.4	0.0	16.7	0.0	6
<i>Galinsoga quadriradiata</i> Ruiz & Pav.	0.0	0.0	2.7	9.1	0.0	0.0	2
<i>Gamochaeta spicata</i>	50.0	53.8	10.8	9.1	16.7	0.0	20
<i>Gnaphalium</i> sp. 1	16.7	15.4	59.5	9.1	66.7	37.5	41
<i>Gnaphalium</i> sp. 2	8.3	61.5	5.4	0.0	8.3	0.0	12
<i>Hieracium avilae</i> H.B.K.	0.0	0.0	2.7	0.0	0.0	0.0	1
<i>Hypochaeris radicata</i> L.	50.0	100.0	35.1	27.3	41.7	0.0	40
<i>Hypochaeris sessiliflora</i> H.B.K.	0.0	15.4	10.8	0.0	8.3	0.0	7
<i>Laennecia filaginoides</i> DC.	41.7	0.0	2.7	18.2	0.0	0.0	8
<i>Laestadia muscicola</i> Sch.Bip. ex Wedd.	58.3	84.6	32.4	0.0	25.0	0.0	33
<i>Lourteigia stoechadifolia</i> (L.f.) R.M. King & H. Rob	0.0	0.0	0.0	0.0	8.3	18.8	4
<i>Mikania laurifolia</i> Willd.	0.0	0.0	0.0	0.0	8.3	0.0	1
<i>Noticastrum marginatum</i> (H.B.K.) Cuatrec.	58.3	61.5	40.5	0.0	16.7	0.0	32
<i>Pentacalia americana</i> (L.f.) Cuatrec.	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Praxelis pauciflora</i> (H.B.K.) R.M.King & H.Rob.	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Psilactis brevilingulata</i> Sch.Bip. ex Hemsl.	8.3	0.0	0.0	9.1	0.0	0.0	2
<i>Schkuhria pinnata</i> (Lam.) Cabrera	75.0	23.1	0.0	0.0	0.0	0.0	12
<i>Sonchus oleraceus</i> L.	0.0	0.0	0.0	9.1	0.0	0.0	1
<i>Stevia lucida</i> Lag.	25.0	7.7	83.8	72.7	91.7	62.5	64
<i>Stevia rhombifolia</i> H.B.K.	0.0	7.7	5.4	0.0	25.0	0.0	6
<i>Stevia serrata</i> Cav.	8.3	23.1	5.4	18.2	16.7	0.0	10
<i>Tagetes zipaquirensis</i> Humb. & Bonp.	0.0	7.7	2.7	0.0	0.0	6.3	3
<i>Taraxacum officinale</i> Weber ex F.H. Wigg.	0.0	7.7	0.0	18.2	0.0	0.0	3
<i>Vasquezia anemonifolia</i> (H.B.K.) S.F.Blake	66.7	23.1	13.5	9.1	0.0	0.0	17
Asteraceae indet.	0.0	0.0	0.0	9.1	8.3	6.3	3

	<i>Micr</i> grassl. Ia	<i>Anth</i> grassl. Ib	<i>Bacc-</i> <i>Dodo</i> IIa	<i>Dalea</i> scrub IIb	<i>Myrs-</i> <i>Dodo</i> IIIa	dwarf forest IIIb	total occ.
Basellaceae							
<i>Anredera brachystachys</i> (Moq.) Sperling	0.0	0.0	0.0	18.2	8.3	18.8	6
Boraginaceae							
<i>Cordia cylindrostachya</i> (Ruiz & Pav.) Roem. &	0.0	0.0	5.4	27.3	33.3	50.0	17
Brassicaceae							
<i>Halimolobos hispidula</i> (DC.) O.Schulz	0.0	0.0	0.0	0.0	0.0	12.5	2
<i>Lepidium trianae</i> Thell.	16.7	0.0	2.7	45.5	0.0	6.3	9
<i>Raphanus sativus</i> L.	0.0	7.7	0.0	0.0	0.0	0.0	1
Bromeliaceae							
<i>Puya</i> sp.	0.0	0.0	2.7	0.0	33.3	12.5	7
<i>Tillandsia biflora</i> Ruiz & Pavón	0.0	0.0	10.8	0.0	0.0	18.8	7
<i>Tillandsia incarnata</i> H.B.K.	0.0	0.0	18.9	18.2	58.3	81.3	29
<i>Tillandsia usneoides</i> (L.) L.	0.0	0.0	2.7	9.1	25.0	43.8	12
<i>Tillandsia</i> sp. 1	0.0	0.0	5.4	45.5	91.7	87.5	32
<i>Tillandsia</i> sp. 2	0.0	0.0	0.0	0.0	0.0	6.3	1
Cactaceae							
<i>Opuntia schumanii</i>	0.0	0.0	16.2	18.2	0.0	18.8	11
<i>Opuntia</i> sp.	0.0	0.0	2.7	0.0	0.0	0.0	1
Campanulaceae							
<i>Lobelia</i> sp.	8.3	0.0	0.0	0.0	0.0	0.0	1
Caryophyllaceae							
<i>Arenaria lanuginosa</i> (Michx.) Rohrb.	0.0	15.4	29.7	18.2	33.3	12.5	21
<i>Cardionema multicaule</i> DC.	33.3	0.0	0.0	0.0	0.0	0.0	4
<i>Paronychia bogotensis</i> Triana & Planch.	0.0	0.0	10.8	9.1	16.7	12.5	9
<i>Scleranthus annuus</i> L.	16.7	0.0	2.7	0.0	0.0	0.0	3
<i>Silene gallica</i> L.	0.0	7.7	0.0	0.0	0.0	0.0	1
<i>Spergula arvensis</i> L.	0.0	0.0	0.0	9.1	8.3	0.0	2
<i>Spergularia villosa</i> (Pers.) Camb.	16.7	0.0	0.0	0.0	0.0	0.0	2
Chenopodiaceae							
<i>Chenopodium</i> sp.	0.0	0.0	0.0	9.1	0.0	0.0	1
Commelinaceae							
<i>Tripogandra multiflora</i> (Sw.) Raf.	33.3	0.0	40.5	36.4	66.7	50.0	39
Convolvulaceae							
<i>Dichondra argentea</i> Humb. & Bonpl. ex Willd.	8.3	15.4	0.0	0.0	0.0	0.0	3
<i>Evolvulus bogotensis</i> Oostr.	41.7	0.0	54.1	27.3	50.0	12.5	36
Crassulaceae							
<i>Echeveria bicolor</i> (H.B.K.) E. Walther	0.0	0.0	35.1	54.5	75.0	93.8	43
Crassulaceae indet.	0.0	0.0	0.0	0.0	0.0	6.3	1

	<i>Mier</i> grassl. Ia	<i>Anth</i> grassl. Ib	<i>Bacc-</i> <i>Dodo</i> IIa	<i>Dalea</i> scrub IIb	<i>Myrs-</i> <i>Dodo</i> IIIa	dwarf forest IIIb	total occ.
Cyperaceae							
<i>Bulbostylis</i> aff. <i>funckii</i> (Steud.) C.B. Clarke	33.3	38.5	48.6	0.0	25.0	0.0	30
<i>Carex bonplandii</i> H.B.K.	0.0	0.0	8.1	0.0	0.0	0.0	3
<i>Eleocharis dombeyana</i> H.B.K.	0.0	0.0	0.0	9.1	0.0	0.0	1
<i>Fuirena incompleta</i> Nees	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Rhynchospora nervosa</i> (Vahl) Boeck.	25.0	69.2	89.2	36.4	100.0	56.3	70
<i>Rhynchospora</i> sp.	50.0	69.2	40.5	18.2	50.0	18.8	41
Elaeocarpaceae							
<i>Vallea stipularis</i> L.f.	0.0	0.0	0.0	0.0	0.0	6.3	1
Ericaceae							
<i>Gaultheria erecta</i> Vent.	0.0	0.0	2.7	0.0	0.0	0.0	1
<i>Pernettya prostrata</i> (Cav.) DC.	0.0	0.0	0.0	0.0	0.0	6.3	1
Euphorbiaceae							
<i>Chamaesyce thymifolia</i> (L.) Millsp.	8.3	53.8	27.0	9.1	58.3	0.0	26
<i>Croton bogotanus</i> Cuatrec.	0.0	0.0	8.1	0.0	50.0	43.8	16
Fabaceae							
<i>Dalea coerulea</i> (L.f.) Schinz & Thell.	0.0	0.0	10.8	100.0	8.3	18.8	19
<i>Desmodium molliculum</i> (H.B.K.) DC.	16.7	15.4	75.7	45.5	100.0	81.3	62
<i>Dioclea sericea</i> H.B.K.	0.0	0.0	0.0	0.0	16.7	12.5	4
<i>Medicago lupulina</i> L.	16.7	7.7	0.0	0.0	0.0	0.0	3
<i>Medicago polymorpha</i> L.	16.7	7.7	0.0	9.1	0.0	0.0	4
<i>Spartium junceum</i> L.	0.0	0.0	2.7	9.1	0.0	0.0	2
<i>Trifolium pratense</i> L.	0.0	30.8	5.4	0.0	0.0	0.0	6
<i>Trifolium repens</i> L.	16.7	30.8	13.5	18.2	0.0	0.0	13
<i>Vicia graminea</i> Sm.	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Zornia diphylla</i> (L.) Pers.	41.7	0.0	37.8	0.0	16.7	0.0	21
Flacourtiaceae							
<i>Xylosma spiculifera</i> (Tul.) Triana & Planch.	0.0	0.0	13.5	9.1	83.3	93.8	31
Geraniaceae							
<i>Pelargonium</i> sp.	0.0	0.0	0.0	0.0	0.0	6.3	1
Hypericaceae							
<i>Hypericum mexicanum</i> L.	0.0	0.0	2.7	0.0	0.0	0.0	1
<i>Hypericum silenoides</i> Juss.	33.3	69.2	27.0	0.0	16.7	0.0	25
<i>Hypericum</i> sp.	0.0	0.0	8.1	9.1	8.3	6.3	6
Hypoxidaceae							
<i>Hypoxis humilis</i> H.B.K.	16.7	7.7	18.9	9.1	8.3	0.0	12
Iridaceae							
<i>Sisyrinchium chilense</i> Hook.	25.0	30.8	2.7	0.0	0.0	0.0	8
Juncaceae							
<i>Juncus capillaceus</i> Lam.	33.3	0.0	13.5	27.3	8.3	6.3	14
<i>Juncus tenuis</i> Willd.	0.0	0.0	0.0	0.0	0.0	12.5	2

	<i>Micr</i> grassl. Ia	<i>Anth</i> grassl. Ib	<i>Bacc-</i> <i>Dodo</i> IIa	<i>Dalea</i> scrub IIb	<i>Myrs-</i> <i>Dodo</i> IIIa	dwarf forest IIIb	total occ.
Lamiaceae							
<i>Salvia amethystina</i> J.E.Sm	0.0	0.0	0.0	0.0	16.7	0.0	2
<i>Salvia palaeifolia</i> H.B.K.	0.0	0.0	27.0	18.2	41.7	62.5	27
<i>Stachys bogotensis</i> H.B.K.	0.0	0.0	5.4	0.0	0.0	0.0	2
Liliaceae							
<i>Anthericum humboldtii</i> Henst.	0.0	0.0	0.0	0.0	8.3	0.0	1
Lythraceae							
<i>Cuphea serpyllifolia</i> H.B.K.	33.3	69.2	91.9	54.5	100.0	75.0	77
Malvaceae							
<i>Gaya bermannoides</i> H.B.K.	0.0	0.0	0.0	0.0	25.0	18.8	6
<i>Modiola caroliniana</i> (L.) G.Don	8.3	0.0	0.0	18.2	0.0	0.0	3
<i>Pavonia sepium</i> A.St.Hil.	0.0	0.0	0.0	0.0	0.0	6.3	1
Melastomataceae							
<i>Bucquetia glutinosa</i> (L.f.) DC.	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Chaetolepis microphylla</i> (Bonpl.) Miq.	8.3	0.0	13.5	0.0	25.0	0.0	9
<i>Miconia squamulosa</i> (H.Karst. ex Triana)	0.0	0.0	18.9	0.0	25.0	81.3	23
Mimosaceae							
<i>Acacia decurrens</i> Willd.*	8.3	7.7	5.4	18.2	0.0	6.3	7
Myricaceae							
<i>Morella pubescens</i> (Humb. & Bonpl. ex Willd.)	0.0	0.0	2.7	0.0	16.7	0.0	3
Myrsinaceae							
<i>Myrsine guianensis</i> (Aublet) Kuntze	0.0	0.0	62.2	36.4	100.0	100.0	55
Myrtaceae							
<i>Myrcianthes leucocyla</i> (Ortega) McVaugh	0.0	0.0	0.0	0.0	33.3	62.5	14
Oenotheraceae							
<i>Oenothera multicaulis</i> Ruiz & Pavón	25.0	46.2	21.6	9.1	0.0	0.0	18
<i>Oenothera</i> sp.	16.7	7.7	0.0	9.1	0.0	0.0	4
Orchidaceae							
<i>Aa colombiana</i> Schltr.	0.0	23.1	2.7	0.0	8.3	6.3	6
<i>Cyclopogon elatus</i> (Sw.) Schltr.	0.0	7.7	10.8	36.4	16.7	37.5	17
<i>Epidendrum elongatum</i> Jacq.	0.0	0.0	21.6	45.5	58.3	43.8	27
<i>Epidendrum</i> sp.	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Habenaria</i> sp.	0.0	0.0	2.7	0.0	0.0	0.0	1
<i>Odontoglossum ramulosum</i> Lindl.	0.0	0.0	18.9	0.0	66.7	50.0	23
<i>Pleurothallis</i> sp.	0.0	0.0	0.0	0.0	0.0	12.5	2
<i>Stelis</i> sp.	0.0	0.0	5.4	0.0	0.0	12.5	4
<i>Telipogon nervosus</i> (L.f.) Druce	0.0	0.0	0.0	0.0	16.7	18.8	5
Orchidaceae indet. 1	0.0	7.7	2.7	0.0	0.0	0.0	2
Orchidaceae indet. 2	0.0	0.0	2.7	27.3	0.0	12.5	6
Orchidaceae indet. 3	0.0	7.7	2.7	9.1	8.3	12.5	6

	Micr grassl. Ia	Anth grassl. Ib	Bacc- Dodo IIa	Dalea scrub IIb	Myrs- Dodo IIIa	dwarf forest IIIb	total occ.
Oxalidaceae							
<i>Oxalis corniculata</i> Lourt.	58.3	76.9	70.3	0.0	66.7	18.8	54
<i>Oxalis</i> sp.	0.0	0.0	2.7	0.0	0.0	0.0	1
Passifloraceae							
<i>Passiflora bogotensis</i> Benth.	0.0	0.0	48.6	27.3	75.0	75.0	42
Piperaceae							
<i>Peperomia galioides</i> H.B.K.	0.0	0.0	5.4	45.5	58.3	93.8	29
<i>Peperomia microphylla</i> H.B.K.	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Peperomia rotundata</i> var. <i>rotundata</i> H.B.K.	0.0	0.0	2.7	0.0	25.0	68.8	15
<i>Piper bogotense</i> C. DC.	0.0	0.0	0.0	0.0	0.0	6.3	1
Plantaginaceae							
<i>Plantago linearis</i> H.B.K.	66.7	23.1	13.5	36.4	16.7	0.0	22
Poaceae							
<i>Aegopogon cenchroides</i> Humb. & Bonpl. ex Willd.	0.0	46.2	48.6	0.0	33.3	18.8	31
<i>Anthoxanthum odoratum</i> L.	0.0	76.9	48.6	9.1	33.3	43.8	40
<i>Aristida laxa</i> Cav.	91.7	69.2	91.9	36.4	100.0	37.5	76
<i>Bothriochloa saccharoides</i> (Sw.) Rydb.	50.0	15.4	43.2	27.3	41.7	0.0	32
<i>Bouteloua simplex</i> Lag.	41.7	0.0	0.0	9.1	0.0	0.0	6
<i>Brachypodium distachyon</i> L.	16.7	0.0	5.4	9.1	0.0	6.3	6
<i>Bromus catharticus</i> Vahl.	0.0	0.0	2.7	0.0	16.7	6.3	4
<i>Bromus pitensis</i> H.B.K.	0.0	0.0	2.7	0.0	8.3	0.0	2
<i>Chloris submutica</i> H.B.K.	33.3	15.4	10.8	9.1	8.3	0.0	12
<i>Cortaderia bifida</i> Pilg.	0.0	0.0	5.4	0.0	0.0	6.3	3
<i>Dichanthelium viscidellum</i> (Scribn.) Gould	0.0	7.7	8.1	9.1	0.0	0.0	5
<i>Elionurus</i> sp.	0.0	0.0	5.4	0.0	25.0	25.0	9
<i>Eragrostis intermedia</i> Hitchc.	66.7	7.7	37.8	36.4	41.7	18.8	35
<i>Eragrostis pastoensis</i> (H.B.K.) Trin.	0.0	0.0	5.4	18.2	0.0	0.0	4
<i>Eragrostis tenuifolia</i> (A.Rich.) Hochst. ex Steud.	41.7	53.8	59.5	18.2	75.0	6.3	46
<i>Holcus lanatus</i> L.	0.0	0.0	8.1	0.0	16.7	6.3	6
<i>Jarava ichu</i> Ruiz & Pav.	16.7	15.4	45.9	81.8	83.3	62.5	50
<i>Lycurus phalaroides</i> H.B.K.	58.3	30.8	75.7	45.5	91.7	12.5	57
<i>Microchloa kunthii</i> Desv.	91.7	23.1	21.6	0.0	8.3	0.0	23
<i>Nassella mucronata</i> (H.B.K.) R.Pohl	25.0	7.7	24.3	36.4	41.7	6.3	23
<i>Panicum</i> sp.	8.3	0.0	10.8	0.0	8.3	0.0	6
<i>Paspalum pilgerianum</i> Chase	33.3	7.7	16.2	0.0	41.7	12.5	18
<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	100.0	84.6	75.7	90.9	33.3	50.0	73
<i>Piptochaetium panicoides</i> (Lam.) E. Desv.	66.7	46.2	43.2	9.1	33.3	6.3	36
<i>Schizachyrium tenerum</i> Nees	0.0	0.0	5.4	9.1	8.3	0.0	4
<i>Setaria parviflora</i> (Poir.) Kerguelén	50.0	76.9	35.1	18.2	83.3	31.3	46
<i>Sporobolus indicus</i> (L.) R.Br.	66.7	23.1	29.7	36.4	16.7	12.5	30
<i>Trachypogon plumosus</i> (Humb. & Bonpl. ex Willd.)	0.0	0.0	5.4	9.1	16.7	6.3	6
<i>Tripogon spicatus</i> (Nees) Ekman	33.3	0.0	5.4	0.0	0.0	0.0	6
Poaceae indet.	8.3	0.0	10.8	0.0	8.3	18.8	9
Polygalaceae							
<i>Monnina obtusifolia</i> H.B.K.	0.0	0.0	35.1	72.7	58.3	100.0	44
<i>Polygala paniculata</i> L.	50.0	76.9	45.9	18.2	50.0	0.0	41

	<i>Micr</i> grassl. Ia	<i>Anth</i> grassl. Ib	<i>Bacc-</i> <i>Dodo</i> IIa	<i>Dalea</i> scrub IIb	<i>Myrs-</i> <i>Dodo</i> IIIa	dwarf forest IIIb	total occ.
Polygonaceae							
<i>Muehlenbeckia tamnifolia</i> (H.B.K.) Meissner	0.0	0.0	2.7	18.2	0.0	12.5	5
<i>Polygonum aviculare</i> L.	0.0	0.0	0.0	9.1	0.0	0.0	1
<i>Rumex acetosella</i> L.	8.3	61.5	24.3	0.0	0.0	12.5	20
Primulaceae							
<i>Anagallis arvensis</i> L.	8.3	7.7	0.0	9.1	0.0	0.0	3
Rhamnaceae							
<i>Condalia thomasi</i> Fernández-Alonso	0.0	0.0	16.2	9.1	66.7	81.3	28
Rosaceae							
<i>Hesperomeles goudotiana</i> (Decne.) Killip	0.0	23.1	43.2	18.2	66.7	68.8	40
<i>Lachemilla aphanoides</i> (Mutis ex L.f.) Rothm.	0.0	53.8	16.2	0.0	8.3	0.0	14
<i>Lachemilla orbiculata</i> (Ruiz & Pavón) Rydb.	0.0	0.0	0.0	0.0	0.0	6.3	1
<i>Margyricarpus pinnatus</i> (Lam.) Kuntze	83.3	100.0	83.8	81.8	66.7	31.3	76
<i>Rubus guianensis</i> Focke	0.0	0.0	0.0	0.0	0.0	6.3	1
Rosaceae indet.	0.0	0.0	2.7	0.0	0.0	0.0	1
Rubiaceae							
<i>Borreria anthospermoides</i> DC.	33.3	84.6	89.2	0.0	91.7	43.8	66
<i>Galium aschenbornii</i> Schauer	0.0	0.0	18.9	18.2	50.0	25.0	19
<i>Galium corymbosum</i> Ruiz & Pavón	0.0	7.7	5.4	0.0	16.7	12.5	7
<i>Galium mexicanum</i> H.B.K.	0.0	0.0	0.0	0.0	0.0	18.8	3
<i>Galium obovatum</i> H.B.K.	0.0	0.0	2.7	0.0	50.0	68.8	18
<i>Ptychotria bogotensis</i> Standl.	0.0	0.0	2.7	0.0	50.0	81.3	20
Sapindaceae							
<i>Dodonaea viscosa</i> Jacq.	8.3	7.7	81.1	27.3	100.0	68.8	58
Scrophulariaceae							
<i>Alonsoa meridionalis</i> (L.f.) Kuntze	0.0	0.0	8.1	0.0	16.7	6.3	6
<i>Castilleja arvensis</i> Schltdl. & Cham.	0.0	0.0	5.4	0.0	16.7	0.0	4
<i>Castilleja fissifolia</i> L.f.	0.0	0.0	18.9	9.1	58.3	50.0	23
<i>Castilleja integrifolia</i> L.f.	0.0	7.7	13.5	0.0	8.3	0.0	7
<i>Mecardonia procumbens</i> (Mill.) Small	8.3	30.8	16.2	18.2	0.0	0.0	13
Solanaceae							
<i>Cestrum tomentosum</i> L.f.	0.0	0.0	2.7	0.0	8.3	50.0	10
<i>Lycianthes lyciodes</i> (L.) Hassl.	0.0	0.0	5.4	54.5	16.7	31.3	15
<i>Solanum nigrescens</i> Martens & Gal.	0.0	0.0	2.7	18.2	0.0	25.0	7
Urticaceae							
<i>Parietaria debilis</i> Forster	0.0	0.0	2.7	0.0	0.0	0.0	1
Verbenaceae							
<i>Duranta mutisii</i> L.f.	0.0	0.0	5.4	9.1	33.3	75.0	19
<i>Lantana boyacana</i> Moldenke	66.7	23.1	62.2	100.0	66.7	43.8	60
<i>Lippia hirsuta</i> L.f.	0.0	0.0	0.0	0.0	8.3	18.8	4
<i>Verbena litoralis</i> H.B.K.	33.3	15.4	0.0	9.1	0.0	0.0	7
<i>Verbena trifida</i> H.B.K.	0.0	7.7	8.1	9.1	8.3	0.0	6

Vegetation patterns and succession

	<i>Micr</i> grassl. Ia	<i>Anth</i> grassl. Ib	<i>Bacc-</i> <i>Dodo</i> IIa	<i>Dalea</i> scrub IIb	<i>Myrs-</i> <i>Dodo</i> IIIa	dwarf forest IIIb	total occ.
Violaceae							
<i>Hybanthus parviflorus</i> (Mutis ex L.f.) Baill.	0.0	0.0	13.5	9.1	8.3	6.3	8

Chapter 3.

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

J.P. Groenendijk, J.F. Duivenvoorden, N. Rietman, and A.M. Cleef, in press, *Plant Ecology*

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 relevés in grassland and shrubland types in different stages of recovery, and in relatively little disturbed endemic *Condalia thomasi* 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 coerulea* 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 coerulea* 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 thomasi* (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.

Table 3.1. Initially hypothesized successional affinity of the "restoration species".

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

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 relevés to obtain the data on vegetation structure and diversity. We applied sequential aerial photograph interpretation to infer the disturbance history of the revee 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.

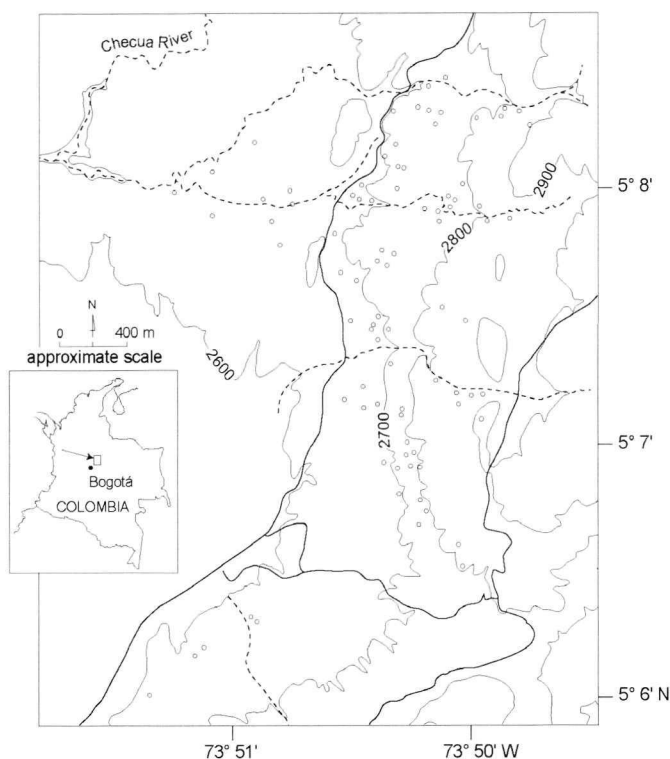


Figure 3.1. Locations of the vegetation relevés in the study area, indicated by circles.

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* – *Condaliatum*, or “*Condalia* forest”, by Van der Hammen (1997). It reaches heights up to

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*, *Anthoxanthum 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 releves 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 NH_4OAc (pH = 7), and quantified by atomic absorption spectrophotometry. Contents of available Ca, Mg, K, and Na were summed to obtain total available bases (TB). Organic C was oxidized by $\text{K}_2\text{Cr}_2\text{O}_7$ in acid medium (Walkley-Black method) and measured by titration with $\text{Fe}(\text{NH}_4)_2(\text{SO}_4)_2$. Cation exchange capacity (CEC) was measured in 1N NH_4OAc (pH = 7).

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*: $\geq$ 5% cover of low (< 1.5 m) shrubs, and < 5% cover of higher woody plants; *high shrubland*: $\geq$ 5% cover of high ($\geq$ 1.5 m) shrubs, and $\geq$ 10% overall woody cover; *dwarf forest*: $\geq$ 5% tree cover, and $\geq$ 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

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 $z = b_0 + b_1 \cdot [\text{expl. var. 1}] + \dots + b_8 \cdot [\text{expl. var. 8}]$

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 relevées. Variance Inflation Factors (VIF's) did not exceed 2.5.

Results

In the 101 relevées, 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 relevées, 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. coerulea*, although showing an increase in frequency towards dwarf forest, was least often found in dwarf forest relevées 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.

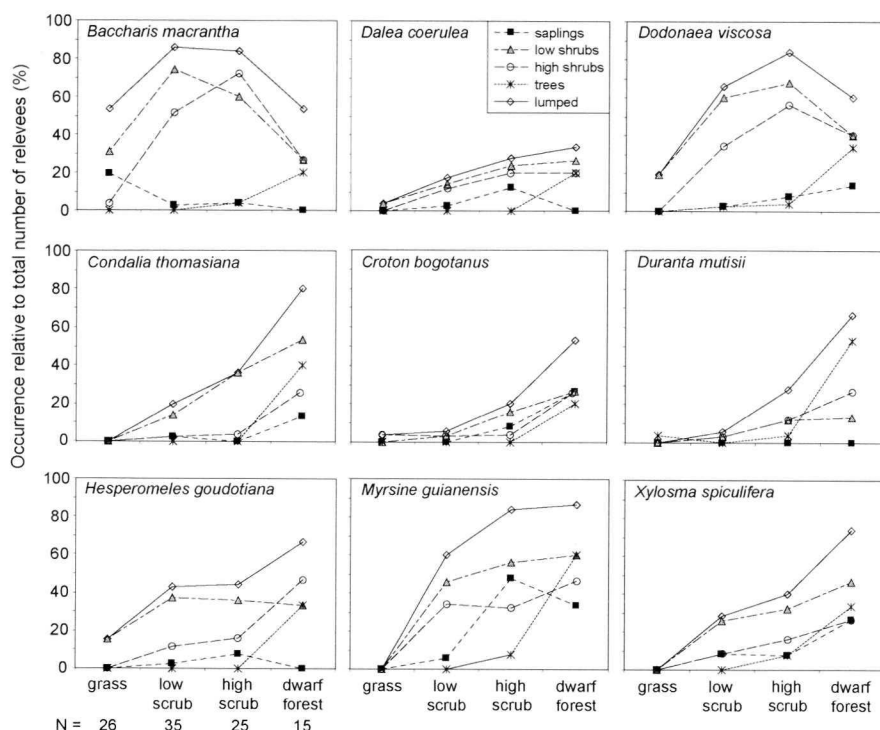


Figure 3.2. Fraction of occurrences of juveniles, low shrubs, high shrubs, trees and all stages lumped, in the four structural vegetation types, for each of the nine restoration species.

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 relevés. Especially *M. guianensis*, but also *C. bogotanus* and *X. spiculifera*, were represented with saplings mostly in high scrub and dwarf forest.

The χ^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 χ^2 -test for independence of total (lumped) occurrences of the species in the four structural vegetation types.

	χ^2	<i>p</i>
<i>Baccharis macrantha</i>	11.96	0.008
<i>Dalea coerulea</i>	7.33	0.062
<i>Dodonaea viscosa</i>	23.76	0.000
<i>Condalia thomasiana</i>	32.33	0.000
<i>Croton bogotanus</i>	21.64	0.000
<i>Duranta mutisii</i>	33.83	0.000
<i>Hesperomeles goudotiana</i>	11.33	0.010
<i>Myrsine guianensis</i>	46.59	0.000
<i>Xylosma spiculifera</i>	25.43	0.000

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 *unstability* (containing empty cells only) were omitted.

	PC soil texture	PC soil chemistry	grazing period	development	degradation	stability	unstability
H'	-0.152	0.086	-0.331	0.224	-0.060	-0.248	0.040
PC soil texture (clayey soils)		0.368	0.005	-0.052	0.023	-0.064	0.095
PC soil chemistry (high nutr. & org. C)			-0.384	0.163	-0.021	-0.113	-0.045
grazing period				-0.088	0.114	0.032	-0.008
development					-0.200	-0.391	-0.507
degradation						-0.168	-0.218
stability							-0.427

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 thomasiana*, *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. thomasiana*, *C. bogotanus*, *M. guianensis* and *X. spiculifera*, and marginally so for *D. coerulea*. Only *C. thomasiana* showed a significant positive response to Shannon's H' . Six species showed a significantly negative association with grazing period: *D. viscosa*, *C. thomasiana*, *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.

	<i>H'</i>	soil PCs		grazing period	develop- ment	degra- dation	stability
		clayey texture	high cont. nutr., C _{org}				
<i>Baccharis macrantha</i>	0.161 -	0.041 +	0.786 +	0.173 -	0.261 +	0.904 +	0.594 +
<i>Dalea coerulea</i>	0.478 +	0.005 +	0.065 +	0.783 -	0.874 +	0.806 +	0.217 +
<i>Dodonaea viscosa</i>	0.673 -	0.310 -	0.193 -	0.000 -	0.161 -	0.541 +	0.194 +
<i>Condalia thomasiana</i>	0.016 +	0.000 -	0.007 +	0.022 -	0.951 -	0.330 -	0.461 -
<i>Croton bogotanus</i>	0.070 +	0.026 -	0.019 +	0.378 -	0.344 +	0.624 +	0.140 +
<i>Duranta mutisii</i>	0.264 +	0.049 -	0.438 +	0.050 -	0.068 -	0.243 -	0.326 -
<i>Hesperomeles</i>	0.290 +	0.248 +	0.598 +	0.009 -	0.130 -	0.402 -	0.433 -
<i>Myrsine guianensis</i>	0.132 +	0.101 -	0.040 +	0.000 -	0.090 -	0.920 +	0.664 -
<i>Xylosma spiculifera</i>	0.512 +	0.286 -	0.045 +	0.002 -	0.420 -	0.175 -	0.417 -

X. spiculifera. 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 macrantha* 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 mutisii*, *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

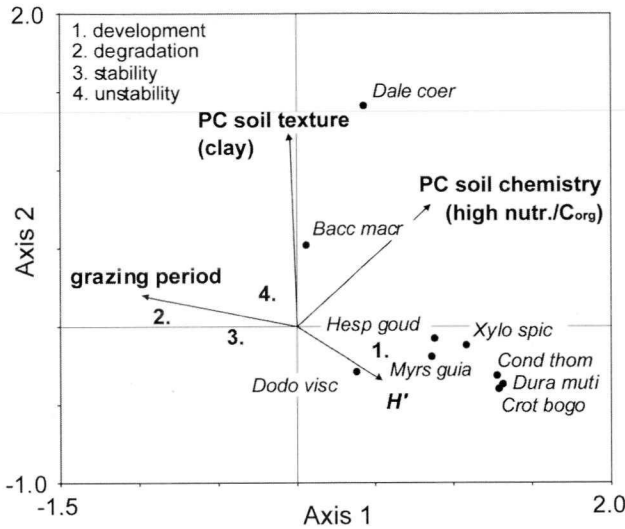


Figure 3.3. CCA ordination diagram displaying the nine restoration species and explanatory variables. Species are indicated by dots, with truncated names. Centroids of the nominal disturbance history variables were plotted as numbers, as indicated above-left.

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.

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

Although *Dalea coerulea* 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 reveeues. 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 reveeues, and to the single reveeue the description by Van der Hammen (1997) was based on.

Secondly, the remaining three species, *Hesperomeles gondotiana*, *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 relevés. 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. gondotiana*, *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. coerulea* 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. Cavellier 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 Wessenbeeck *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.

Acknowledgments

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Chapter 4.

Role of soil seed bank in recovery of semi-arid Andean forests in Colombia

J.P. Groenendijk, M. van der Linden, J. Struik, and J.F. Duivenvoorden, submitted to *Basic and Applied Ecology*

Abstract

Soil seed banks of five vegetation types (grassland, low scrub, high scrub, dwarf forest, and plantation forest) were studied in a semi-arid part of the Colombian Andes, in order to assess the potential for regeneration of the mature (native) dwarf forest. Seeds in soil samples taken at 0-5 and 5-10 cm were allowed to germinate in a greenhouse for a period of 12 weeks. A total of 22429 germinated seeds were recorded, represented by 110 species, which were classified according to their growth form and position in the successional series of the vegetation in the area. Seeds from woody late-successional species were hardly recorded in pioneer vegetation types, where artificial seed supply or seedling plantation seems the best way to accelerate natural regeneration. Especially in grasslands, the only woody species abundantly found in the soil seed bank was *Baccharis macrantha*, an important species of the first woody stages of succession. Pioneer shrubs that act as perch or shelter deserve attention in conservation management in severely degraded areas.

Introduction

Drylands in the tropics generally have suffered more human population pressure than the humid tropics, and hence most of their ecosystems have been severely altered (Aronson *et al.* 2002; Aronson *et al.* 1993; Murphy & Lugo 1986). Because of the diminishing productivity and changing economic incentives, much formerly (over-) exploited land in Latin America has nowadays been abandoned and has become available for recovery of natural woody vegetation (Aide *et al.* 1995). The (semi-)arid Andean zones, in addition, have particularly few remnants of natural vegetation due to high population pressure and are susceptible to erosion (Coppus *et al.* 2003). Restoration of the nowadays highly threatened Andean forests is an urgent objective in many parts of Latin America, in terms of conservation of biodiversity and of valuable ecosystem functions, mainly water and soil protection.

In many cases, lack of ecological knowledge of the local ecosystem composition and processes hampers restoration and rehabilitation. Assessment of the capacity of a landscape or ecosystem to recover without human efforts is an important preliminary step in vegetation restoration. Natural vegetation succession is often limited 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), and hence plantation or other means to jump-start successions might be necessary.

Recruitment by plants of available sites is driven either by soil seed banks or by recently dispersed seed. Since seeds from nearby forest often reach the soil within tens of meters (Cubiña & Aide 2001), soil seed banks are often the main determinants of secondary vegetation composition. Composition and density of soil seed banks are influenced by different factors related to human disturbance. Fragmentation of surrounding forest acting as seed sources also reportedly affects seed availability on a given site (Nepstad *et al.* 1991; Gorchoy *et al.* 1993; Guevara & Laborde 1993; Vieira *et al.* 1994). Agricultural practices have been shown to strongly affect soil seed banks (Quintana-Ascencio *et al.* 1996; Wijdeven & Kuzee 2000; Moffatt & McLachlan 2003).

The semi-arid valley of the Checua River in the Colombian Andes – an affluent of the Bogotá River, and important for the water supply of the high plain of Bogotá – has particularly few remnants of natural little disturbed vegetation. Many parts have been abandoned due to a declining agricultural productivity caused by drought, loss of soil fertility and erosion. Moreover, parts of the area have been afforested with *Acacia decurrens*, which nowadays show a very poor recovery in terms of biodiversity and ecological functions. The restoration of the original endemic, and nowadays nearly extinct *Condalia* dwarf forest is a goal of the natural resource authority Corporación Autónoma Regional de Cundinamarca (CAR).

In this study, we evaluated the potential role of soil seed banks in contributing to the regeneration of early and late secondary woody vegetation in dry Andean forests. Because of the heavy fragmentation and reduction of the dwarf forest area, and hence scarcity of seed sources, we expected woody plant taxa to be poorly represented in secondary vegetation. The following questions were addressed: To what degree are early and late secondary woody species represented in the seed bank of young secondary vegetation types? Is the richness of woody taxa in the seed bank at a given site related to the composition of the surrounding or locally standing vegetation? To answer these questions, we sampled soil seed banks in abandoned pastures, secondary scrubs, dwarf forests and *Acacia* forests, and compared these with the local woody standing vegetation.

Methods

Study site

The fieldwork area is at the edge of the high plain of Bogotá, an intramontane basin in the Eastern Cordillera of Colombia (Figure 4.1). It concerns a part of the Checua River valley, affluent to the Bogotá River, situated within the community of Suesca, Cundinamarca. The height above sea level of the study area is between 2550 and 2950 m. The area receives about 700 mm of annual rainfall, generally concentrated in two short rainy periods. Evapotranspiration approximates 1050 mm, leading to an annual deficit of about 350 mm (Claro-Rizo 1995). The mean annual temperature is around 13°C (Van der Hammen 1998).

The study area is a mosaic landscape of grassland, scrub, and fragments of dwarf forest. Five vegetation types were selected for our research.

1. Grassland: pasture co-dominated by *Pennisetum clandestinum*, and either *Anthoxanthum odoratum* or *Microchloa kunthii*.
2. Low scrub: open, low (~1 m) shrub vegetation co-dominated by *Baccharis macrantha* and *Dodonaea viscosa*.
3. High scrub: dense, high (~2 m) shrub vegetation co-dominated by *Dodonaea viscosa* and *Myrsine guianensis*, with a low aboveground cover (generally < 5%) of some late-successional woody species, e.g., *Hesperomeles goudotiana*, *Myrsine guianensis*, and *Xylosma spiculifera*.
4. Dwarf forest: relatively little disturbed forest of about 4-5 m height, characterized by the small trees *Condalia thomasiana* – endemic to the Checua Valley (Fernández-Alonso 1997) – *Croton bogotanus*, *Duranta mutisii*, *Hesperomeles goudotiana*, *Myrsine guianensis*, and *Xylosma spiculifera*. This forest was described as *Xylosmo* – *Condaliatum*, or "Condalia forest", by Van der Hammen (1997).

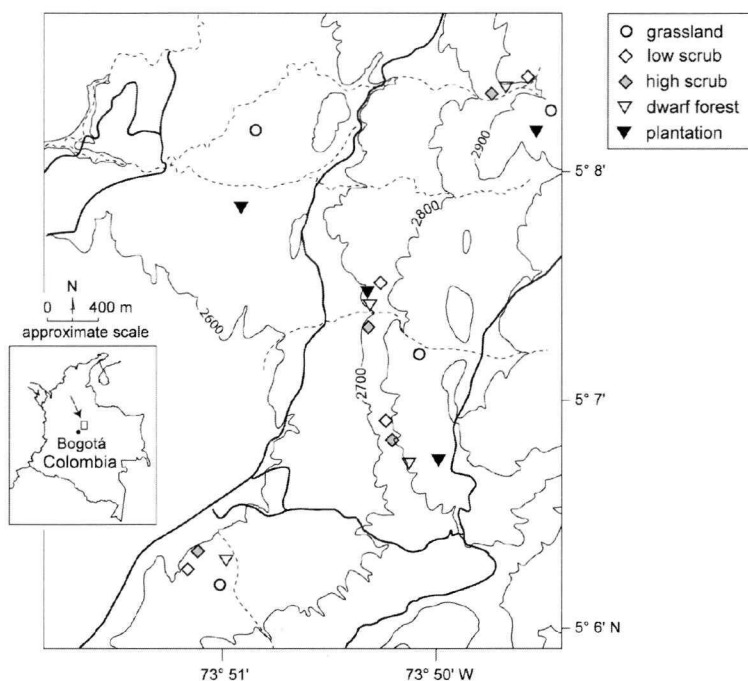


Figure 4.1. Locations of the soil seed bank sampling sites in the study area, indicated by symbols according to the vegetation types.

5. *Acacia* forests: plantation of *Acacia decurrens*, established between 1980-1984. The undergrowth in these forests is poorly developed. The aboveground cover of woody non-planted species remains well below 10%, and total herbaceous cover is generally less than 30%.

Soil and vegetation sampling

In November 2001, in each of the five vegetation types four plots of 30 x 30 m were laid out widely distributed over the area (Figure 4.1). The sides of the plots were situated parallel to the contour lines. In each plot five random points were chosen under the restriction that all points were at least 4 m apart from each other. Around each point, three soil samples of 9 x 9 cm were taken at 0-5 cm and 5-10 cm depth, and pooled for each depth. The litter layer (if present) was included in the upper soil sample. The plot altitude ranged between 2635 and 2912 m above sea level.

A vegetation plot of 70 x 70 m was laid out over each seed bank plot, in such a way that the centres of vegetation and seed bank plots coincided and their sides were parallel. In the vegetation plot, the aboveground cover of woody plant species was recorded. The cover of scrub (low and high shrub vegetation types combined) and dwarf forest surrounding the seed bank plots was estimated on aerial photographs from 1991 (scale 1:10,000, black & white, panchromatic). For this, circles with 200 and 500 m dia-

meters were projected on each seed bank plot. The vegetation cover was then estimated applying a grid overlay of square cells, each corresponding to 25 x 25 m in the field.

Germination in greenhouse

Germination trials were conducted in a ventilated greenhouse, located in a nearby village (Nemocón). A black polypropylene shade cloth, reducing solar radiation by 75%, was installed under the roof. The soil samples were sieved through a sieve of 4.0 mm mesh width to remove branches, leaves, and stones. Seeds or fruits bigger than 4.0 mm - e.g. from *Myrsine guianensis* and *Condalia thomasiana* - were removed from the residual and added to the substrate. Subsequently, the samples were washed over a sieve of 0.19 mm mesh width to reduce their volume, since the period of seedling emergence increase with the thickness of the sample layer when spread out in the trays (Bakker *et al.* 1996). Immediately after this, the sample was thoroughly mixed and split up in two equal parts. One part was gently rubbed with a brick for 20 times, in order to break physical dormancy which is reportedly common in dry woodland shrub seeds (Baskin & Baskin 1998). The other part received no such treatment. Both the rubbed and untreated parts of all samples were - separately - spread out in 22 x 27 x 5 cm shallow plastic trays, after having filled these with sterile potting soil (so-called Fafard Canadian growing mix with Canadian *Sphagnum* peat moss) topped by a 5 mm layer of sterile white sand. The layer of sterile white sand prevented contact between the sample and the potting soil. The bottom of the trays was perforated to drain and air the soil. Additionally, eight control trays were filled with potting soil, the layer of white sand and again a layer of potting soil, in order to detect possible seed contamination from the surroundings of the greenhouse. The total of 408 trays (20 plots x 5 samples x 2 depths x 2 treatments + 8 control) were placed randomly in the greenhouse, and were watered daily. The seeds were allowed to germinate for a period of 12 weeks (December 2001 - March 2002). During this period the number of vascular plant seedlings in each tray was counted weekly. Most seedlings had emerged after 6 weeks. In order to reduce competition, seedlings were removed after identification, or transplanted to a separate pot for later identification. The species identification of the seedlings was made easier by means of a reference seedling collection, grown (in the greenhouse) from seeds collected in the study area during fieldwork. The position of each species in the secondary succession was defined by means of a local vegetation study (Groenendijk *et al.* in press, see Chapter 3). The following categories were distinguished: pioneer (39 species), rural (or weedy) (18 species), late-successional (15 species), unknown (33 species), and planted (*Acacia decurrens*, *Eucalyptus globulus*, *Pinus patula*).

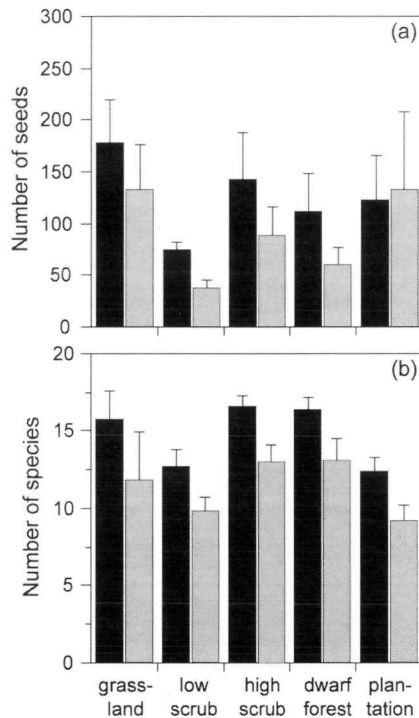


Figure 4.2. Persistent seed bank properties at 0-5 cm and 5-10 cm depth in different vegetation types. a) Average number of germinated seeds per 243 cm². b) Average number of vascular plants species in germinated seeds per 243 cm². Bars represent $\pm$ one standard error from 4 plots per vegetation type. Data from individual plots were averages taken from 5 samples per plot.

Data processing

Per species a paired t-test was used to test for differences in the number of germinated seeds due to the brick rubbing treatment. For nearly all species the rubbing treatment had no significant effect on the germination. Only the seeds from *Dichondra* cf. *evolvulacea* germinated better after rubbing. The numbers of seedlings from rubbed and not rubbed samples were summed in further analyses. Spearman rank correlations were calculated between woody species seed abundance and cover of scrub or forest surrounding the plots. Analyses were done with JMP 3.0 for the Macintosh.

Results

General properties of the germinating seeds

In total, 22429 germinating seeds were counted in the trays, represented by 110 species of which 66 were fully identified (see Appendix). Ten species were counted more than 500 times in the trays. The most abundant species were *Mecardonia procumbens*, and *Hypericum silenoides*, with 3140 and 2744 germinating seeds, respectively. A total of 87 species were found with more than 5 seedlings. Of these, two species (*Hypoxis humilis* and *Lycianthes lycioides*) emerged exclusively in the 0-5 cm soil samples (classified as transient after Thompson *et al.*(1997)), 66 species emerged in majority in the 0-5 cm soil samples (short-term persistent), and another 21 species occurred mostly in the 5-10 soil samples (long-term persistent). Seedlings of *Gamochaeta* sp. (296 seedlings) and *Sonchus oleraceus* (13 seedlings) emerged also in the control trays. These two species and the two transient species were deleted from further analyses.

The average abundance of germinated seeds found in 243 cm² at 0-5 cm varied between 180 in grasslands to 76 in low scrub (Figure 4.2a). On average, between 16.7 and 12.6 vascular species were found at 0-5 cm depth (Figure 4.2b). At 5-10 cm depth the abundance and species richness was generally about 20-45% lower than at 0-5 cm soil depth.

Germinating seeds by species group and growth form

On the basis of all plots at 0-10 cm depth, an average of 56% of the seeds were from pioneer species, 17% from rural (weeds), 4% from late-successional, 22% from unknown, and less than 1% from the planted species group. On average, 90% of the seeds in plots at 0-10 cm depth belonged to herbs, 9% to shrubs, and less than 1% to the remaining forms. A total of 12 species in the seed bank samples were woody (shrub and tree growth forms).

Pioneer herbs dominated the seed bank of all vegetation types regarding seed abundance and species diversity (Figure 4.3a, c). Seeds from late-successional species, both herbaceous and woody, occurred far less abundantly and with lower diversity. These species were least abundantly found in the seed bank of pioneer communities (grassland and low scrub) and plantation forests, and were best represented in dwarf forests (Figure 4.3a-d). Seeds from woody pioneers were mostly found in scrub and dwarf forest, and to a lesser degree in grasslands and plantation forests. In the grassland plots only seeds from two pioneer shrubs (*Baccharis macrantha*, *Chromolaena leivensis*) were found (Table 4.1).

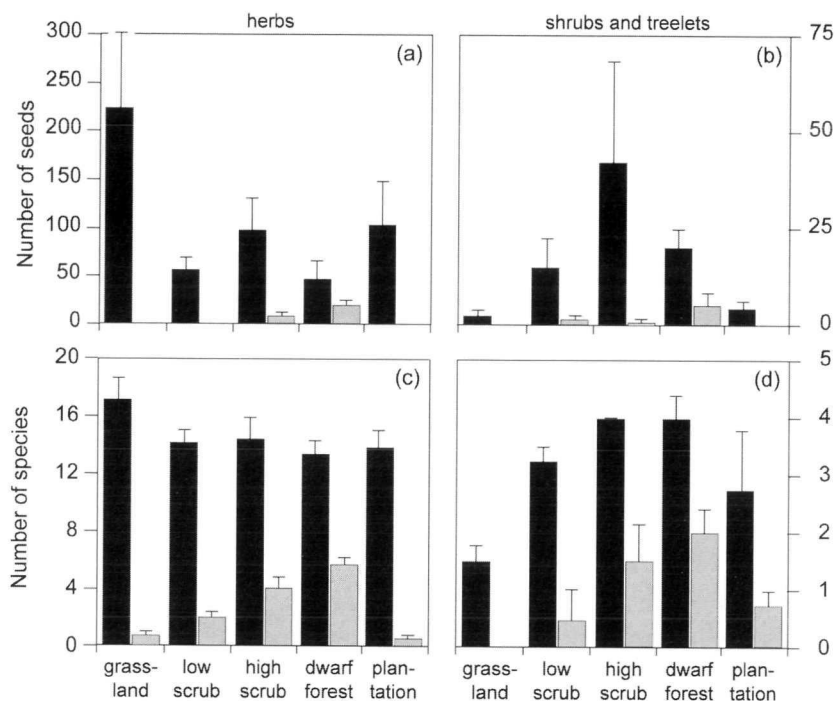


Figure 4.3. Persistent seed bank properties at 0-10 cm depth in different vegetation types for herbs and woody (shrub and tree) species. a) Average number of germinated seeds in 243 cm². b) Average number of vascular plant species in germinated seeds in 243 cm². Bars represent +/- one standard error from 4 plots per vegetation type. Data from individual plots were averages taken from 5 samples per plot.

Woody late-successional species in seed bank and standing vegetation

Many woody late-successional species that were recorded in the standing vegetation were lacking in the seed bank (Table 4.2). *Hesperomeles goudotiana* was the only exception. This species was recorded in the seed bank of just 2 plots from the 13 where it was recorded as small tree or shrub. In contrast, the wind-dispersed pioneer shrubs encountered in this study were generally present in both the seed bank and the standing vegetation. Moreover, most of these species were occasionally found in the soil seed bank, while absent above-ground. Four woody species (*Physalis peruviana*, *Gaya hermannoides*, *Solanum nigrum*, and *Ageratina gracilis*) were found in seed bank, but not in the standing vegetation. The species most abundantly found in the standing vegetation (*Baccharis macrantha*, *Chromolaena leivensis*, and *Dodonaea viscosa*) showed a significant positive correlation between above-ground plant cover and numbers of seeds in the local seed bank.

Table 4.1. Abundance of germinated seeds per 243 cm² at 0–10 cm for woody (shrub and tree) species. Shown are non-zero averages and 1 standard deviation (between brackets) from 4 plots per vegetation type. *N* is the total number of plots where species were recorded in the seed bank.

	grasslands	low scrub	high scrub	dwarf forest	plantation	<i>N</i>
pioneer						
<i>Baccharis macrantha</i>	2.6 (3.4)	12.4 (13.2)	38.2 (52.8)	16.1 (8.5)	3.9 (3.8)	20
<i>Baccharis rupicola</i>				0.1 (0.1)	0.1 (0.1)	3
<i>Chromolaena leivensis</i>	0.2 (0.2)	1.3 (0.8)	2.7 (1.8)	2.5 (2.0)	0.7 (0.9)	16
<i>Stevia lucida</i>		1.2 (1.9)	0.5 (0.3)	0.5 (0.5)	0.1 (0.1)	11
<i>Dodonea viscosa</i>		0.5 (0.5)	1.1 (0.7)	1.5 (1.0)	0.1 (0.1)	12
rural						
<i>Physalis peruviana</i>			0.1 (0.1)	2.0 (2.0)	0.1 (0.1)	6
late-successional						
<i>Gaya hermanoides</i>			0.3 (0.3)	0.2 (0.3)		4
<i>Miconia squamulosa</i>		0.2 (0.3)	0.1 (0.1)		0.1 (0.1)	3
<i>Hesperomeles goudotiana</i>				0.3 (0.3)		2
<i>Solanum nigrum</i>		1.3 (2.5)	0.9 (1.0)	5.0 (6.5)	0.4 (0.5)	10
unknown position						
<i>Ageratina</i> cf. <i>gracilis</i>				1.0 (1.9)		2
planted in plantation						
<i>Acacia decurrens</i>			0.2 (0.3)		8.4 (9.8)	5

This also applied to *Acacia decurrens*. For none of the woody late-successional species was the seed abundance at 0–10 cm associated to the cover of scrub or forests within distances of 200 or 500 m surrounding the plots.

Discussion

Seeds from woody late-successional species hardly available in pioneer vegetation

Woody late-successional species were hardly found in the seed bank of grassland or low scrub, or in that of the *Acacia* plantation. Our study confirmed observations that soil seed banks are often largely dominated by pioneer species, even relatively long after these species have disappeared from the standing vegetation (Quintana-Ascencio *et al.* 1996; Grandin 2001; De Villiers *et al.* 2003). Therefore it seems that settlement of late-successional species in pioneer and plantation communities highly depends on seed dispersal events, as is well known from the humid lowlands in the tropics (Nepstad *et al.* 1991; Gorchoy *et al.* 1993). However, the dispersal from nearby forests into areas of secondary vegetation often covers only short distances (Aide & Cavellier 1994; Holl 1999; Cubiña & Aide 2001). Perches might increase seed dispersal rates of animal-dispersed

Table 4.2. Woody species found in standing vegetation and persistent soil seed bank at 0-10 cm. The asterisk (*) indicates significant ($p < 0.05$) positive Spearman correlation coefficients between plant cover in plots and number of seeds in seed bank.

species	seed dispersal mode	number of plots with species		
		only as plant	in seed bank and as plant	only in seed bank
pioneer				
<i>Baccharis macrantha</i> *	Anemochory	0	18	2
<i>Baccharis rupicola</i>	Anemochory	14	2	1
<i>Chromolaena leivensis</i> *	Anemochory	3	16	0
<i>Dodonaea viscosa</i> *	Anemochory	5	11	1
<i>Stevia lucida</i>	Anemochory	4	8	3
rural				
<i>Physalis peruviana</i>	Endozoochory	0	0	6
late-successional				
<i>Condalia thomasiiana</i>	Endozoochory	10	0	0
<i>Croton bogotanus</i>	Autochory	11	0	0
<i>Dalea coerulea</i>	Barochory	3	0	0
<i>Duranta mutisii</i>	Endozoochory	6	0	0
<i>Gaya bermanoides</i>	Barochory	0	0	4
<i>Hesperomeles goudotiana</i>	Endozoochory	11	2	0
<i>Miconia squamulosa</i>	Endozoochory	11	3	0
<i>Monnina</i> sp.	Endozoochory	12	0	0
<i>Myrciantes leucoxyla</i>	Endozoochory	4	0	0
<i>Myrica</i> sp.	?	4	0	0
<i>Myrsine guianensis</i>	Endozoochory	17	0	0
<i>Psychotria bogotensis</i>	Endozoochory	2	0	0
<i>Solanum nigrum</i>	Endozoochory	0	0	10
<i>Xylosma spiculiferum</i>	Endozoochory	12	0	0
unknown				
<i>Ageratina gracilis</i>	Anemochory	0	0	2
planted				
<i>Acacia decurrens</i> *	Barochory	3	5	0
<i>Eucalyptus globulus</i>	Barochory	1	0	0
<i>Pinus patula</i>	Anemochory/Barochory	6	0	0

species into large patches of open vegetation (Guevara & Laborde 1993; Holl 1998). Successful dispersal events into areas of open pioneer vegetation do not guarantee subsequent establishment and growth. Many late-successional species in general are supposed to have short seed longevities (Fenner 1987; Chapin III 1993). On top of that, severe agricultural disturbances of the soil form an extra factor exhausting seed banks (Guariguata & Ostertag 2001; Quintana-Ascencio *et al.* 1996; Moffatt & McLachlan 2003; Wijdeven & Kuzee 2000). Even when a seed bank is present, recovery might still be hampered by soil properties (*e.g.*, nutrient status, compaction), drought, lack of mycorrhizae, and competition with exotic grasses.

Seed dormancy and greenhouse errors

The optimal germination conditions for many tropical species, especially those restricted to semi-arid zones, are not known. The conditions in the greenhouse may not have favoured germination of many seeds. Also, some seeds may take a lengthy period of time to germinate (Brown 1992). Knowledge on the dormancy type of seeds from especially the woody species found in this study is hardly available. Physical dormancy, though, is reported for *Dalea coerulea* (Baskin & Baskin 1998), *Acacia decurrens* (Beadle 1940) and *Dodonaea viscosa* (Burrows 1995). In spite of this, the brick rubbing treatment had no effect on the germination of the later two species. Also physiological dormancy might occur (*Solanum nigrum*; Baskin and Baskin (1998)). It seems therefore likely that seeds from more species would have germinated if greenhouse conditions would have been more variable, or if the incubation time would have been longer than the 3 months applied in the present study.

Notwithstanding the above considerations we have confidence in the obtained seed bank patterns. Some seeds from the reference collection (e.g., *Croton bogotanus* and *Xylosma spiculiferum*) germinated in the greenhouse, but did not do so in the sample trays, and were safely assumed to be absent from the seed bank samples. Also the observed seed densities were quite comparable to other studies in the tropics. Garwood (1989) and Wijdeven and Kuzee (2000) reported average grassland densities of around 4200 and 4900 seeds/m², respectively, which is even lower than the average density of 7400 seeds/m² found in the grasslands near Checua. In mature forests, these authors found averages of 3700 and 400 seeds/m², respectively, which is of the same magnitude as the dwarf forest average of 4700 seeds/m² in the current study.

Recommendations for vegetation recovery

Given the scarcity of woody late-successional species in the soil seed bank at most sites, and especially in grasslands and low scrub where vegetation recovery (in biomass and diversity) is most urgent, artificial seed supply or seedling plantation could provide the onset to natural regeneration that might never be accomplished under natural conditions. In high scrub, the seed bank starts to contain seeds from species that typically occur in mature dwarf forests. This corresponds to observations that more seedlings from late-successional species occurred in scrub and dwarf forest vegetation than in grasslands (Chapter 3 of this thesis). It reduces the need for enrichment planting with such taxa. Weed control in high scrub would probably enhance the survival of the seedlings from these woody late-successional species.

Especially in grasslands, the only woody species abundantly found in the soil seed bank was *Baccharis macrantha*. This is an important species of the first woody stages of secondary development in the study area (Chapter 3 of this thesis). In grasslands it is often found as seedling. Shrubs of *Baccharis* and *Dodonaea*, genera with several wind

dispersed species that are dominant in pioneer communities in many parts of the dry Andes, might act as perch or shelter for small seed dispersing birds and mammals. Such shrubs and scrub vegetation types deserve attention in conservation management in severely degraded areas (Vieira *et al.* 1994).

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Appendix 4.1. List of vascular plant species found as seeds in soil samples.

Amaranthaceae*Iresine diffusa* Humb. & Bonpl. ex Willd**Apiaceae**cf. *Daucus***Asteraceae***Ageratina* cf. *gracilis* (HBK) R.M. King & H.
Rob.*Asteraceae* sp. 1, 2*Baccharis macrantha* HBK*Baccharis ripicola* HBK*Bidens rubifolia* HBK*Bidens triplinervia* HBK*Gamochaeta* sp.*Chromolaena leivensis* (Hieron.) R. King & H.
Rob.*Chromolaena* sp.*Coryza* sp.*Gnaphalium* sp.*Hypochoeris radicata* L.*Laenecia filaginoides* DC.*Noticastrum marginatum* (HBK) Cuatrec.*Schkura pinnata* (Lam.) Cabrera*Sonchus oleraceus* L.*Stevia lucida* Lag.*Vasquezia anemoneifolia* (HBK) S.F. Blake**Basellaceae***Anredera brachystachys* (Moq.) Sperling**Brassicaceae***Halimolobos hispidula* (DC.) O. Schulz*Lepidium bipinnatifidum* Desv.*Lepidium trianae* Thell.**Caryophyllaceae***Arenaria* cf. *lanuginosa* (Michx.) Rohrb.*Cardionema multicaule* DC.*Cerastium vulgatum* L.*Drymaria corrata* (L.) Willd. ex Schult.*Paronychia bogotensis* Triana & Planch.*Sagina* sp.*Silene gallica* L.*Silene* sp.*Spergularia villosa* (Pers.) Camb.**Chenopodiaceae***Chenopodium* sp.**Commelinaceae***Tripogandra multiflora* (Sw.) Raf.**Convolvulaceae***Dichondra* cf. *evolvulacea* (L.f.) Britton**Crassulaceae***Echeveria bicolor* (HBK) E. Walther**Cyperaceae***Carex* sp.1, 2**Euphorbiaceae***Chamaesyce thymifolia* (L.) Millsp.**Fabaceae***Desmodium* sp.*Trifolium pratense* L.*Trifolium repens* L.*Zornia diphylla* (L.) Pers.**Hypericaceae***Hypericum silenoides* Juss.**Hypoxidaceae***Hypoxis humilis* HBK**Iridaceae***Sisyrinchium chilense* Hook.**Juncaceae***Juncus* sp.*Juncus tenuis* Willd.**Lamiaceae***Stachys bogotensis* HBK**Lythraceae***Cuphea serpyllifolia* HBK**Malvaceae***Gaya hermanoides* HBK*Modiola caroliniana* (L.) G. Don**Melastomataceae***Miconia squamulosa* (H Karst. ex Triana)

Triana

Mimosaceae*Acacia decurrens* Willd.**Oenotheraceae***Oenothera multicaulis* Ruiz & Pav.**Oxalidaceae***Oxalis corniculata* Lourt.*Oxalis* sp. 2**Passifloraceae***Passiflora bogotensis* Benth.**Phytolaccaceae***Phytolacca bogotensis* HBK**Piperaceae***Peperomia* sp.

Chapter 4

Plantaginaceae

Plantago linearis HBK

Poaceae

Aristida laxa Cav.

Botriochloa saccharoides (Sw.) Rydb.

Brachypodium dystachion (L.) P. Beauv.

Jarava ichu Ruiz & Pav.

Paspalum sp.

Piptochaetium setifolium Presl.

cf. *Schizachyrium tenerum* Nees

Setaria geniculata P. Beauv.

Sporobolus indicus (L.) R. Br.

Poaceae 16 spp.

Polygonaceae

Rumex acetosella L.

Rumex obtusifolius L.

Primulaceae

Anagallis arvensis L.

Rosaceae

Hesperomeles goudotiana (Ruiz & Pav. ex
Lindl) Hook

Lachemilla sp.

Margyricarpus pinnatus (Lam.) Kuntze

Rubiaceae

Borreria anthospermoides DC.

Galium sp. 1-4

Sapindaceae

Dodonea viscosa Jacq.

Scrophulariaceae

Alonsoa meridionalis (L.f.) Kuntze

Castilleja sp.

Mecardonia precumbens (Mill.) Small

Nuttallanthus subandinus (Diels) D.A. Sutton

Veronica pergrina (HBK) St. John & Warren

Solanaceae

Lycianthes lcyioides (L.) Hassl.

Physalis peruviana L.

Solanum nigrum L.

Verbenaceae

Verbena littoralis HBK

Unidentified

indet. 81

Chapter 5.

Planting pioneers and late-successional species in abandoned dry Andean pastures and scrubs: prospects for restoration

J.P. Groenendijk and J.F. Duivenvoorden, submitted to *Forest Ecology and Management*

Abstract

The results of a plantation experiment with native woody species in the Eastern Cordillera of the Andes, Colombia, are presented. We hypothesized that planted seedlings of native woody pioneers would perform best in open pastures, and that planted seedlings of late-successional shrub and tree species would perform better in shrubland. Additionally, we evaluated the effect of treatments with stones and fertilizer on seedling performance. Moreover, we expected natural succession in the matrix vegetation to be accelerated as an effect of canopy establishment by planted species. Plantation with species mixtures of pioneers, and of late-successional species, were applied in both pastures and shrublands. Seedling performance and matrix vegetation development was monitored from 2000 to 2004. Survival was low for some species, probably caused by drought and night frost. Seedling growth was generally low: pioneer species reached stem heights up to around 1 m, while the late-successional species mostly did not grow significantly. Stone treatments enhanced survival for most species, while the fertilizer addition increased stem growth for late-successional species. A canopy of planted seedlings was established only with pioneer species planted in pastures. In these plots, species turnover rate did not differ from that of control plots. We concluded that pioneer shrubs performed better in pastures than in shrublands. Late-successional species survived better in pastures, but stem growth was higher in shrublands. Stones and fertilizer treatments enhance survival and/or growth rates for a number of species. Changes in species composition were not an effect of the planted canopy. However, total herb cover in these plots did increase as an effect of the plantation. We concluded that succession can possibly be accelerated by a planted canopy, but more time is needed to be able to detect successional changes as an increased turnover, different species composition and invasion of typical late-successional species. It is recommended to use mixtures of pioneer and late-successional species in future plantation trials.

Introduction

Although spontaneous succession has been successful at some sites (Hodacova & Prach 2003; Prach *et al.* 2001), the "let-nature-take-its-course" way of restoring native vegetation has proven to be an unsatisfactory option for many disturbed sites. Secondary succession is often either too slow (Parrotta *et al.* 1997b), or takes a non-desired course (Sarmiento 1997; Gibson & Brown 1992). To accelerate and control the course of secondary succession, technologies based on ecological theories should be conducted (Goosem & Tucker 1995; Golley 1999; Hardwick *et al.* 2004). Plantation of trees, leading to a woody canopy, may accelerate natural succession by permitting typical forest species to establish (Lamb *et al.* 1997). On the other hand, species could be suppressed or even become locally extinct as a consequence of woody canopy establishment.

Natural regeneration of many native vegetation types around the world is often hindered by competition with exotic grasses (Cabin *et al.* 2002; D'Antonio *et al.* 1998), cattle grazing (Hendrix *et al.* 1988), or altered soil properties (Olff *et al.* 1997). Moreover, many late-successional woody species have large seeds with reportedly very short dispersal distances (Aide & Cavellier 1994; Cubiña & Aide 2001), strongly hampering their recruitment of available sites (Wunderle 1997). Perches have increased rates of bird-dispersed seed dispersal (Shiels & Walker 2003; Holl 1998), although these have not been applied in large-scale restoration designs.

Prior to executing a restoration attempt, it is important to gain basic knowledge on habitat requirements of desired species, growing site characteristics of the desired vegetation type, and propagule dispersal abilities (Hardwick *et al.* 2004). Previous vegetation research in our study area (Groenendijk *et al.* in press, see Chapter 3) pointed out that the most important woody species of the climax dwarf forest mostly occur – besides the dwarf forests – in relatively developed secondary scrubs, rarely in open low scrubs, and not in pastures. These species most probably are limited by seed dispersal, and hardly form seed banks either in dwarf forest or in any secondary vegetation (Groenendijk *et al.* in prep., see Chapter 4). Seedlings of these species were rarely found in vegetation surveys, and mostly restricted to developed scrubs and dwarf forest (Groenendijk *et al.* in press, see Chapter 3). The classic facilitation model (Connell & Slatyer 1977) would predict that habitat conditions impede early establishment and growth of these late-successional species. On the other hand, establishment could be merely limited by propagule supply, growth requirements for seedlings being sufficient even in open scrubs or in pastures. In the latter case, artificial insertion of seedlings of these species – even in recently abandoned open fields – may lead to successful introduction.

In this paper we report on the first four years of a succession-based restoration experiment in a semi-arid Andean valley, nowadays nearly deprived of native *Condalia* dwarf forest and suffering from severe erosion. Investigating both the performance of planted seedlings and the development of the existing vegetation, we hypothesized that:

1) seedlings of planted late-successional species perform better in shrublands than in pastures, 2) seedlings of planted pioneer species perform better in pastures than late-successional species, 3) additional treatments compensating environmental stress weaken the expected differences of the first and second hypotheses, 4) establishment of a planted shrub canopy in pastures and open scrubs accelerates succession, 5) species turnover rates will be higher in pastures than in shrublands.

We planted both pioneer shrubs and late-successional shrubs and treelets in pastures and in open shrubby vegetation. The latter is the least developed scrub type in the area, dominated by the pioneer shrubs *Baccharis macrantha* and *Dodonaea viscosa* (Groenendijk & Cleef in prep.; Van der Hammen 1997; Groenendijk *et al.* in press, see Chapters 2 and 3). After reporting on performance of planted seedlings in the different experimental series, we investigated differences in successional indicators of the matrix vegetation in the plots where a woody canopy of planted seedlings was established. Succession, defined as a directional temporal change in species composition or relative abundances (Pickett & McDonnell 1989), is expressed in species turnover rates, changing species composition, changes in vegetation structure, and (woody) species establishment and extinction.

Methods

Study area

The fieldwork area is at the edge of the high plain of Bogotá, an intramontane basin in the Eastern Cordillera of Colombia (Figure 5.1). It concerns a part of the Checua River valley, affluent to the Bogotá River, situated within the municipality of Suesca, Cundinamarca. The height above sea level of the study area is between 2550 and 2950 m.

The zone receives about 700 mm of annual rainfall, generally concentrated in two short rainy periods. Evapotranspiration approximates 1050 mm annually, leading to a deficit of about 350 mm (Claro-Rizo 1995). The mean annual temperature is around 13°C (Van der Hammen 1998). During dry periods, night frost frequently occurs.

The area has a hilly terrain morphology. Most of the hills are built up by sandstones belonging to the Guadalupe Formation (Cretaceous). 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 sites show a natric B horizon primarily containing clay, organic material, and

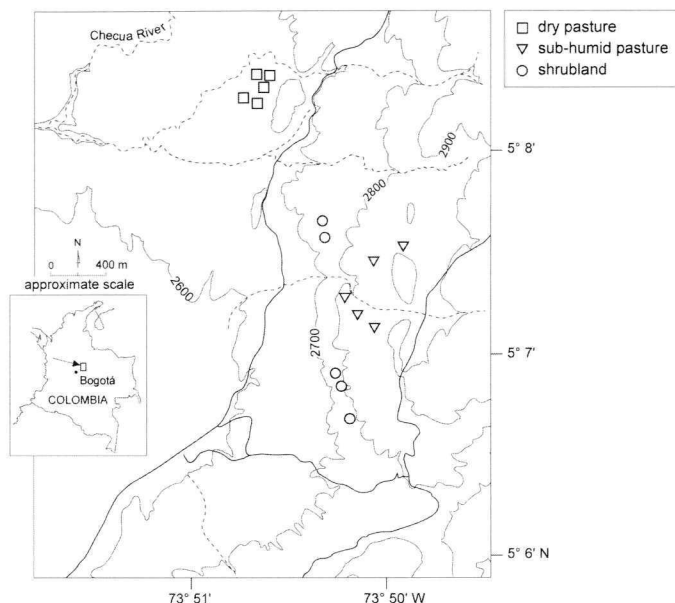


Figure 5.1. Locations of the clusters of experimental plots in the study area, indicated by symbols according to the matrix vegetation type.

sodium. 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. However, in the higher parts of the hills, where more humid conditions prevail, this horizon is often found. Slope deposits and fine alluvial caps have caused local variations in soil properties.

The study area is a mosaic landscape of grassland, scrubs, planted exotics' forest, and fragments of dwarf forest (Groenendijk & Cleef in prep., see Chapter 2). The dry andean dwarf forest was described as *Xylosmo – Condaliatum*, or “*Condalia* forest”, by Van der Hammen (1997). One of the characteristic treelets, *Condalia thomasiana* (Rhamnaceae), is a recently discovered endemic of this particular zone (Fernández-Alonso 1997). Disturbances have been common and severe, and exotic grasses have large cover values. Plantations with exotics - mostly *Acacia decurrens* - 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 1997, 1998); pers. obs.).

Plantation species

Nine species of shrubs and treelets were selected for this experiment. All of these are native to the *Condalia* dwarf forest zone and commonly found there in woody pioneer stands and/or in late-successional dwarf forest patches. Their successional

Table 5.1. Numbers of individuals of woody species planted per plot, as applied in the different mixtures. Average stem length per species is given, with standard deviations between brackets. Ph = sub-humid pasture; Pd = dry pasture; S = shrubland.

species	family	successio- nal affinity	individuals per plot		initial stem length (cm)
			pioneer mixture		late-succ. mixture
			Pd	Ph, S	Pd, Ph, S
Pioneer mixture					
<i>Baccharis macrantha</i>	Asteraceae	pioneer	63	94-95	32.8 (9.0)
<i>Dalea coerulea</i>	Fabaceae	pioneer	63		41.1 (36.0)
<i>Dodonaea viscosa</i>	Sapindaceae	pion.-mid	63	94-95	17.2 (7.3)
Late-successional mixture					
<i>Condalia thomasiana</i>	Rhamnaceae	late			15 9.5 (5.3)
<i>Croton bogotanus</i>	Euphorbiaceae	late			40 27.1 (21.1)
<i>Duranta mutisii</i>	Verbenaceae	late			40 32.7 (14.2)
<i>Hesperomeles goudotiana</i>	Rosaceae	mid-late			14 16.3 (16.3)
<i>Myrsine guianensis</i>	Myrsinaceae	mid-late			40 5.0 (2.3)
<i>Xylosma spiculifera</i>	Flacourtiaceae	mid-late			40 25.0 (8.1)

affinity was investigated by Groenendijk *et al.* (in press, see Chapter 3), and is summarized in Table 5.1. *Dodonaea viscosa* was categorized as a mid-successional species, but was included in the pioneer mixture because it is mostly co-dominant with *Baccharis macrantha* in pioneer scrubs. Similarly, *Hesperomeles goudotiana*, *Myrsine guianensis* and *Xylosma spiculifera* were classified as mid-successional, but were included in the late-successional plantation mixture because of their frequent co-occurrence with the three other species of that mixture in dwarf forest patches. We chose to plant greenhouse-grown seedlings in stead of sowing seeds, thus skipping the germination stage in which most plant species are vulnerable.

Seeds of all species were collected from the vegetation present at the study site. The plant material for the initial planting was produced in two different nurseries owned by the Corporación Autónoma Regional de Cundinamarca (CAR). Plantlets received applications of fertilizers and fungicides on a regular basis during the production and maintenance period in the nurseries. At the moment of plantation in the field, the seedlings were in 707 cm³ nursery bags. *D. coerulea* was grown in bags with a volume of 2389 cm³.

Experimental design

Three vegetation types were selected for this research: two types of abandoned pastures, and a scrub type representing the least developed, low-stature woody stage (Groenendijk & Cleef in prep., see Chapters 2 and 3; Groenendijk *et al.* in press). The non-planted vegetation will hereafter be referred to with the term "matrix vegetation".

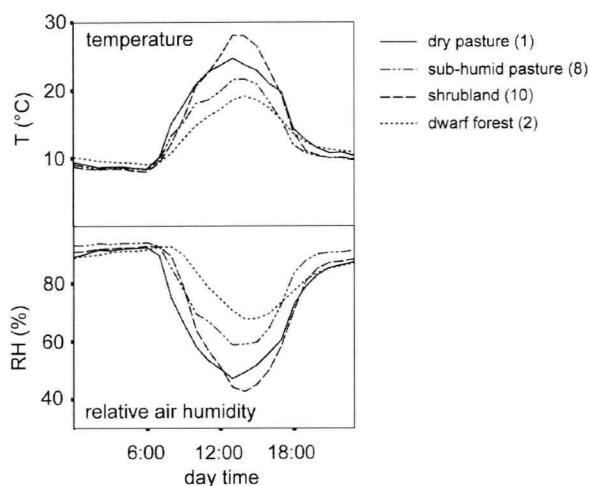


Figure 5.2. Temperature and relative air humidity during the day, at 10 cm above ground level in the three vegetation types selected for the plantation experiment, and in dwarf forest. Lines indicate the average over the number of dataloggers per vegetation types (between brackets), and over the days from 28 November to 11 December 2000.

Dry pasture (Pd): low, open pasture co-dominated by *Pennisetum clandestinum* and *Microblosa kunthii*. Sparse presence of woody Asteraceae (mostly *Baccharis macrantha* and *Stevia lucida*), but with a cover of < 1%. The soils shows a natric B horizon under a strongly leached hardpan, sometimes topped with a cap of alluvial sand (< 5 cm). Around 35% of the surface was bare soil, and the height of the vegetative parts of the herb layer generally did not surpass 10 cm.

Sub-humid pasture (Ph): pasture co-dominated by *Pennisetum clandestinum* and *Anthoxanthum odoratum*, found near or at the summit of the hills. Cover of < 1% of *B. macrantha* and other shrubs. Soils also have a natric B horizon, but the upper horizon is darker and a hardpan has mostly not developed. Bare soil cover was around 20%, and herbaceous vegetative height was about 10 cm.

Shrubland (S): open, low scrub co-dominated by *Baccharis macrantha* and *Dodonaea viscosa*. Cover of the shrub layer is 8 – 17%, and the canopy height is generally between 60 and 150 cm. Dwarf forest species (e.g., *Myrsine guianensis*, *Xylosma spiculifera*, *Hesperomeles goudotiana*) are present, but have low cover values. The herb layer is mostly dominated by the graminoids *Rhynchospora nervosa*, *Lycurus phalaroides* and *Aristida laxa*. Mostly found on slopes with a colluvial soil.

Figure 5.2 gives an indication of microclimatic differences (measured at 10 cm above the soil) between the three vegetation types, and a comparison with *Condalia* dwarf forest, obtained in a two weeks' transition period from rainy to dry season (Groenendijk, unpublished results). Clearly higher temperatures were measured in dry pastures and shrublands around 2:00 PM, while the relative air humidity drops to lower values, as

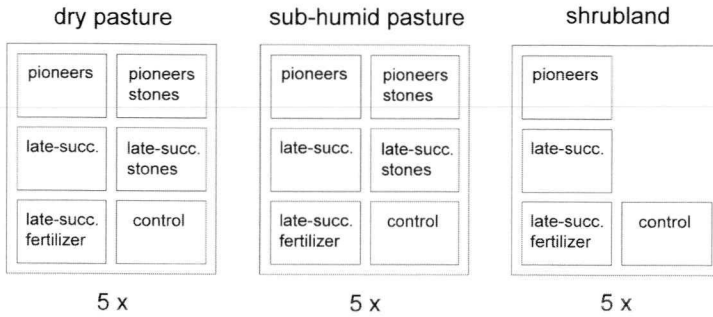


Figure 5.3. Schematic representation of the experimental set-up of the study.

compared to sub-humid pastures and dwarf forest.

The plantation was established in May – June 2000. In each of the three vegetation types, five plots of 10 x 15 m were established and planted with seedlings of pioneer species. Another five plots were planted with seedlings of the six late-successional species. Repeats of both the pioneers' series and the late-successional series were carried out with two separate additional treatments (Figure 5.3). The stones treatment consisted of three or four stones – of about 10 cm diameter – placed around each individual plant in the plots concerned, about a week after planting. The stone treatment was not applied in shrublands, because we considered those to already have a micro-climate affected by shrubs and tussock grasses. Additionally, the series of plots planted with late-successional species was repeated with fertilizer treatment. A quantity of 20 g of "triple-15" fertilizer (15% of both N, P, and K, with additional trace elements) was applied superficially in the soil, at some 10 cm distance in the upslope direction of each plant. This was done in July 2000, about a month after planting, when rain was still frequent.

We organized the series of experimental plots in barbed wire fenced clusters. Each cluster contained one plot of the combinations of planted species mixture and additional treatment, and a control plot, for a particular vegetation type, as shown in Figure 5.3. The minimum distance between plots within a cluster was 10 m. Hence, the clusters of both dry and sub-humid pasture each contained six plots, and those of shrubland four plots. Thus, a total of 80 experimental plots were laid out for the experimental setup.

Soil samples were taken at the beginning of the experiment, from each of the five clusters. In the control plots, five subsamples of superficial (0 - 5 cm) mineral soil were taken, from the four corners and the center of the plot. The contents of available K, Na, Mg, Ca, Al, and organic C in the samples, as well as pH and texture, were analyzed in the laboratories of the Instituto Geográfico Agustín Codazzi (IGAC, Bogotá). For details

Table 5.2. Soil properties of the vegetation types. Values are averages of the five blocks, with standard deviations between brackets. C_{org} = organic Carbon; CEC = Cation exchange capacity. Soil parameters are expressed as percentage (texture, C_{org} , Al saturation, and base saturation); or $cmol^+/kg$ (CEC, cations, and total bases).

	Dry pasture (Pd)	Sub-humid pasture (Ph)	Shrubland (S)
sand	55 (14)	47 (14)	50 (10)
silt	34 (13)	27 (11)	35 (5)
clay	11 (2)	25 (9)	15 (7)
pH	6.0 (0.2)	5.6 (0.2)	5.3 (0.1)
C_{org}	0.6 (0.3)	2.2 (0.9)	2.4 (0.4)
CEC	3.9 (0.9)	13.5 (5.9)	11.3 (2.4)
Ca	1.3 (0.4)	3.3 (1.5)	3.4 (1.1)
Mg	0.5 (0.2)	1.6 (0.8)	1.6 (0.3)
K	0.3 (0.1)	0.4 (0.2)	0.2 (0.0)
Na	0.0 (0.0)	0.1 (0.0)	0.1 (0.0)
Al *	-	0.3 (0.2)	0.4 (0.5)
Al satur.	-	8.3 (13.7)	6.7 (6.5)
tot. bases	2.1 (0.7)	5.4 (2.5)	5.3 (1.4)
base satur.	53.4 (8.9)	28.5 (18.9)	46.4 (4.5)

* not measured at pH > 5.5

on the soil analysis procedures, the reader is referred to Groenendijk *et al.* (in press, see Chapter 3). The analyses showed that dry pastures have relatively sandy soils with a high pH, and low contents of organic C and available cations (Table 5.2), as compared to sub-humid pastures and shrublands.

Plantation: within-plot

Every plantation plot had 189 individuals planted at 1 meter's distance, in a regular triangular pattern. As three different combinations of species were applied in the experimental setup, each had its own basic species quantities (Table 5.1) and spatial distribution pattern. The patterns were designed in such a way that the distribution of each species was more or less regular, without severe clustering of a certain species at a certain place in the plots.

The first pioneer mix, consisting of *Baccharis bogotensis* and *Dodonea viscosa* only, was simply planted in an alternating way, resulting in either 95 *B. bogotensis* and 94 *D. viscosa* per plot, or the reverse (Table 5.1). The second pioneer mix had 63 individuals of *B. bogotensis*, *D. viscosa*, and *Dalea coerulea* planted in a simple alternating way. This mixture was only applied in dry pastures, because *D. coerulea* is common around these areas, and does not occur in sub-humid pastures nor in *B. macrantha* – *D. viscosa* scrubs (Groenendijk & Cleef in prep., see Chapter 2). The late-successional species mixture consisted of different quantities of each of the six species, due to differences in availability.

The seedlings were planted in such a way the species were regularly spread over the plot. A hole of about 20 cm depth was made, in which the plantlet was inserted with all the earth of the nursery bag it was grown in. In November 2000, dead seedlings were replaced by living ones of the same species. Individuals that showed high mortality of leaves or an otherwise bad condition were also replaced by vigorous ones.

Monitoring of vegetation

Survival, length and cover of the planted seedlings were monitored in October - November 2000 (taken as the initial length), October 2001, and August 2004. The stem length of every individual was measured from the ground up to the upper living bud or leaf base. Cover of each planted species, and the total planted canopy cover, was estimated visually as percentage of the plot area. At the same time, the composition and abundance of all non-planted vascular plant species (the matrix vegetation) was recorded in all of the experimental plots, including the control plots. Vegetation structural data – bare ground, herb cover, shrub cover – were also recorded.

Data analysis

Survival of the planted seedlings in 2004 was analyzed on plot level for each species. The arcsine – square root transformed percentages of surviving seedlings in 2004 were tested by means of ANOVA for differences due to the vegetation type, and effects of additional treatments, *i.e.*, stones or fertilizer. The ANOVA's were executed in three separate series: a) One-way analysis of differences between vegetation types, including only those plots that had not received fertilizer or stone treatment; b) Two-way analysis of the effect of stone treatment, and its interaction with pasture type, thus excluding scrub plots and fertilized plots; c) Two-way analysis of the effect of fertilizer treatment, and its interaction with vegetation type, thus excluding stone-treated plots. Post-hoc multiple comparisons were carried out by means of Tukey's test, in case of overall significant differences.

Differences in stem length of the planted seedlings that had survived over the four years' period were analyzed for each species, by means of Kruskal-Wallis tests (ANOVA could not be applied because of unequal sample sizes and variances). The dependent variable of the test was the residual fraction of the log-transformed length in 2004 after linear regression on the log-transformed initial length at planting time. A first series of Kruskal-Wallis tests was performed with vegetation type as explanatory factor, and a second series with additional treatment as explanatory factor. The plots included in the between-vegetation analyses were those without stones or fertilizer treatments. Plots analyzed for the between-treatments test were those of dry pasture and sub-humid pasture, while those of *D. coerulea* were dry pasture plots only. Post-hoc multiple comparisons were done by means of Dunn's test, with $\alpha = 0.05$, as explained by Zar (1999). The spatial position of planted individuals, with respect to the plot border and planted neigh-

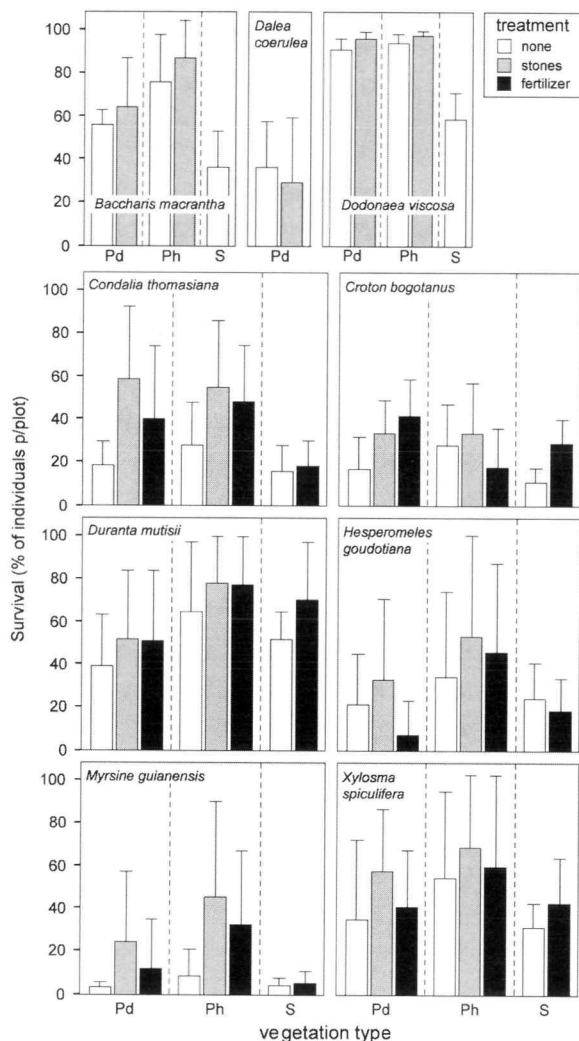


Figure 5.4. Survival of planted seedlings for each species expressed in percentage of total planted per plot, clustered per vegetation type and additional treatment. Error bars indicate ± 1 SD. $N = 5$ plots for all combinations. Pd = dry pasture; Ph = sub-humid pasture; S = shrubland.

bours, was assumed to have negligible effects on seedling performance, after preliminary analyses.

The development of the matrix vegetation was analysed using a number of indicators. The relative species turnover from 2000 to 2004 was calculated for each plot, as follows (Krieger *et al.* 2003; Schoener 1988):

$$TO = \frac{E + I}{S_1 + S_2}$$

where E = the number of species found in 2000, but not in 2004; I = the number of species found in 2004, but not in 2000; S_1 = the total number of species found in 2000; S_2 = the total number of species found in 2004. This index is inversely related to Jaccard's similarity coefficient. The turnover rates were tested for significant differences between vegetation types and planted species mixtures (including control plots), by means of ANOVA. All above-mentioned statistical analyses were performed with SPSS version 11.0 (SPSS 2001), except Dunn's Multiple Comparisons, which were calculated in MS Excel.

Directional changes in species composition in the plots were analyzed by means of a Principal Components Analysis (PCA) of the correlation matrix of plots, including the samples of both 2000 and 2004 in one ordination. The analysis was done separately for the three vegetation types. Prior to that, Detrended Correspondence Analyses (DCA) revealed gradients of 1.80, 2.78, and 1.91 SD length for dry pasture, sub-humid pasture and shrubland, respectively. All ordinations were performed with the Canoco program, version 4.0 (Ter Braak & Šmilauer 1999).

Results

Performance of planted seedlings

Survival

While the average survival percentages on plot-level of *Dalea coerulea* were below 40%, the other two pioneer species performed better, with over 90% survival for *D. viscosa* seedlings in pasture plots (Figure 5.4). *Myrsine guianensis* performed least in terms of survival, the percentage surviving seedlings mostly remaining below 35%. The remaining five late-successional species had survival percentages around 50%.

Survival on plot-level of seedlings of the pioneer species *B. macrantha* and *D. viscosa* was higher in at least one of the two pasture types than in shrublands, while no differences were detected for any of the late-successional species (Table 5.3). Stone treatment had a significant survival-enhancing effect for *D. viscosa*, *C. thomasi*, and *M. guianensis*. Fertilizer addition enhanced survival of *C. bogotanus*, but only in dry pastures and scrubs.

Growth

Individual growth of planted seedlings was generally poor: the average length of the planted individuals after four years was around or well below 50 cm for all late-successional species. The pioneer species mostly reached a height between 50 and 100 cm, *Dalea coerulea* often above 120 cm. Average growth rates were around zero or negative for all late-successional species, except *Myrsine guianensis* that attained a rate of 0

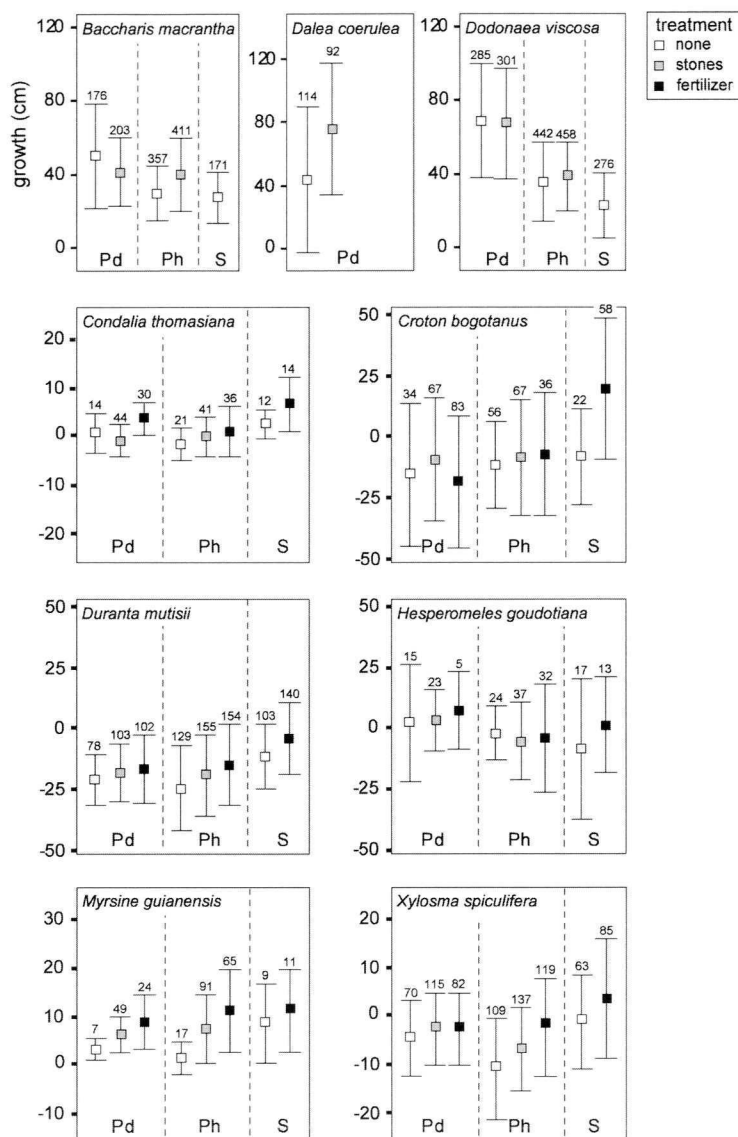


Figure 5.5. Average growth (cm) of surviving planted seedlings for each species over a four years' period, clustered per vegetation type. Error bars indicate ± 1 S.D. N is indicated above each error bar. Pd = dry pasture; Ph = sub-humid pasture; S = shrubland.

– 10 cm growth over the four years' period (Figure 5.5). Planted seedlings of *X. spiculifera*, *D. mutisii*, and *C. bogotanus* appeared to have “shrunk”, i.e., the upper living leaves or buds died. Some species, mainly *Xylosma spiculifera* and *Croton bogotanus*, showed reiteration from the base after mortality of the main above-ground stem.

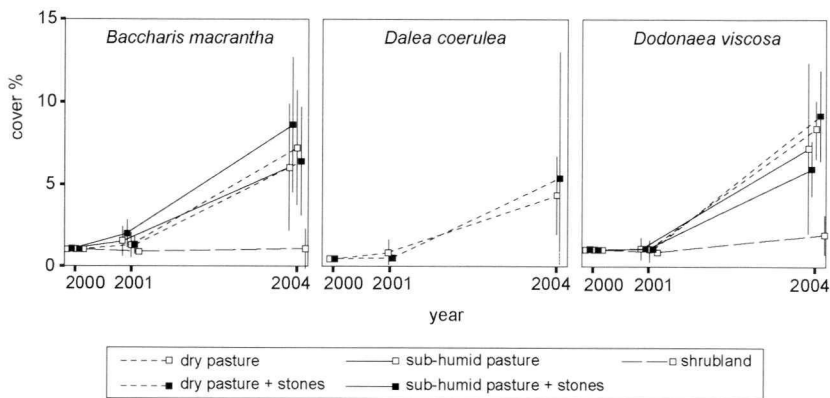


Figure 5.6. Average increase in cover percentages of planted pioneer species between 2000 and 2004. Error bars indicate ± 1 S.D. $N = 5$ for all averages.

Four out of six late-successional species showed a higher growth in shrubland plots (without stones or fertilizer) than in those of at least one of the pasture types, and *D. mutisii* and *X. spiculifera* more than in those of both pasture types (Table 5.4). Contrarily, the pioneer shrubs *B. macrantha* and *D. viscosa* showed the highest growth in dry pastures. The pioneers *B. macrantha* and *D. coerulea* showed a higher overall growth rate for stones-treated seedlings than non-treated ones, although this does not hold for *B. macrantha* in dry pasture plots (Figure 5.5). This was also the case for the late-successional species *D. mutisii*, *M. guianensis*, and *X. spiculifera*. All late-successional species except *H. goudotiana* showed enhanced growth as a result of fertilizer addition. Although we could not test for interaction effects between vegetation type and treatment, the benefit of fertilizer looked greater in shrubland than in pastures for *C. thomasiana* and *C. bogotanus*.

Cover

Total cover of the planted seedlings reached average values between 10 - 20% only in pasture plots planted with pioneer species (Figure 5.6). The three pioneer species showed an increase up to – on average – at least 5% in the pasture plots, *B. macrantha* and *D. viscosa* remaining sparse in shrubland plots. In the dry pasture pioneer-planted plots, total cover values of about 20% were reached in both untreated and stones-treated plots, while in the sub-humid ones total cover was around 15%. The six late-successional species *C. thomasiana*, *C. bogotanus*, *D. mutisii*, *H. goudotiana*, *M. guianensis* and *X. spiculifera* did not increase their cover in any of the plots, nor did the total cover of late-successional planted seedlings.

Table 5.4. Differences in growth of planted seedlings for each species, between vegetation types and between treatments, tested by Kruskal-Wallis tests and Dunn's Multiple Comparisons. Vegetation types: Ph = sub-humid pasture; Pd = dry pasture; S = shrubland. Additional treatments: n = no treatment; s = stones; f = fertilizer. See text for explanation. *N* is given in Figure 5. *Pd was not significantly different from either Ph or S.

GROWTH	between vegetation types			between treatments			
				stones		fertilizer	
	H _c	<i>p</i>	Dunn's M.C.	H _c	<i>p</i>	H _c	<i>p</i>
Pioneer mixture							
<i>Baccharis macrantha</i>	88.82	0.000	Pd>Ph=S	25.11	0.000	s>n	
<i>Dalea coerulea</i>	-	-		10.70	0.001	s>n	
<i>Dodonaea viscosa</i>	358.16	0.000	Pd>Ph>S	1.30	0.253		
Late-successional mixture							
<i>Condalia thomasi</i>	9.99	0.007	S>Ph*	0.14	0.707	15.30	0.000 f>n
<i>Croton bogotanus</i>	1.59	0.449		3.47	0.063	8.97	0.003 f>n
<i>Duranta mutisii</i>	58.79	0.000	S>Ph=Pd	20.99	0.000	s>n	62.79 0.000 f>n
<i>Hesperomeles goudotiana</i>	0.23	0.890		0.02	0.897	0.82	0.365
<i>Myrsine guianensis</i>	10.12	0.006	S=Pd>Ph	30.05	0.000	s>n	28.96 0.000 f>n
<i>Xylosma spiculifera</i>	35.49	0.000	S>Pd>Ph	15.72	0.000	s>n	51.99 0.000 f>n

Development of the matrix vegetation

Species turnover rates

In the dry pasture plots, a total of 75 species was found in 2000, and 83 in 2004. In sub-humid pastures, these numbers were 98 and 100 for 2000 and 2004, respectively, and in shrubland plots 137 and 143. There were no patterns in species increase per plot over time. The number of annual species, on average, slightly decreased in most plantation series, but again there were no patterns. Average turnover rates varied between 0.20 and 0.30 for dry pasture and shrubland plots, and between 0.30 and 0.40 for sub-humid plots. This difference was significant (ANOVA, $F = 6.05$, $p < 0.005$). No differences in turnover rates were found between planted species mixtures or between additional treatments. Moreover, control plots did not have *TO* rates different from those of planted plots.

Directional changes in species composition

Since pasture-plots planted with pioneer species were the only ones yielding a total planted canopy cover between 10 – 20%, meaning a substantial change with respect to the initial situation, we restrict to showing the analyses of vegetation development only for these plots, and control plots. Changes in the remaining plots are probably not an effect of the plantation.

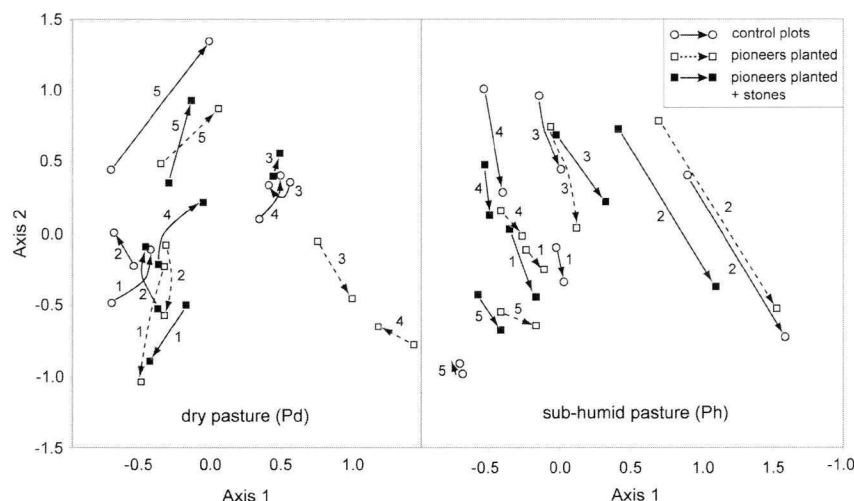


Figure 5.7. PCA ordination diagrams of non-planted matrix vegetation, comparing the situation in 2000 with that of 2004. Symbols represent plots, the arrow indicating change from 2000 to 2004. The numbers along each arrow indicates the cluster to which the corresponding plot belongs. Percentages of explained variation by the first and second axis are 9.0%, 8.2% (Pd); 9.6%, 7.6% (Ph).

Figure 5.7 shows the results of the PCA's executed for dry pasture and sub-humid pasture plots. Changes in species composition over time were reflected in movement of individual plots in ordinal space, with arrows connecting the coordinates of a particular plot in 2000 with those of the situation in 2004. Generally, the arrows indicating changes over time for the control plots do not have a different length from those of the planted plots, so changes in the principal patterns of species composition and abundance were of a comparable magnitude. The five clusters of plots within the vegetation types were mostly occupying a certain part of ordinal space. In dry pasture, control plots and stone-treated pioneer-planted plots changed mostly towards higher axis 1 values, while untreated pioneer-planted plots showed no particular pattern. In sub-humid pastures, nearly all plots moved towards lower axis 2 values, and slightly higher axis 1 values. Resumingly, planted plots did not show changes in principal patterns of species composition other than those visible in control plots.

Species involved in vegetation changes

In pasture plots, we found a few herb species normally found in shrublands (Table 5.5). Woody species invading pasture plots were mostly pioneers. *Dalea coerulea* was found in pioneer-planted dry pasture plots, most probably offspring from the planted seedlings. The commonly planted exotic *Acacia decurrens* invaded five shrubland plots.

In dry pasture plots, among the species mostly increasing their cover over time were the grasses *Botriochloa saccharoides*, *Aristida laxa*, *Sporobolus indicus*, and *Pennisetum clan-*

Table 5.5. Vascular plant species that have invaded the plantation plots. Values are numbers of plots where a species has invaded ($N = 5$). C = control plots; P = pioneer-planted; Ps = P with stones; L = late-successional species planted; Ls = L with stones; Lf = L with fertilizer.

herbs	growth form	affinity	dry pasture					sub-humid pasture					shrubland					
			C	P	Ps	L	Ls	Lf	C	P	Ps	L	Ls	Lf	C	P	L	Lf
<i>Arenaria lanuginosa</i> (Michx.) Rohrb.	prostrate herb																	
<i>Chelanthus bonariensis</i> (Willd.)	fern	scrub undergrowth	1				1	1										
<i>Ditassa longiloba</i> Benth.	vine	scrub undergrowth											1					
<i>Epidendrum elongatum</i> Jacq.	herb	degraded sites								1								
<i>Evolverus bogotensis</i> Oostr.	prostrate herb	pasture / scrub									1							
<i>Habenaria</i> sp.	herb	scrub undergrowth																
<i>Hypoxis humilis</i> H.B.K.	herb	pasture / scrub						1										
<i>Linaria</i> cf. <i>canadensis</i> (L.) Dum.	herb	scrub / <i>Acacia</i> forest																1
<i>Lupinus</i> sp.	herb	pasture											1					
<i>Ophioglossum nudicaule</i> L.f.	fern	pasture						1										
<i>Oxalis debilis</i> Kunth	herb	pasture / scrub																1
<i>Pellaea ternifolia</i> (Cav.) Link	fern	scrub undergrowth	1				1	2										
<i>Peperomia</i> sp.	prostrate herb	dwarf forest undergrowth											1	1				
<i>Rhynchospora nervosa</i> (Vahl) Boeck.	herb	pasture / scrub					2											
<i>Stevia serrata</i> Cav.	herb	pasture																1
<i>Acacia decurrens</i> Willd.	tree	planted exotic																1
<i>Arytaphyllum nitidum</i> (Kunth)	subshrub	rocky outcrops																2
<i>Baccharis trinacata</i> (L.f.) Pers.	subshrub	rocky outcrops									1							
<i>Chaetolepis microphylla</i> (Bonpl.) Miq.	subshrub	rocky outcrops																1
<i>Cordia</i> sp.	treelet	dwarf forest canopy																
<i>Croton bogotanus</i> Cuatrec.	treelet	dwarf forest canopy																1
<i>Dalea coerulea</i> (L.f.) Schinz & Thell.	shrub	pioneer shrub	4		2													
<i>Dodonaea viscosa</i> Jacq.	shrub	pioneer shrub	1															1
<i>Gaillheria erecta</i> Vent.	subshrub	rocky outcrops											1					
<i>Lycianthes lycioides</i> (L.) Hassl.	shrub	dwarf forest undergrowth																
<i>Solanum nigrescens</i> Martens & Gal.	shrub	exotic / undergrowth						1										
<i>Stevia lucida</i> Lag.	shrub	pioneer shrub											1	1	1	1		
total			0	7	2	4	3	4	2	4	2	1	7	0	1	3	2	5

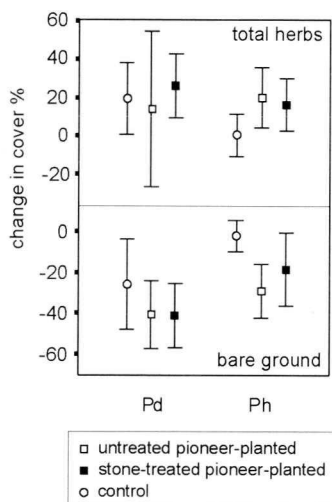


Figure 5.8. Average cover change of total herbs and bare ground, in pasture plots without plantation and plots planted with pioneer shrub species, expressed as difference in cover % from 2000 to 2004. Error bars represent 1 S.D. $N = 5$ for all combinations.

destinum. The shrub *Baccharis macrantha* also increased cover. In sub-humid pastures, the common grass *Anthoxanthum odoratum* decreased in cover, while *Rhynchospora nervosa* and *Cyperus aggregatus* became more abundant. In shrublands, the most common woody species became more abundant (*B. macrantha*, *Dodonaea viscosa*), together with the spreading herbs *Cuphea serpyllifolia* and *Rhynchospora nervosa*. The grass *Aristida laxa* declined its cover.

Changes in vegetation structure

Figure 5.8 shows that the control plots in sub-humid pasture hardly revealed any changes in total herb cover or bare ground area, while most of the pioneer-planted ones clearly did show an increased herb cover, and a decreased bare ground area. In dry pastures, no strong differences between control and planted plots were detected regarding herb cover, while the decrease in bare ground was higher in planted plots than in control plots. Changes in cover of the woody layers were not displayed because the cover estimation error is probably comparable to the expected changes in cover over the study period.

Discussion

Planted seedlings performance

The planted pioneer species *Baccharis macrantha* and *Dodonaea viscosa* clearly performed better in pastures than in shrublands, in terms of survival, stem growth and crown cover. Contrarily to our hypothesis, most late-successional species survived better in pastures as well. However, stem growth for these species was higher in shrubby vegetation. The high overall rates of mortality, mostly for late-successional species, could be explained by night frosts, which have been exceptionally severe during the dry periods of January to March 2001 and January to March 2004 (CAR, unpublished data; R. Peña, pers. comm. 2004). In addition, drought has probably been another major cause of mortality.

The positive effect of the stone treatment on survival of nearly all species suggests desiccation stress for naturally germinated seedlings in both dry and sub-humid grasslands. Apart from soil humidity maintenance, an observedly high presence of soil fauna and crickets, spiders, small snails etcetera probably provide some nutrient supply. Growth of *D. viscosa* was positively related to soil moisture level in Australian semi-arid woodland (Hodgkinson 1992). Preliminary analyses of pF-ring samples showed that, in dry pastures, soil moisture retention between 0 – 30 cm depth was very low (mostly below 5%), while in sub-humid pastures it ranged between 10 – 15%. We expected the effect of the stone treatment to be inversely related to soil moisture retention. However, we found no significant interaction between the effect of the stone treatment and pasture type on survival, although the difference in average survival between non-treated and stone-treated plots were somewhat higher in dry pastures for *C. thomasi*, *C. bogotanus* and *X. spiculifera*. Furthermore, the positive effect of stones on stem growth of several species planted in sub-humid pastures was mostly not found in dry pastures, or less strongly so. It even appeared negative for *B. macrantha* in dry pastures. We speculate that soil fauna – especially worms –, more abundantly found in sub-humid pastures (and shrublands), could have improved soil characteristics (structure and nutrient mineralization). The attractive function of the stones for soil fauna could thus help the planted seedlings to profit from these additional benefits.

Fertilizer addition generally increased growth, and not better survival, of the late successional species. The degree of increase in nutrient uptake by seedlings – causing enhanced performance – resulting from fertilizer addition, depends on local soil physical and chemical characteristics. Fertilizer can be expected to make less difference in soils where the added nutrients are relatively well available. Preliminary analyses (separate from those presented in Table 2) suggested that levels of total N, P, and K were low in dry pastures (mostly below 0.1% N, 0.05% P₂O₅, and 0.2% K₂O, respectively), relatively high in shrublands (above 0.25%, 0.08%, and 0.2%) and intermediate in sub-humid pas-

tures. However, the positive effect of fertilizer on performance of *C. bogotanus* seedlings was strongest in relatively nutrient-rich shrublands. For the other late-successional species (except *H. goudotiana*), similarly, the effect was most prominent in either shrubland or sub-humid pasture. Apparently, conditions for nutrient uptake in shrublands and sub-humid pastures were better than in pastures. Soil moisture, important for nutrient mobility (Marschner 1986; Jensen *et al.* 2003), is low and strongly fluctuating in dry pastures. Moreover, relatively small fractions of clay, and low contents soil organic material were found in the soils of dry pastures, which suggests a low nutrient-buffering capacity: in semi-arid volcanic soils of the Lesser Antilles, fertilizer N in soil was found to be lost more rapidly when soil OM contents were low (Chotte *et al.* 1998). We do not have any data on growth limitation by nutrients for any of the planted species.

In shrublands, low growth rates and cover could be explained by competition for water with the abundant bunchgrasses and shrubs. Seedling survival of *D. viscosa* was negatively related to presence of tussock grass in semi-arid Australian grassland (Harrington 1991). The cover of non-planted shrubs is probably not sufficient to provide buffering of relative air humidity and temperature fluctuations, since the late-successional species did not survive more in shrublands. Additionally, the shallow soils of these sites could also explain low overall growth rates. The late-successional species considered here are favoured by a certain minimum level of soil humidity, which could be conserved if (woody) vegetation cover is sufficient. Probably, the cover of the non-planted shrub layer in the shrubland plots was not high enough to have such a facilitating effect, and the observed performance of late-successional species was even less than in pastures.

Since planted seedlings could compete with neighboring ones, there could be an effect of number and species composition of planted neighbours on performance. At this stage of the experiment, considering the small size of most seedlings, we do not expect such effects to have played a role until now, but – depending on root development and (lateral) crown development – this could play a major role in the future.

Although we did not consider the germination phase of the woody species, but in stead focused on survival and growth of planted seedlings, our results indicate that the lack of natural establishment of late-successional species in open vegetation, and even in the shrublands used in this study, is hampered by environmental conditions.

Development of vegetation: accelerated succession?

The only effect measured in planted plots that did not occur in control plots was an increase in herb cover, obviously inversely related to a decrease in bare ground area. Hence, instead of a mere effect of grazer exclusion, this is an effect of planted canopy establishment. This might be regarded as the first onset to accelerated succession. Shrub crowns at least facilitated horizontal spread of already present herb species. However, the *Baccharis-Dodonaea* (-*Dalea*) canopy has only recently established, and hence microclimatic changes, if any, have not yet had the chance to measurably influence estab-

lishment of species. Growth of shrubs and treelets is slow, especially of the late-successional ones, so establishment of a canopy will take place over a scale of decades, in stead of years. Establishment of late-successional species not only depends on a suitable habitat eventually formed by a planted canopy, but also on propagule availability. Seed banks of most late-successional species are very sparse, especially in pastures (Groenendijk *et al.* in prep., see Chapter 4).

Turnover rates were higher in sub-humid pastures than in dry pastures, in spite of less initial bare ground surface and hence less available sites for germination. Species turnover is generally believed to be higher in habitats with high nutrient availability and soil moisture (Prach *et al.* 1993; Luken 1990; Tilman 1988), although extreme conditions have lower turnover rates (Burrows 1990). Shrublands were found to have a lower turnover rate as compared to grasslands, which is consistent with results from many other authors (Bornkamm 1981; Burrows 1990; Myster & Pickett 1994; Prach *et al.* 1993). This has been attributed to longer life spans of late-successional invading species (Connell & Slatyer 1977), and more competition for resources (Tilman 1988).

Control plots showed changes in species composition similar to planted ones, irrespective of the planted species mixture or the treatment. This was hardly surprising, since survival and growth of the planted seedlings during the four years' period was not enough to establish a woody canopy in many plots. Moreover, even after closure of a woody canopy, processes of colonization still take time. The different directions of change in species composition, as revealed by PCA, should probably be interpreted as few changes at all; the picture is "strongly zoomed" on small changes. This is supported by the low fraction of explained variance by the principal components: mostly below 10%. The changes that did occur, *i.e.*, increased cover of graminoids, were most likely to be attributed to exclusion of grazing cattle by the fences.

Conclusions and recommendations

The pioneer species used in this experiment are applicable in plantation experiments in abandoned pastures, given that their survival rates are high and growth is sufficient as to form a significant canopy. Further trials and restoration attempts might include combination of pioneers and late-successional species. During canopy formation of the pioneers, the late-successional species could at least survive, and growth conditions for the latter might improve after some lateral crown growth of *B. macrantha* and *D. viscosa*. Especially if the seedlings would be treated with (a combination of) stones and fertilizer, chances of successful efforts might be further enhanced. Although growth is very slow – the rates reported in this paper concern increases of (tens of) centimeters stem length per year –, the effects of these treatments are clear.

Since both growth and propagule availability of the desired species are low, successional changes will probably become evident after a relatively long period. We have no data that permit speculation about the length of the time span needed for regenera-

tion of *Condalia* dwarf forest, but we feel that using plantations we could at least overcome a part of the seed dispersal limitation. If collected seeds would be sown out as an alternative for seedling plantation, the loss of individuals would be much higher, and the time span for establishment would be even longer. This would not be desirable, in view of the urgent need for restoration in many sites.

The methods used in restoration or rehabilitation practices should be affordable for developing countries, but also effective. The costs of plantation are relatively high, partly because of the nursery procedures. However, since the cost of labor is relatively low in most tropical countries, plantation, even with survival-enhancing application of stones, could be an affordable way for many institutions to rehabilitate endangered sites.

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Chapter 6.

Insertion of native species in the understory of *Acacia decurrens* plantations: perspectives for conversion into natural vegetation

J.P. Groenendijk and J.F. Duivenvoorden, submitted to *Restoration Ecology*

Abstract

We examined the possibilities for conversion of *Acacia decurrens* plantations to native *Condalia* dwarf forest in a dry part of the Colombian Andes, by inserting native late-successional species under the planted canopies. Performance of planted seedlings in *Acacia* forest was compared with that in open secondary vegetation. Moreover, we investigated the effect of site differences, *Acacia* canopy cover and fertilizer application on seedling performance. Late-successional species generally perform better in *Acacia* plantations than in open vegetation, while the reverse was true for pioneer shrubs, which had very low survival rates under plantations. Fertilizer had a positive effect on performance of some species, but not enough to justify its use in large-scale restoration attempts. We concluded that underplanting of late-successional *Condalia* dwarf forest species give good prospects for conversion of *Acacia* forests into native vegetation.

Introduction

All over the tropics, exotic rapid-growing tree species have been planted extensively for timber production and protection against erosion. These planted forests generally have a number of drawbacks in terms of ecological function, *e.g.*, high water consumption and evaporation, and low levels of animal and plant diversity (Lugo 1997; Van der Hammen 1998; Van Wessenbeeck *et al.* 2003). Therefore, the possibilities for conversion of these exotics' forests to natural vegetation have gained interest, and a catalytic effect of tree plantations for natural regeneration has been shown by many authors (Yirdaw 2001; Fimbel & Fimbel 1996; Geldenhuys 1997; Parrotta 1992, 1993, 1995). However, this catalytic effect depends on (lack of) management, planted species, distance to natural forest, site degradation, and grazing (Hofstede *et al.* 2002; Parrotta *et al.* 1997b), and consequently there are many sites where regeneration is hampered (Van der Hammen 1998; Cortés *et al.* 1990; Hofstede *et al.* 2002; Hofstede *et al.* 1998).

The experience available to date has mainly been obtained from *Pinus* and *Eucalyptus* plantations. Especially in subtropical semi-arid areas, *Acacia decurrens* has been commonly used in forestry in many parts of the world, and subsequently became naturalized and invasive (Haysom & Murphy 2003). However, to our knowledge, no published information is available on understory development in *A. decurrens* plantations.

In spite of the above-mentioned promising reports on natural regeneration in the understory of planted forests, this seems not to be the case in the *A. decurrens* forests treated in this paper, which are situated in a semi-arid intermontane valley in the Colombian Andes. The understory of the planted *Acacia decurrens* forests is very poor in terms of biodiversity and has a low cover of herbs and shrubs (Van der Hammen 1998, 1997). A thick litter cap is formed by leaves and pods shedded by *A. decurrens*, and moss cover can reach up to 80%. These could have a negative influence on seedling establishment in the understory. Planted tree species, mostly being pioneers, are generally expected to be replaced by late-successional native species (Lugo 1997). Although a longevity of 10 – 15 years has been suggested for *A. decurrens* by Arredondo *et al.* (1998), the plantations of this species in our study area are still in a good state after 20 – 25 years, and rejuvenating occurs both inside and outside the forested area. Native woody species have hardly (re-) established in the planted forest understory, so either environmental conditions are not suited, or seeds do not enter the forest. Regarding the latter, soil seed banks are indeed dominated by weedy herbs, and virtually lack native woody species (Groenendijk *et al.* in prep., see Chapter 4).

The question raises whether one should use (mostly very costly) underplanting of native species to overcome the above-mentioned obstacles to natural regeneration and replacement of planted trees. Examples of native forest species plantation experiments in exotics' forests have come from the Asian lowland tropics (Ashton *et al.* 1997, 1998). In

these studies, performance of inserted late-successional species was found to depend largely on openness of the *Pinus caribaea* canopy, and was poor under completely closed canopies. Good performance of planted seedlings indicate limitation of the considered species by seed dispersal, and would justify further experimentation with artificial (partial) clearings of the originally planted exotic trees. If, on the other hand, seedlings would not be able to grow, environmental conditions would have to be modified – which could include canopy opening – in order to enhance regeneration. From plantation experiments in open secondary vegetation, we found that pioneer shrub species performed well in abandoned pastures, while late-successional species mostly had higher growth rates in shrubby vegetation (Groenendijk & Duivenvoorden in prep., see Chapter 5). Moreover, fertilizer addition proved to enhance performance of late-successional species. Natural recruitment of this late species group is mostly restricted to dense-canopy dwarf forests (Groenendijk *et al.* in press, see Chapter 3).

In this paper, we address the question whether plantation of pioneer and/or late-successional species gives prospects for conversion into a vegetation of native species, based on performance of planted species. Prospects are good if the understory environment of planted forests are suited for plantation, *i.e.*, if it permits establishment and growth of woody plants that will further develop after cutting of the *Acacia*'s. We expected that: 1. seedlings of late-successional species perform better than those of pioneer species, when planted in *Acacia* forest; 2. late-successional species perform better in *Acacia* forest than in open vegetation, and the reverse for pioneer species. Moreover, we investigated whether performance of planted species can be enhanced by fertilizer addition, and which site factors might further be influencing performance. The questions will be addressed by comparing the performance of planted seedlings in *Acacia* forests among sites with different characteristics and among vegetation types.

Methods

Study site

The fieldwork area is at the edge of the high plain of Bogotá, an intramontane basin in the Eastern Cordillera of Colombia (Figure 6.1). It concerns a part of the Checua River valley, affluent to the Bogotá River, situated within the municipality of Suesca, Cundinamarca. The elevation above sea level of the study area is between 2700 and 2900 m.

The zone receives about 700 mm of annual rainfall, generally concentrated in two short rainy periods. Evapotranspiration approximates 1050 mm annually, leading to a deficit of about 350 mm (Claro-Rizo 1995). The mean annual temperature is around 13° C (Van der Hammen 1998). During dry periods, night frost frequently occurs.

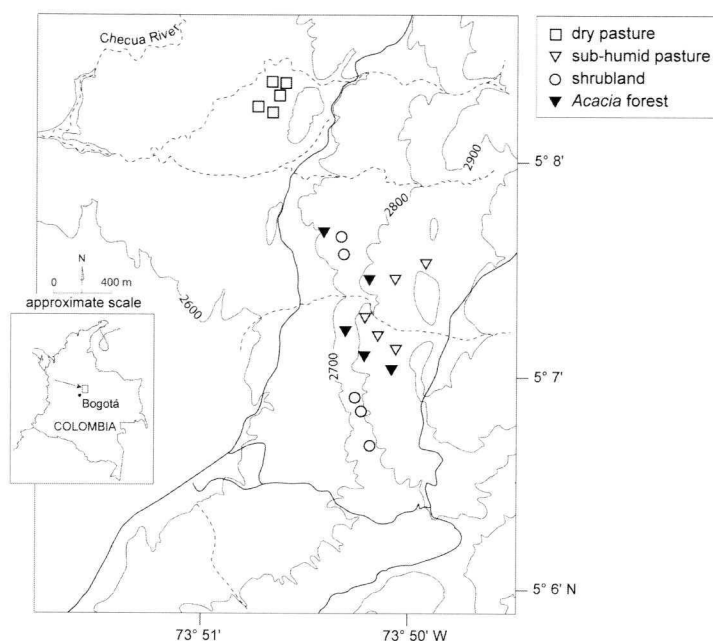


Figure 6.1. Locations of the clusters of experimental plots in the study area, indicated by symbols according to the matrix vegetation type.

The study site is on a slope consisting of Tertiary sandstone, covered by a volcanic ash cap of about 20-70 cm thick, which has locally been disturbed or removed due to erosion and landslides. Soils formed in this ash cap show a thin A horizon and a natric B horizon primarily containing clay, organic material, and sodium. Locally, erosion has exposed the underlying sandstone.

The vegetation consists of a mosaic landscape of grassland, scrubs, planted exotics' forest, and fragments of native dry Andean dwarf forest. This dwarf forest was described as *Xylosmo – Condaliatum*, or “*Condalia* forest”, by Van der Hammen (1997). One of the characteristic treelets, *Condalia thomasi* (Rhamnaceae), is a recently discovered endemic of this particular zone (Fernández-Alonso 1997). Disturbances have been common and severe, and exotic grasses have large cover values. The native *Condalia* dwarf forest and secondary vegetation types of the area have been described in more detail elsewhere (Groenendijk & Cleef in prep., see Chapter 2; Van der Hammen 1997).

Plantations of *Acacia decurrens* were established by the Corporación Autónoma Regional de Cundinamarca (CAR) in the 1980s, mostly on grasslands and low open scrubs that most probably were cleared before seedling insertion. Tree height ranged from 7 to 14 m. Nowadays, these planted forests have a poor undergrowth, with a total herb cover generally between 10 - 30%, and a shrub cover mostly below 1% (Groenen-

Table 6.1. Numbers of individuals of woody species planted per plot, as applied in the different mixtures. Average initial stem length per species is given, with standard deviations between brackets.

species	family	successional affinity	individuals per plot	stem length at planting (cm)
			pioneer mixture	late-succ. mixture
Pioneer mixture				
<i>Baccharis macrantha</i>	Asteraceae	pioneer	94 - 95	39.1 (9.3)
<i>Dodonaea viscosa</i>	Sapindaceae	pioneer-mid	94 - 95	17.3 (7.5)
Late-successional mixture				
<i>Croton bogotanus</i>	Euphorbiaceae	late	40	29.5 (21.9)
<i>Duranta mutisii</i>	Verbenaceae	late	55	29.3 (13.1)
<i>Hesperomeles gondotiana</i>	Rosaceae	mid-late	14	38.7 (24.5)
<i>Myrsine guianensis</i>	Myrsinaceae	mid-late	40	5.8 (2.7)
<i>Xylosma spiculifera</i>	Flacourtiaceae	mid-late	40	24.0 (12.5)

dijk, unpublished data). Graminoids, mostly *Piptochaetium panicoides* and *Rhynchospora nervosa*, dominated the herb layer, together with *Cuphea serpyllifolia* and *Chaptalia excapa*. The only common woody species was *Chromolaena leivense*, a small slender shrub. The often dense mats of mosses covered mostly more than 40%, especially in the higher parts of the study area. Species composition of the understory mostly depended on elevation above sea level and *Acacia decurrens* canopy cover. The trees shed a lot of leaves and pods, leading to a litter cap mostly completely covering the soil.

Preliminary measurements of microclimate (at 10 cm above the soil) in the vegetation types of the study area indicated that *Acacia* forests mostly have temperatures and relative air humidity comparable to those of *Condalia* dwarf forests.

Plantation species

Seven species of shrubs and treelets were selected for this experiment. All of these are native to the *Condalia* dwarf forest zone and commonly found there, either in woody pioneer stands and/or in late-successional dwarf forest patches. Their successional affinity was investigated by Groenendijk *et al.* (in press, see Chapter 3), and is summarized in Table 6.1. *Dodonaea viscosa* was categorized as a mid-successional species, but was included in the pioneer mixture because it is mostly co-dominant with *Baccharis macrantha* in pioneer scrubs. Similarly, *Hesperomeles goudotiana*, *Myrsine guianensis* and *Xylosma spiculifera* were classified as mid-late-successional, but were included in the late-successional plantation mixture because of their frequent co-occurrence with the three other species of that mixture in dwarf forest patches. We chose to plant greenhouse-grown seedlings instead of sowing seeds, thus skipping the germination stage in which most plant species are vulnerable.

Seeds of all species were collected from the vegetation present at the study site. The plant material for the initial planting was produced in two different nurseries owned by the Corporación Autónoma Regional de Cundinamarca (CAR). Plantlets received applications of fertilizers and fungicides on a regular basis during the production and maintenance period in the nurseries. At the moment of plantation in the field, the seedlings were in 707 cm³ nursery bags.

Site and plot selection

Fifteen experimental plots of 150 m² (10 x 15 m) were laid out in *A. decurrens* stands for the experimental setup. We organized the experimental plots in five clusters, *i.e.*, barbed wire fenced groupings of plots. Each cluster contained: (1) one plot planted with the pioneer species mixture; (2) one plot planted with the late-successional species mixture; (3) one plot planted with the late-successional species mixture, and treated with fertilizer. Throughout this paper, the term “planted seedling” is preserved for the seedlings of the native species used in our experiment, and “*Acacia* forest” for the *A. decurrens* plantation.

The *Acacia* trees, inserted in the 1980s by the CAR, were planted in or next to artificially created infiltration trenches following the contour lines. We selected sites where the *Acacia* rows were at least 10 m apart, in order not to have the infiltration trenches in the experimental plots. The plots within a cluster were laid out at at least 10 m distance from each other. The clusters were established with at least 150 m distance between them (Figure 6.1).

Plantation plots were also established in three types of open secondary vegetation: dry pasture, sub-humid pasture, and open scrub. These plots are treated in more detail elsewhere (Groenendijk & Duivenvoorden in prep., see Chapter 5). Plantation procedures in these plots were highly similar to those of the *Acacia* plantation plots, except for a few differences explained below. The dry pastures, at the pediments, were dominated by grasses and annual herbs, mostly *Microchloa kunthii*, *Schbcuria pinnata* and the exotic *Pennisetum clandestinum*. Around 35% of the soil surface was without any vegetation or litter cover. Soil conditions were relatively harsh: low OM contents, low nutrient availability and low water retention. The sub-humid pastures, found at higher elevations, had a denser vegetation cover, and were co-dominated by *Pennisetum clandestinum* and *Anthoxanthum odoratum*. Soils were more nutrient-rich. Shrublands were mostly found on midslopes, and dominated by *Baccharis macrantha* and *Dodonaea viscosa*, covering between 8 – 17%.

Plantation and performance monitoring

Two different combinations of species were applied in the experimental setup, and each species had different numbers of individuals planted per plot (Table 6.1). The patterns were designed in such a way that the distribution of each species was more or

less regular, without severe clustering of a certain species at a certain place in the plots. Every plot had 189 individuals planted at 1 m distance, in a regular triangular pattern. The pioneer mix, consisting of *Baccharis bogotensis* and *Dodonea viscosa* only, was simply planted in an alternating way, resulting in either 95 *B. bogotensis* and 94 *D. viscosa* per plot, or the reverse. The late-successional species mixture consisted of different quantities of each of the five species (Table 6.1), due to differences in availability. The seedlings were planted in such a way that the species were regularly spread over the plot.

The same plantation patterns were applied in the plots established in dry and sub-humid pastures, and shrublands. Additionally, 15 seedlings of *Condalia thomasiana* were included (at the cost of *Duranta mutisii* seedlings) in the late-successional mixtures applied to these vegetation types. Furthermore, *Dalea coerulea* (L.f.) Schinz & Thell. (Fabaceae) was included in the pioneer mixture, in the dry pasture plots only. Assuming that these species did not have any neighbouring influence other than that of the remaining species in the plots, we do not report on them in this paper. The reader is referred to the paper by Groenendijk and Duivenvoorden (in prep., see Chapter 5) for more detailed results on these species.

Each seedling was inserted in a dug-out hole of about 20 cm depth, with all the earth of the nursery bag it was grown in. The fertilizer treatment was only applied to the late-successional species mixture. A quantity of 20 g of "triple-15" fertilizer (15% of both N, P, and K, with additional trace elements) was applied superficially in the soil, at some 10 cm distance in the upslope direction of each plant. This was done in July 2000, about two months after planting, when rain was still frequent. In November 2000, dead seedlings were replaced by living ones of the same species. Individuals that showed high mortality of leaves or an otherwise bad condition were also replaced by vigorous ones.

The length of the stem of every individual was measured from the ground up to the upper living bud or leaf base. In case the leading stem was dead, the highest upgoing branch was caught for the measurement. The length of the planted seedlings was measured in October 2000 (taken as the initial length), October 2001, and August 2004. Cover percentage of each planted species, and the total planted canopy cover, was also estimated.

Soil samples were taken from each of the five clusters. In the control plots, five subsamples of superficial (0 - 5 cm) mineral soil were taken, from the four corners and the center of the plot. The contents of available K, Na, Mg, Ca, Al, and organic C in the samples, as well as pH and texture, were analyzed in the laboratories of the Instituto Geográfico Agustín Codazzi (IGAC, Bogotá). For details on the soil analysis procedures, the reader is referred to Groenendijk *et al.* (in press, see Chapter 3).

Data analysis

Survival of the planted seedlings in 2004 was compared with that in the sub-humid pasture, dry pasture, and scrub plots, for each species, by subjecting arcsine-

square-root transformed percentages of surviving individuals to ANOVA. For this one-way ANOVA, only the non-fertilized plots were included. Post-hoc multiple comparisons were made by means of Tukey's test. Between-vegetation-type differences in relative stem growth of the planted seedlings that had survived were analyzed per species, by means of Kruskal-Wallis tests (ANOVA could not be applied because of highly unequal sample sizes and variances). Relative growth was calculated, per individual seedling, as the stem growth over the four years' period divided by the initial stem length. Post-hoc multiple comparisons were done by means of Dunn's test, following Zar (1999).

The effects of fertilizer application and site differences (cluster effect) on survival of planted seedlings were tested by means of logistic regression, for each species separately. Clusters were entered as dummy variables. Since each single dummy of this set of five is perfectly correlated to the other four, one dummy had to be left out of the logistic regression, and the effect of the entered dummies is given as compared to the one left out. To be able to assess the effect of each cluster as compared to the other, we ran four repeats of logistic regression, each with a different cluster dummy variable excluded.

Effects of clusters on stem growth was tested with a Kruskal-Wallis test for the two pioneer shrubs *Baccharis macrantha* and *Dodonaea viscosa*. These effects, together with that of fertilizer application was investigated by means of two-way ANOVA's for the late-successional species. Levene's test revealed differences in variance among groups for *Duranta mutisii* and *Xylosma spiculifera*. However, both the ratios of largest to smallest group sizes and the ratios of largest to smallest variances ($F_{\max}$) were below 2 for both species.

The relation between canopy cover of the *Acacia decurrens* trees and performance of the planted seedlings was investigated on plot level by linear regression, for each species. For survival, this was done with arcsine-square-root transformed percentages surviving seedlings per plot. Averages of stem growth per plot were used as a dependent variable for the growth analysis.

All statistical analyses were done in SPSS 11.0, except for Dunn's multiple comparisons which were calculated in MS Excel.

Results

Site characteristics

Different environmental characteristics were found between the plantation clusters (Table 6.2). Cluster 1 is at the high end of the elevation gradient, and has a relatively sandy soil with a high content of available phosphorus. Cluster 5 has the lowest elevation a.s.l., and was also distinguished by low nutrient availability, as shown by the

Table 6.2. Values of environmental variables for the five *Acacia* forest clusters, and mean values for the five clusters each in dry pasture (Pd), sub-humid pasture (Ph), and shrubland (S). C_{org} = organic Carbon; CEC = Cation exchange capacity. Soil parameters are expressed as percentage (texture, C_{org} , base saturation); $cmol^+/kg$ (CEC, kations); or ppm (P_{av}).

environmental factor	cluster of <i>Acacia</i> forest plots					open secondary vegetation (means)		
	1	2	3	4	5	Pd	Ph	S
sand	64	38	46	44	56	55	47	50
silt	26	38	40	36	36	34	27	35
clay	10	24	14	20	8	11	25	15
pH	5.2	5.3	5.3	5.4	5.4	6.0	5.6	5.3
C_{org}	2.5	2.9	2.3	2.3	1.9	0.6	2.2	2.4
CEC	11.2	14.1	9.1	13.5	8.8	3.9	13.5	11.3
Ca	3.8	5.0	2.3	3.6	2.5	1.3	3.3	3.4
Mg	1.5	2.0	1.3	1.7	1.3	0.5	1.6	1.6
K	0.2	0.2	0.2	0.2	0.2	0.3	0.4	0.2
Na	0.0	0.1	0.1	0.1	0.1	0.0	0.1	0.1
Total bases	5.6	7.2	3.8	5.6	4.2	2.1	5.4	0.4
Base saturation	50.0	51.5	42.2	41.3	47.1	53.4	28.5	6.7
P_{av}	4.2	2.5	1.6	3.3	3.3			
elevation a.s.l.	2900	2850	2835	2820	2720	2630	2870	2760

low CEC, organic C and total bases. As to these soil characteristics, cluster 3 is rather comparable to cluster 5. Clusters 2 and 4 are intermediate in terms of soil texture, soil chemical characteristics and elevation above sea level.

Between-species differences in performance

A strong difference in fractions of surviving seedlings was found between species: the pioneer shrub *Baccharis macrantha* had the lowest fraction (6.2% on average) of surviving plantlets as compared to the remaining species (Figure 6.2a). *Dodonaea viscosa* and *Hesperomeles goudotiana* had survival percentages around 25%. The remaining four late-successional species *Croton bogotanus*, *Duranta mutisii*, *Myrsine guianensis* and *Xylosma spiculifera* had mean survival percentages above 60%.

Growth was generally poor: both the pioneer and the late-successional species increased stem length with a few centimeters (Figure 6.2b). Only *C. bogotanus* showed a spectacular growth in some of the plots: although the overall average was around 100 cm, many individuals reached 3 m or more, especially in the plots at higher elevation, which is probably related to a somewhat higher precipitation and air humidity. The pioneer species *B. macrantha* and *D. viscosa* also increased their average stem height, to around 80 cm and 45 cm on average, respectively.

C. bogotanus, again, was the only species that substantially increased its cover percentage in a part of the plots, up to 9% in a fertilized plot, and 12% in the non-

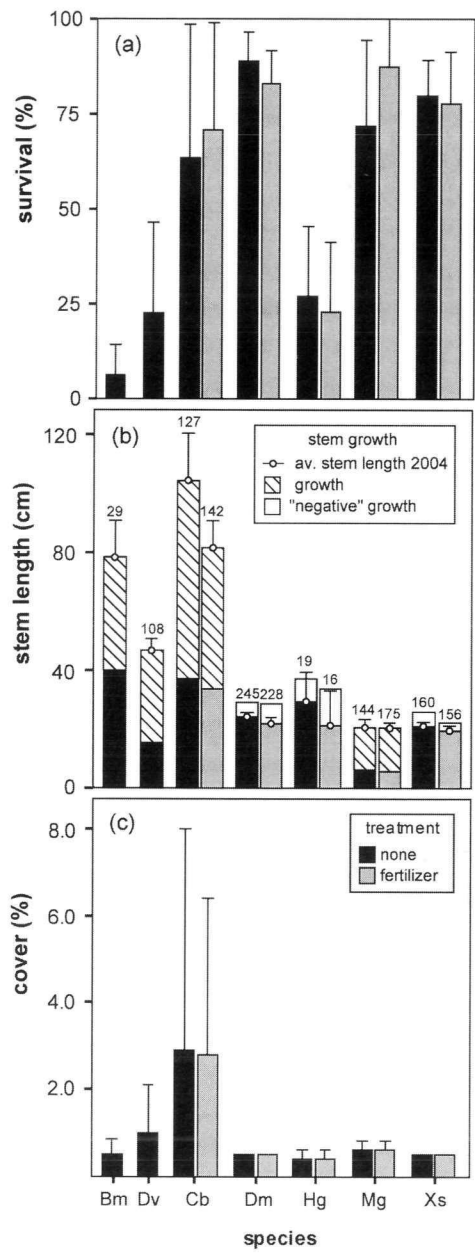


Figure 6.2. Performance of planted seedlings in *Acacia decurrens* forest, expressed in (a) survival; (b) stem length; and (c) cover %. Bm = *Baccharis macrantha*; Dv = *Dodonaea viscosa*; Cb = *Croton bogotanus*; Dm = *Duranta mutisii*; Hg = *Hesperomeles gondotiana*; Mg = *Myrsine guianensis*; Xs = *Xylosma spiculifera*. Errorbars indicate 1 SD. Errorbars in panel (b) correspond to the growth part. N = 5 plots per species for (a) and (c), and indicated in the figure for (b) (*i.e.*, number of individuals).

Table 6.3. Performance of planted seedlings in *Acacia* forest understory as compared to open vegetation types, for each species. Survival percentages per plot were compared by ANOVA and Tukey's Multiple Comparisons, and stem growth by Kruskal-Wallis tests and Dunn's Multiple Comparisons. A = *Acacia* planted forest; Ph = sub-humid pasture; Pd = dry pasture; S = shrubland. The plots included in these analyses did not receive any additional treatment.

	survival			growth		
	F	<i>p</i>	Tukey's M.C.	<i>H_c</i>	<i>p</i>	Dunn's M.C.
pioneer mixture						
<i>Baccharis macrantha</i>	21.62	0.000	Ph>S>A*	70.05	0.000	Pd=Ph>S*
<i>Dodonaea viscosa</i>	25.21	0.000	Ph=Pd>S>A	217.31	0.000	Pd>Ph=A>S
late-successional mixture						
<i>Croton bogotanus</i>	5.76	0.007	A>S=Pd*	99.51	0.000	A>Ph=Pd=S
<i>Duranta mutisii</i>	4.66	0.016	A>Pd*	173.15	0.000	A>S>Ph=Pd
<i>Hesperomeles goudotiana</i>	0.21	0.889		1.77	0.621	
<i>Myrsine guianensis</i>	21.52	0.000	A>Pd=Ph=S	30.47	0.000	A=S>Ph*
<i>Xylosma spiculifera</i>	2.40	0.106		41.67	0.000	S>A=Pd>Ph

*Vegetation types not significantly different from *Acacia* forest are not displayed.

fertilized plot of the same cluster (Figure 6.2c). The remaining species, both the pioneers and the late-successional ones, did not significantly increase their cover over the four years' period.

Performance in Acacia forest as compared to open vegetation

Pioneer species showed the lowest fraction of surviving seedlings when planted in *Acacia* forest understory, as compared to plantations in pastures and shrubland (Table 6.3). Stem growth rates of *B. macrantha* in *Acacia* forest were not different from those in open vegetation. Growth of *D. viscosa* was higher in *Acacia* plantations than in shrublands, but not higher than in pastures. Contrarily, the late-successional species *C. bogotanus*, *D. mutisii*, and *M. guianensis* tended to perform best in *Acacia* understories, or at least not significantly less than in any of the open vegetation types. Growth of *X. spiculifera* in *Acacia* forest was higher than that in sub-humid pastures only.

Factors influencing seedling performance in Acacia forest

An inverse relation was found between cover of *Acacia decurrens* trees and survival of *Dodonaea viscosa* ($F = 10.26$, $p = 0.049$; $\beta = -0.880$). The remaining species showed no significant relations between *Acacia* cover and performance, either for fertilized or non-fertilized plots.

Site characteristics, as expressed by the cluster dummy variables, had a significant effect on survival of most species, except *Hesperomeles goudotiana* (Table 6.4). In cluster 4, most species had a relatively low survival, while this was generally higher in clusters 1

Table 6.4. Results of multiple logistic regression testing for effects of cluster and fertilizer application on survival of planted seedlings. B = partial regression coefficient; p = probability. Numbers in the multiple comparisons column are cluster numbers; numbers not appearing are not significantly different from any of the others.

	overall		cluster effect		fertilizer	
	χ^2	p	p	multiple comparisons	B	p
pioneer mixture						
<i>Baccharis macrantha</i>	44.66	0.000	0.001	1=3>2=4	-	-
<i>Dodonaea viscosa</i>	114.7	0.000	0.000	3>1=2; 1>4=5; 2>5	-	-
late-successional mixture						
<i>Croton bogotanus</i>	159.7	0.000	0.000	1=2>5>4>3	0.534	0.048
<i>Duranta mutisii</i>	26.76	0.000	0.000	1=2=3=5>4	-0.544	0.034
<i>Hesperomeles goudotiana</i>	22.38	0.000	0.507		-0.258	0.535
<i>Myrsine guianensis</i>	57.24	0.000	0.000	1=2=5>3=4	1.122	0.000
<i>Xylosma spiculifera</i>	10.19	0.070	0.074	2>4=5	-0.123	0.620

Table 6.5. Results of ANOVA testing for effects of cluster and fertilizer application on relative stem growth of planted seedlings of the late-successional mixture. Significant differences between clusters are indicated in Figure 3.

	cluster		fertilizer		cluster * fertilizer	
	F	p	F	p	F	p
<i>Croton bogotanus</i>	29.49	0.000	0.29	0.590	1.71	0.149
<i>Duranta mutisii</i>	3.22	0.013	1.21	0.272	3.78	0.005
<i>Hesperomeles goudotiana</i>	0.06	0.982	1.17	0.289	0.28	0.842
<i>Myrsine guianensis</i>	35.68	0.000	13.54	0.000	5.07	0.001
<i>Xylosma spiculifera</i>	6.50	0.000	10.69	0.001	6.74	0.000

and 2. The pioneer shrub *Dodonaea viscosa* had a higher relative stem growth in cluster 3 than in cluster 5 (Kruskal-Wallis test, $\chi^2 = 10.18$, $p = 0.038$; Dunn's test: $p < 0.05$), while for *Baccharis macrantha* no differences were found (Kruskal-Wallis test, $\chi^2 = 3.48$, $p = 0.324$). Again, *H. goudotiana* was the only late-successional species that showed no differences in relative growth across clusters (Table 6.5). In general, cluster 1 revealed the highest growth rates, while the lowest growth rates were mostly found in clusters 3 and 5 (except for *D. viscosa* and *X. spiculifera*). Moreover, an effect of fertilizer application, interacting with the cluster, was found for *D. mutisii*, *M. guianensis* and *X. spiculifera*. *D. mutisii* had the highest growth rates in the non-fertilized plot of cluster 1, while in cluster 4 fertilizer did increase growth (Figure 6.3). The positive effect of fertilizer application on *M. guianensis* was only apparent in clusters 4 and 5. For *X. spiculifera*, growth rates were lowest in the non-fertilized plots of clusters 2 and 4. So, fertilizer had a growth-enhancing effect in cluster 4, as opposed to the general pattern in the remaining clusters.

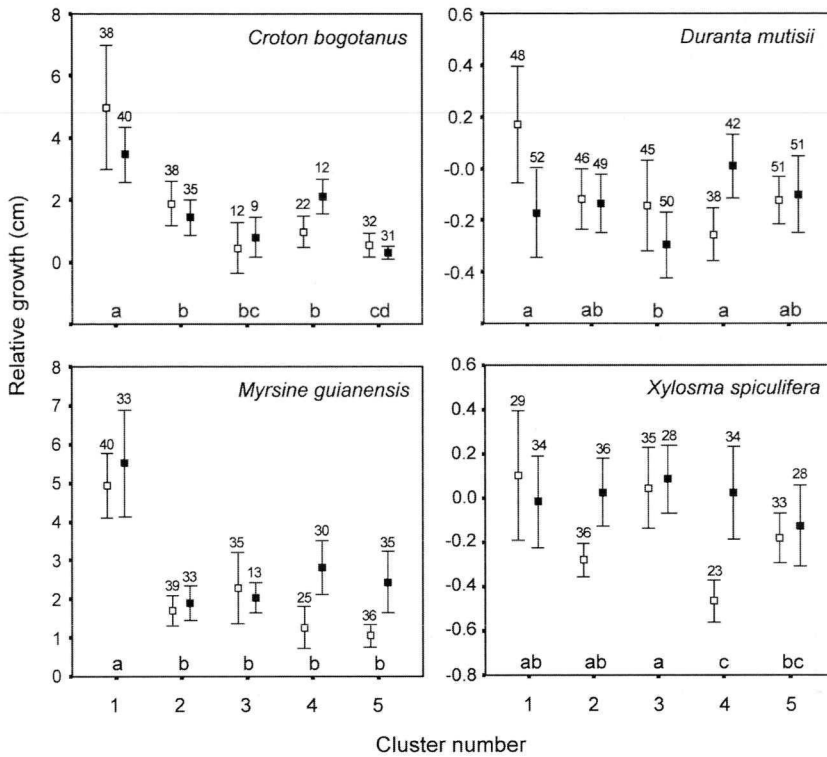


Figure 6.3. Relative growth of planted seedlings in *Acacia decurrens* forest, for the four late-successional species that had significant between-site differences (Table 5). Errorbars indicate 1 SD. *N* is given above the error bars for each average. Clusters sharing letters displayed above the category axis were not significantly different (Tukey's multiple comparisons test).

Discussion

The two pioneer species used in this study, *B. macrantha* and *D. viscosa*, showed a very low survival in the understory of *A. decurrens* forests. The seedlings that survived did, on average, double their stem length over the four years' period. Except for *H. goudotiana*, the late-successional dwarf forest species survived better: generally between 60 – 90%. Growth was generally poor for all species, except for *Croton bogotanus* which reached heights of several meters in some plots. So at least in terms of survival, performance of the late-successional species in *Acacia* forest understory was better than that of pioneer shrubs.

Pioneers clearly had a higher survival in pastures and open scrubs than in *Acacia* forest, but growth was either not different or in the middle of the range. Three out of five late-successional dwarf forest species, *C. bogotanus*, *D. mutisii*, and *M. guianensis*, performed better when planted under an *Acacia* canopy than in open vegetation, in terms of both survival and growth. The density of the *Acacia* canopy did not show to be of any

influence on performance of planted seedlings except for *Dodonaea viscosa*, which had a higher survival when the canopy was relatively open. An experimental design on a smaller scale, with smaller plots and small-scale assessment of irradiation might have given clearer relationships in this respect. Ashton *et al.* (1997, 1998) found that performance of planted seedlings of native Sri Lankan rainforest in artificial *Pinus caribaea* forests was better when parts of the canopy were removed. Apparently, there is a trade-off between the beneficially higher air humidity and reduced temperature fluctuations on the one hand, and reduced solar irradiation on the other.

Most probably, these differences are explained by the light demand of the pioneer shrubs, and the shade tolerance of the late-successional species. In natural circumstances, *B. macrantha* seedlings are generally found in pastures, while those of the dwarf forest species mostly occur in high scrub and dwarf forest (Groenendijk *et al.* in press, see Chapter 3).

Site effects other than *Acacia* cover, however, were much more apparent. We feel that the higher performance of species in cluster 1 is due to the higher elevation of the latter, and with that, a higher air and soil humidity. Water stress is most probably strongly limiting survival and growth for both pioneer and late-successional species of the Andean dwarf forest zone (Groenendijk & Duivenvoorden in prep., see Chapter 5), although shady conditions obviously limited performance of the pioneer species. Moreover, available phosphorus, a limiting nutrient, is higher in cluster 1. The relatively low survival in clusters 3 and 5 might be due to a somewhat lower humidity (mainly the lower-altitude cluster 5) and soil nutrient availability.

Fertilizer addition had a positive effect on survival or growth of three species. However, the differences in growth due to fertilizer application were very small. Soil nitrogen availability might have been increased by the planted *Acacia* trees: many *Acacia* species have root nodules with N-fixing bacteria (New 1984), and *Rhizobium* bacteria have indeed been found in nodules of *A. decurrens* (Alarcón *et al.* 1997). Although phosphorous availability is generally limited in dry volcanic ash soils due to either too low or too high pH values (Marschner 1986), addition apparently improved performance of seedlings in a few cases only. *A. decurrens*, not limited by N, might have been able to profit more from the added phosphorus than the seedlings planted for this experiment, thus enhancing below-ground competition for the native species and reducing their performance. However, we have no explanation for the strong effect of fertilizer being restricted to cluster 4, since this cluster is relatively nutrient-rich. The benefits of fertilizer application for native species development in *Acacia* forests of our study area are small, and most probably will not outweigh the costs.

We concluded that the late-successional species used in this study, except *H. gondotiana*, can be planted successfully under *Acacia* canopies. Survival rates are fairly high, and – after a period of seedling establishment – growth and cover will probably increase after opening of the *Acacia* canopy. Since the latter species in our study area

commonly rejuvenates, and has a life span of at least 25 years, thinning should be executed after establishment of the seedlings. Care should be taken that seedlings do not grow vertically at the cost of lateral extension, since that might reduce their performance and subsequent regeneration of *Condalia* dwarf forest after removal of the nursing *Acacia*.

Furthermore, *A. decurrens* could possibly be included in a future experiment on restoration of native vegetation on abandoned pastures. If this species would be planted sparsely, the ecological disadvantages of this species could be outweighed by its positive effect on performance of late-successional *Condalia* dwarf forest species. *A. decurrens* reportedly reaches a height of four meters or more, at four to six years after plantation, both in our study area and in Chile (Perea Rojas 1992; Ovalle *et al.* 1995; Arredondo *et al.* 1998).

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Chapter 7.

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 leivensis*). *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

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 coerulea* and *Baccharis macrantha*. 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 levees 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 assessed based on their life history characteristics (mainly occurrence of seedlings), structure 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 forest, *Hesperomeles goudotiana*, *Myrsine guianensis* and *Xylosma spiculifera*, were found relatively often in *Baccharis* – *Dodonaea* scrubs, also as juveniles, and were also considered mid-successional species, although they never co-dominate in pioneer scrubs. The remaining three dwarf forest species, *Condalia thomasiana*, *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

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 re-sprouting 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.

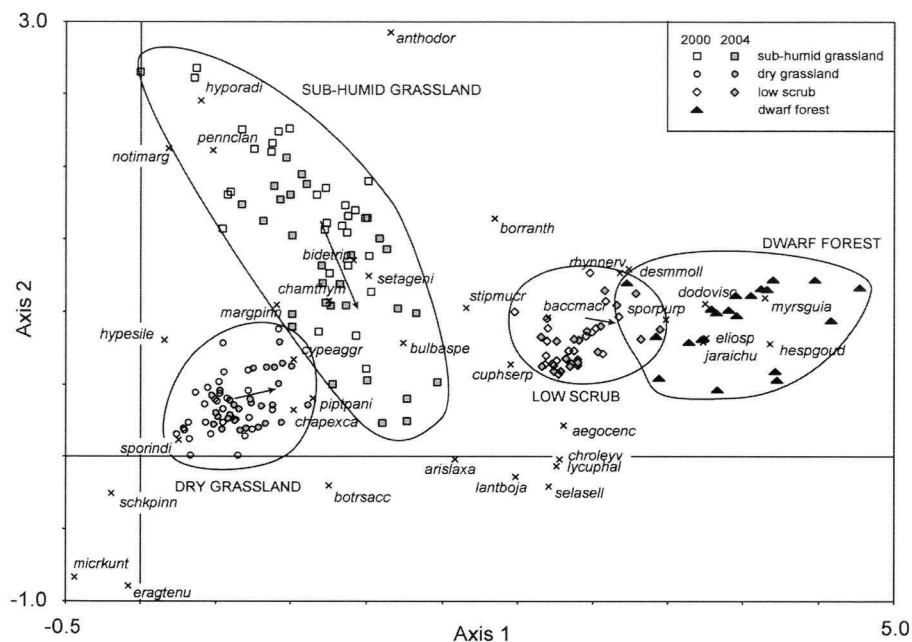


Figure 7.1. Ordination diagram of a DCA carried out on species abundances in the vegetation of the experimental plots (excluding the planted seedlings), and of dwarf forest vegetation releves. For the experimental plots, the situation of 2000 and that of 2004 were included. Samples are indicated by symbols (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 *Schkura pinata*, 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 *Antboxanthum 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 instead 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 treelet 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, instead 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.

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Summary

Introduction

Severe degradation of ecological systems in drylands has mainly been caused by increased human populations and subsequent over-exploitations. "Original" ecosystems are generally believed to have a high complexity and species diversity on the one hand, and high values for ecosystem functions related to water retention and soil conservation on the other. Hence, it is essential from the point of view of both nature conservationists and farmers to stop degradation processes and restore the natural vegetation to an acceptable level of biodiversity and other ecosystem functions. 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.

Secondary succession (*i.e.*, succession after disturbance) often proceeds too slow or takes a non-desired course due to abiotic or biotic barriers, such as increased and strongly fluctuating soil temperatures and decreased local soil humidity. A lack of seed dispersal is apparent in many abandoned fields: many forest species have been shown to disperse their seeds over a few tens of meters only. On top of that, seedlings often face competition with exotic pasture grasses for light, water, and nutrients.

Ecological restoration, defined as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed", can be put into practice in various ways, ranging from directly reassembling a predefined historic ecosystem with a certain set of species, to a mere halt to degradation and a redirection of a disturbed ecosystem towards an "original" one. The latter would be an effort that relies on subsequent natural recovery (soil formation processes, vegetation succession). The choice of restoration or rehabilitation methods depends (apart from the desired characteristics of the ecosystem) largely on the degree of site degradation, and might be aimed at halting disturbance, restoring soil properties, and promoting establishment of desired organisms. Experiences with plantation of native species are still relatively sparse, although many experiments have been initiated. Most of these are in the humid tropics. The importance of shrubs in the facilitation of succession, especially in areas with a Mediterranean climate, has been stressed.

This thesis reports on the onset of an restoration experiment of late-successional dwarf forest in the Checua River valley at the northern edge of the high plain of Bogotá, 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 were:

- Which types of vegetation are present in the study area, and which pathways of (secondary) succession are likely to occur?

- Is seed dispersal a limiting factor for the 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 the planting of native species give prospects for conversion of exotics' forests into native vegetation?

The fieldwork area was a semi-arid intramontane basin in the Eastern Cordillera of Colombia between 2550 - 2950 m.a.s.l., at the edge of the high plain of Bogotá, which is one of the most populated and intensely cultivated regions in the Colombian Andes. The study area is a mosaic landscape of grassland, scrubs, planted exotics' forest, and fragments of dwarf forest. Severe erosion formed crevices up to several meters depth throughout the area. The dry andean *Condalia* dwarf forest, endemic to the area, was defined as the "original" ecosystem for the area. Plantations with *Acacia decurrens* 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.

Results of this research

In Chapter 2, I present a study on vegetation patterns in the study area, as a basis for the restoration experiment treated in Chapters 5 and 6. Successional pathways were explained by means of environment and disturbance history data. We laid out 101 relevés in grassland and shrubland types in different stages of recovery, and in relatively little disturbed endemic *Condalia* dwarf forests. Based on a TWINSPLAN classification we recognized two types of grasslands, three scrub types and a dwarf forest type. The dry pastures of the peditments 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 *Pennisetum clandestinum*, *Anthoxanthum odoratum* and other graminoids. Most woody species invading the pastures are asteraceous shrubs. *B. macrantha* reaches a co-dominant status together with *Dodonaea viscosa* in pioneer scrubs. 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 coerulea* and *Baccharis macrantha*. Understoreys were mostly species-poor, and the overall vegetation cover was relatively low. CCA was applied to relate

species composition to environment, disturbance history and to the spatial configuration of the relevés. Abiotic factors mostly related to species composition were soil nutrient richness and soil organic matter content. Invasion of grasslands by woody species is pioneered by *Baccharis macrantha* and *Dodonaea viscosa*. *Dalea coerulea* was the predominant woody species on truncated clayey soils, which will probably not support *Condalia* dwarf forest. This exploratory study will be of use in the set-up of future succession-based restoration experiments.

Chapter 3 treats the successional affinity of the nine woody species used in the plantation experiment (*Baccharis macrantha*, *Dalea coerulea*, *Dodonaea viscosa*, *Condalia thomasiiana*, *Croton bogotanus*, *Duranta mutisii*, *Hesperomeles goudotiana*, *Myrsine guianensis* and *Xylosma spiculifera*), inferred from the structure, diversity and disturbance history of the vegetation where these occurred. The data for this study were obtained from the same 101 relevés as those used for Chapter 2. 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 coerulea* 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 most probably pioneered by *Baccharis macrantha* and followed by *Dodonaea viscosa*. *Dalea coerulea* 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: *B. macrantha* is a true pioneer, while *D. viscosa* is a pioneer tending to mid-successional affinity. *M. guianensis*, *H. goudotiana* and *X. spiculifera* are late-successional species, but not as clearly so as *C. thomasiiana*, *C. bogotanus* and *D. mutisii*. One species was considered not to be part of the above-mentioned successional series: *D. coerulea* is a woody pioneer on eroded clay soils, but persists and co-dominates old scrub stands on these soil types.

Chapter 4 reports on soil seed banks of five vegetation types (grassland, low scrub, high scrub, dwarf forest, and plantation forest), which were studied in order to assess the potential for regeneration of mature dwarf forest. Seeds in soil samples taken at 0-5 and 5-10 cm were allowed to germinate in a greenhouse for a period of 12 weeks. A total of 22429 germinated seeds were recorded, represented by 110 species, which were classified according to their growth form and position in the successional series of the vegetation in the area. Seeds from woody late-successional species were hardly recorded in pioneer vegetation types, where artificial seed supply or seedling plantation seem the best way to accelerate natural regeneration. Especially in grasslands, the only woody species abundantly found in the soil seed bank was *Baccharis macrantha*, an important species of the first woody stages of succession. Pioneer shrubs that act as perch or shelter deserve attention in conservation management in severely degraded areas.

The results of a plantation experiment with native woody species are presented in Chapter 5. We hypothesized that planted seedlings of native woody pioneers would perform best in open pastures, and that planted seedlings of late-successional shrub and tree species would perform better in shrubland. Additionally, we evaluated the effect of treatments with stones and fertilizer on seedling performance. Moreover, we expected natural succession in the matrix vegetation to be accelerated as an effect of canopy establishment by planted species. Plantation with species mixtures of pioneers, and of late-successional species, were applied in both pastures and shrublands. Seedling performance and matrix vegetation development were monitored from 2000 to 2004. Survival was low for some species, probably caused by drought and night frost. Seedling growth was generally low: pioneer species reached stem heights up to around 1 m, while the late-successional species mostly did not grow significantly. We concluded that pioneer shrubs performed better in pastures than in shrublands. Late-successional species survived better in pastures, but stem growth was higher in shrublands. Stone treatments enhanced survival for most species, while the fertilizer addition increased stem growth for late-successional species. A canopy of planted seedlings was established only with pioneer species planted in pastures. In these plots, species turnover rate did not differ from that of control plots. Hence, changes in species composition were not an effect of the planted canopy. However, total herb cover in these plots did increase as an effect of the plantation. We concluded that succession might indeed be accelerated by a planted canopy, but more time is needed to be able to detect successional changes as an increased turnover, different species composition and invasion of typical late-successional species. It is recommended to use mixtures of pioneer, mid-, and late-successional species in future plantation trials.

Chapter 6 reports on performance of planted seedlings of seven species (a subset of the nine species mentioned before) in the understorey of *Acacia decurrens* forests. A catalytic effect of exotic tree plantations for natural regeneration, mostly by mitigating soil temperature and humidity fluctuations, has been shown by many authors. 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. Consequently there are many examples of hampered understorey development in the tropics. We examined the possibilities for conversion of *Acacia decurrens* plantations to native *Condalia* dwarf forests, by inserting native woody species under the planted canopies. Performance of planted seedlings in *Acacia* forest was compared with that in open secondary vegetation. Moreover, we investigated the effect of site differences, *Acacia* canopy cover and fertilizer application on seedling performance. Late-successional species generally performed better in *Acacia* plantations than in open vegetation, while the reverse was true for pioneer shrubs, which had very low survival rates under plantations. We concluded that planting of late-successional *Condalia* dwarf forest species give good prospects for conversion of *Acacia* forests into native vegetation.

Conclusions and recommendations

Accelerated succession by means of plantation of woody species could possibly be achieved in the future, but no substantial succession has been shown to occur in the first four years of this project. Other vegetation characteristics of the experimental plots have generally changed very little over the period 2000 – 2004. Both pasture types are still far from similar to the woody vegetation types. Some scrub plots are floristically relatively similar to *Condalia* dwarf forests, but the vegetation stature of these plots is clearly lower and less dense. Successional changes were probably not linked to any canopy closure of the planted seedling assemblage, 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.

Apart from environmental effects, understorey 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 and species traits (reproductive strategy, 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.

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. 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. 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, and that pioneers might be limited by other nutrients than late-successional species. However, this remains to be investigated for the species of the dwarf forest region, and probably also for the plant species of most other successional seres worldwide.

Further succession-based restoration experiments

Baccharis macrantha – *Dodonaea viscosa* scrubs seem an essential stage to be passed in the course of vegetation succession towards *Condalia* dwarf forests. Further plantation exper-

iments in the study area therefore should include *B. macrantha* and *D. viscosa*. In one single plantation effort, seedlings of pioneer shrub and mid/late-successional treelet species could be planted. I would expect that the pioneer shrubs form a relatively closed canopy within five years or so, after which the dwarf forest species start to grow.

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

For the conversion of *Acacia* forest into "natural" woody vegetation, planting of *Condalia* dwarf forest species might give promising results. More experiments are needed to determine when the *Acacia* canopy should be thinned or cleared, and to assess the effects of this activity on growth rates of the planted 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. *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 a fast 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.

Resumen

Introducción

La degradación severa de los ecosistemas de zonas áridas ha sido causada principalmente por el aumento de las poblaciones humanas y por consiguiente la sobre-explotación. Se considera, por lo general, que los ecosistemas "originales" tienen por un lado, un alto grado de complejidad y de diversidad de especies y por el otro lado, alto grado de funcionamiento ecológico (retención de agua y conservación de suelos). Por lo tanto, desde un punto de vista tanto agrícola como conservacionista, es necesario detener los procesos de degradación y restaurar la vegetación natural hasta cierto nivel de biodiversidad y funcionamiento ecológico aceptable. La mayor parte del conocimiento sobre la recuperación de los bosques tropicales proviene de los bosques de tierras bajas y de las zonas montañas húmedas. Las zonas montañas secas han sido virtualmente inexploradas a este respecto. Producto de barreras bióticas o abióticas como altas y fluctuantes temperaturas del suelo y baja humedad local del suelo, la sucesión vegetal secundaria (*i.e.*, la sucesión después de eventos de perturbación) con frecuencia transcurre muy despacio, o se desarrolla hacia un tipo de vegetación no deseada. En muchos campos abandonados hay una aparente ausencia de dispersión de semillas, en donde muchas especies del bosque dispersan sus semillas a sólo pocos metros. Además, las plántulas frecuentemente compiten por luz, agua y nutrientes con pastos exóticos.

La restauración ecológica, definida como "el proceso de la recuperación asistida de un ecosistema degradado, dañado o destruido", se puede poner en práctica de varias formas. Una forma consiste en el restablecimiento de un ecosistema histórico predefinido con un grupo particular de especies. Otra forma consiste en frenar el proceso de degradación y redirigir el desarrollo de un ecosistema perturbado hacia el ecosistema "original". El éxito de esta opción dependería de la recuperación natural sucesiva (procesos de formación de suelos y sucesión de la vegetación). La selección de los métodos para la restauración o la rehabilitación depende (aparte de las características deseadas del ecosistema) del grado de degradación del sitio y de la necesidad de detener la perturbación, restaurar las propiedades del suelo o estimular el establecimiento de organismos deseados. La experiencia con la plantación de especies nativas es todavía relativamente escasa, aunque se han iniciado muchos experimentos. La mayoría de estos experimentos han resaltado la importancia de los arbustos para la facilitación de la sucesión vegetal, particularmente en áreas mediterráneas.

Esta tesis presenta el inicio de un experimento de restauración del bosque enano seco, nativo en el valle del río Checua, en la franja norte de la Sabana de Bogotá, con base en la idea de la aceleración de la sucesión vegetal gracias a un dosel cerrado de especies leñosas plantadas. Durante la realización de este esfuerzo de restauración, adquirir el conocimiento básico sobre los requisitos ambientales de las especies deseadas, las características de los

sitios de crecimiento del tipo de vegetación deseado y la capacidad de dispersión de los propágulos. Las preguntas principales del proyecto eran:

- ¿Qué tipos de vegetación están presentes en el área del estudio y qué formas de sucesión (secundaria) podrían ocurrir?
- ¿Es la dispersión de semillas un factor limitante para el desarrollo del matorral secundario y del bosque enano?
- ¿Cómo es el éxito de establecimiento de especies pioneras y especies de sucesión tardía plantadas en tipos de vegetación secundaria abierta?
- ¿Puede acelerarse la sucesión natural en pastizales por medio de la plantación de especies nativas leñosas?
- ¿Cómo es el éxito de establecimiento de especies pioneras y especies de sucesión tardía plantadas en el sotobosque de los bosques exóticos de *Acacia decurrens*?
- ¿La plantación de especies nativas puede ser provechosa para la conversión de bosques con especies exóticas en bosques de vegetación nativa?

El área del estudio es un valle intramontano semiárido de la Cordillera Oriental, entre 2550 y 2950 m.s.n.m., en la franja norte de la Sabana de Bogotá, la cual es una de las regiones más pobladas y cultivadas de los Andes Colombianos. El paisaje es un mosaico de pastos, matorrales, bosques plantados con especies exóticas, y unos fragmentos pequeños de bosque enano. El bosque enano seco de *Condalia*, endémico de la zona, se designó como el ecosistema "original" del área. Existen también plantaciones de *Acacia decurrens* establecidas entre 1980 y 1984 con fines de conservación de los suelos. Sin embargo, en estas plantaciones el desarrollo del sotobosque ha sido insignificante y por lo tanto la recuperación de las funciones ecológicas ha sido poca en comparación con el bosque enano seco de *Condalia*.

Resultados de esta investigación

En el capítulo 2 se presenta un estudio acerca de los patrones de vegetación en la zona del Valle del Río Checua, como base para el experimento de restauración ecológica planteado en los capítulos 5 y 6. El objetivo consistió en explicar las líneas de sucesión por medio de factores ambientales y datos de la historia de la perturbación. Se establecieron 101 levantamientos de vegetación tanto en pajonales y en matorrales en diferentes estados de regeneración, como en fragmentos de bosque enano de *Condalia thomasi* relativamente poco perturbados. Con base en una clasificación TWINSPAN, se reconocieron dos tipos de pajonales, tres tipos de matorrales y un tipo de bosque enano. Los pajonales secos del piedemonte generalmente tienen una cobertura vegetal baja y una abundancia relativamente alta de hierbas (anuales) de la familia Asteraceae. Los pajonales sub-húmedos de alta elevación tienen una cobertura relativamente alta de *Pennisetum clandestinum*, *Anthoxanthum odoratum* y otras graminíoides. La mayoría de las especies leñosas invasoras son arbustos de Asteráceas. *Baccharis macrantha* llega a codominar los matorrales pioneros, junto con *Dodonaea viscosa*. Remanentes del bosque enano se encontraron por lo general en sitios inclinados y rocosos, en comparación con los matorrales pioneros y de sucesión tardía florísticamente similares. Esto

se atribuyó al supuesto desprecio de dichas pendientes rocosas y poco accesibles de parte de los ganaderos para el establecimiento de pastos, dejándolos relativamente poco perturbados. En las partes gravemente erosionadas del área de estudio en donde arcillas Terciarias han quedado expuestas, se encontraron arbustales dominados por *Dalea coerulea* y *Baccharis macrantha*. El sotobosque es pobre en especies y tiene una cobertura vegetal baja. Se aplicó un CCA para relacionar la composición de especies con las variables ambientales, la historia de la perturbación y con la ubicación espacial de los levantamientos. Los factores abióticos más correlacionados con la composición de especies fueron la disponibilidad de nutrientes y el contenido de materia orgánica en el suelo. La invasión de los pajonales por especies leñosas es iniciada por *Baccharis macrantha* y *Dodonaea viscosa*. *Dalea coerulea* es la especie leñosa dominante en los suelos erosionados y arcillosos, los cuales probablemente no soportan el bosque de *Condalia*. El presente estudio explorativo sirve para el diseño de futuros experimentos de restauración basados en la sucesión.

El capítulo 3 trata las afinidades sucesionales de las nueve especies leñosas usadas en el experimento de plantación (*Baccharis macrantha*, *Dalea coerulea*, *Dodonaea viscosa*, *Condalia thomasiensis*, *Croton bogotanus*, *Duranta mutisii*, *Hesperomeles goudotiana*, *Myrsine guianensis* y *Xylosma spiculifera*). Estas afinidades se dedujeron a partir de la estructura vegetal, la biodiversidad y la historia de la perturbación de los sitios en donde se encontraron las especies mencionadas. Los datos usados para este estudio se obtuvieron de los mismos levantamientos de vegetación utilizados en el capítulo 2. La historia de la perturbación de los sitios durante los últimos 60 años se obtuvo a partir de una serie de fotografías aéreas (1941-1991). Se aplicaron análisis de correspondencia canónica (CCA) y regresiones logísticas para relacionar la composición de especies con la diversidad, el medio abiótico y la historia de perturbación. Las nueve especies mostraron una preferencia por ciertos grupos de estructura vegetal. Se encontró además, una clara relación entre la ocurrencia de especies y la diversidad de la vegetación. *Baccharis macrantha* y *Dalea coerulea* resultaron relativamente resistentes al pastoreo, mientras que las demás especies reaccionaron de manera negativa. Así mismo, el contenido de arcillas, la disponibilidad de bases y el contenido de carbón orgánico en el suelo fueron factores importantes para la ocurrencia de las especies. La invasión de pajonales por especies leñosas es probablemente iniciada por *Baccharis macrantha*, seguida por *Dodonaea viscosa*. *Dalea coerulea* se encontró por lo general en suelos erosionados arcillosos. Se perfeccionó la clasificación hipotética de las nueve especies de plantación en la categoría de pioneras o de sucesión tardía: *B. macrantha* es una especie pionera, mientras *D. viscosa* tiende a ser afín a la sucesión mediana. *M. guianensis*, *H. goudotiana* y *X. spiculifera* son especies de sucesión tardía pero que aún aparecen antes que *C. thomasiensis*, *C. bogotanus* y *D. mutisii*, en la serie sucesional. Sólo una especie estuvo fuera de la serie sucesional: *D. coerulea*, especie pionera leñosa de suelos erosionados arcillosos, pero persistente y codominante en matorrales maduros de este tipo de suelo.

En el capítulo 4 se presenta un estudio acerca de los bancos de semillas encontrados en cinco tipos de vegetación (i.e., pajonal, matorral bajo, matorral alto, bosque enano y

bosque plantado de *Acacia decurrens*). El objetivo era determinar el potencial de regeneración de bosque enano maduro. Se tomaron muestras de suelo a de 0-5 y de 5-10 cm de profundidad. Estas se dispusieron en bandejas y se dejaron germinar las semillas presentes durante un periodo de 12 semanas en un invernadero. Se registró un total de 22429 semillas germinadas pertenecientes a 110 especies, las cuales se clasificaron de acuerdo a su forma de crecimiento y a su posición en la serie sucesional de la vegetación nativa de la zona de estudio. Semillas de especies leñosas de sucesión tardía fueron muy escasas en tipos de vegetación pionera, en donde la adición artificial de semillas o la siembra de plántulas parece la mejor forma de acelerar la regeneración natural. La única especie leñosa encontrada en los bancos de semillas, especialmente en los suelos de los pastos, fue *Baccharis macrantha*, una especie importante de las primeras fases arbustivas de la sucesión vegetal. Las especies arbustivas pioneras utilizadas como perchas para aves o refugio merecen atención para el manejo y la regeneración de las áreas gravemente degradadas.

Los resultados del experimento de plantación con especies nativas leñosas se presentan en el capítulo 5. Nuestra hipótesis inicial fue que el rendimiento de las plántulas de plantas pioneras nativas leñosas sería mejor cuando plantadas en pastizales abiertos y que el rendimiento (supervivencia y crecimiento del tallo) de las plántulas de especies nativas leñosas de sucesión tardía sería mayor cuando son sembradas en matorrales. Adicionalmente, evaluamos los efectos del tratamiento de las plántulas con piedras protectoras y con fertilizante sobre el rendimiento. Esperábamos que la sucesión natural en la matriz de vegetación (*i.e.*, la vegetación presente no plantada) se vería acelerada por el establecimiento de un dosel de especies plantadas. La siembra de especies pioneras y mezcladas con especies de sucesión tardía, se realizó tanto en pastizales como en matorrales. El rendimiento de las plántulas se monitoreó durante cuatro años, desde 2000 al 2004. La supervivencia fue baja para algunas especies, probablemente a causa de la sequía y las heladas. El crecimiento de las plántulas generalmente fue bajo: las especies pioneras alcanzaron alturas del tallo alrededor de un metro, mientras que la mayoría de las especies de sucesión tardía no crecieron significativamente. Concluimos que el rendimiento de los arbustos pioneros fue mayor en pastizales que en matorrales. Las especies de sucesión tardía sobrevivieron más en pastizales, pero el crecimiento del tallo fue mayor en matorrales. El tratamiento con piedras aumentó la supervivencia de la mayoría de las especies, mientras que la aplicación de fertilizante aumentó el crecimiento del tallo para las especies de sucesión tardía. Solamente en pastizales plantados con especies pioneras en pastizales fue posible establecer un dosel con cobertura significativa. En éstas parcelas, el grado de recambio no difirió al de las parcelas testigo. Por lo tanto, los cambios en la composición de especies no fueron efecto del dosel plantado. En las mismas parcelas, Sin embargo, la cobertura total de hierbas aumentó como consecuencia la plantación. Concluimos que la sucesión puede ser acelerada por un dosel plantado, pero se necesita suficiente tiempo para poder detectar cambios sucesionales en términos de un grado de recambio elevado, cambios en la composición de especies y la invasión de especies típicas de vege-

tación madura. Se recomienda aplicar mezclas de especies tanto pioneras como de sucesión mediana y tardía en futuros experimentos de plantación.

El capítulo 6 presenta el rendimiento de las plántulas de siete especies (un subgrupo de las nueve especies usadas en los capítulos anteriores), sembradas en el sotobosque de bosques anteriormente plantados de *Acacia decurrens*. Diferentes estudios han reportado que la plantación de árboles foráneos genera un efecto catalítico debido a que se amortiguan las fluctuaciones de temperatura y de humedad del suelo. Sin embargo, el grado catalítico de tal plantación depende del manejo de sitio (perturbación), la(s) especie(s) plantada(s) (posibles efectos alelopáticos), la distancia a un eventual bosque nativo (fuente de semillas), propiedades del suelo y el pastoreo. Por lo tanto, existen muchos ejemplos de desarrollo impedido de sotobosque en el trópico. Examinamos las posibilidades para la conversión de plantaciones de *Acacia decurrens* en bosque enano nativo de *Condalia*, mediante la adición de especies leñosas bajo el dosel del bosque de *Acacia*. Se comparó el rendimiento de las plántulas sembradas en el bosque de *Acacia* y en varios tipos de vegetación secundaria abierta. Adicionalmente, investigamos el efecto del sitio de plantación, la cobertura del dosel de *Acacia* y la aplicación de fertilizante sobre el rendimiento de las plántulas. Las especies tardías generalmente se desempeñaron mejor en el sotobosque de *Acacia* que en la vegetación secundaria abierta en contraste con las especies pioneras, las cuales presentaron una alta mortalidad en el bosque plantado. Se concluyó que la plantación de especies de sucesión tardía es una buena alternativa para la conversión de los bosques de *Acacia decurrens* en bosque enano nativo.

Conclusiones y recomendaciones

La sucesión acelerada por medio de la plantación (siembra) de especies leñosas posiblemente se podrá lograr en el futuro. No obstante en los cuatro primeros años de esta investigación no se presentó una substancial sucesión vegetal. Los dos tipos de pastizales todavía se encuentran florísticamente diferentes de los tipos de vegetación leñosa. Algunas parcelas experimentales de matorral tendieron a asemejarse florísticamente al bosque enano de *Condalia*, pero la vegetación es claramente mas baja y menos densa que el bosque enano. Los cambios sucesionales no parecen estar relacionados con un eventual cerramiento del dosel plantado, sino más bien con la exclusión del ganado. La única respuesta detectada estadísticamente fue el incremento de la cobertura herbácea total en las parcelas de pastizal plantadas con especies pioneras. No obstante, se espera que, durante los próximos años ocurran cambios más contundentes en las parcelas plantadas en comparación con las parcelas control, por lo menos en los pastizales. En el último monitoreo, el dosel de las parcelas plantadas había alcanzado una cobertura hasta del 20%, el cual sólo se alcanzó de forma reciente. Tal parece que los cambios microclimáticos estaban comenzando a suceder y quizás aún no eran muy fuertes. Se necesita un monitoreo microclimático para medir una posible relación entre los cambios vegetales con la humedad y la temperatura de suelo y del aire.

Además de los efectos ambientales, el desarrollo del sotobosque en la zona de estudio estuvo limitado por la oferta de propágulos. Por lo tanto, la escala temporal, en la que un substancial recambio de especies tendría lugar depende tanto de las características del sitio como de las propiedades de las especies (*e.g.*, estrategia reproductiva, historia de vida, requisitos de germinación). El monitoreo a largo plazo de las parcelas experimentales es esencial para entender cómo se desarrollará el bosque enano de *Condalia* apartir de pastizales o matorrales, bien sea con o sin la siembra de plántulas. Hasta el momento, la mayoría de las publicaciones acerca de la plantación de especies nativas con fines de restauración vegetal se ha enfocado en el rendimiento de las plántulas sembradas. Aparte de los datos presentados en el capítulo 5 de esta tesis no existen datos disponibles sobre el monitoreo y desarrollo de pastizales después de la siembra de de especies leñosas.

Las diferencias entre el rendimiento de especies pioneras y tardías puede explicarse por diferentes estrategias de absorción de nutrientes y por la fotosíntesis. Aunque es difícil hacer al respecto, tal parece que las especies de sucesión tardía son más rapidamente afectadas por la sequía (disminuyendo la tasa fotosintética) que las pioneras. Se puede esperar que las pioneras tengan una mayor capacidad de absorción de nutrientes cuando la concentración de nutrientes solubles es baja en comparación con las especies tardías. En adición, las pioneras y las tardías podrían ser limitado por diferentes nutrientes. Sin embargo, esto aún no ha sido investigado para las especies de la zona del bosque enano, así como para muchas especies de plantas de otras series sucesionales en el mundo.

Futuros experimentos de restauración basados en la sucesión

La limitación por dispersión de semillas se podría remediar por medio de la adición de semillas de especies deseadas. Experimentos de adición de semillas podrían llevarse a cabo con especies del bosque enano, en matorrales con diferentes coberturas de dosel y sotobosque, con el fin de definir una cobertura límite bajo la cual el desarrollo de las especies de bosque enano sea exitoso.

Con base en la idea que los arbustales de *Baccharis macrantha* y *Dodonaea viscosa* son una fase esencial en el curso de la sucesión vegetal hacia el bosque enano de *Condalia*, futuros experimentos de plantación en esta zona, deberían incluir estas dos especies. Además, se podrían mezclar plántulas de arbustos pioneros y de arbustos o arbolitos de sucesión tardía. Dentro de los primeros cinco años las pioneras deberían formar un dosel de substancial cobertura (>30%), lo cual permitiría a las especies de bosque enano comenzar a crecer.

Para la conversión de los bosques de *Acacia* hacia una vegetación leñosa “natural”, la plantación de especies del bosque enano de *Condalia* puede ser una estrategia prometedora. Se necesitan más experimentos para establecer el momento de poda, raleo y tala de las *Acacias* y para conocer los efectos de estas actividades sobre el crecimiento de las especies nativas y en la sucesión vegetal. Debido a la capacidad de rebrote de *A. decurrens* a partir de sus raíces, la erradicación completa puede ser laboriosa y necesitar de repetidos esfuerzos. Pese a la mala fama de las especies de árboles foráneas en proyectos de plantación – aspecto

del que no difiero, en particular cuando se trata de monocultivos de *A. decurrens* – no deberíamos excluir del todo la *Acacia* en esfuerzos de plantación enfocados a forzar un salto en la sucesión. *A. decurrens* se podrían utilizar en el establecimiento del "matorral catalítico", junto con *B. macrantha*, *D. viscosa* y algunas especies de bosque enano medianas y tardías. *A. decurrens* puede expandir rápidamente su copa y es un posibleme fijador de nitrógeno, por lo que la plantación (y la vegetación no plantada) puede aprovecharse de ella. un monitoreo y manejo permanente serían necesarios para controlar, ralea y talar las *Acacias* en un cierto momento.

Samenvatting

Introductie

De aantasting van ecosystemen in droge gebieden is voornamelijk veroorzaakt door bevolkingsgroei en een daaruit voortkomende over-exploitatie. Over het algemeen is men ervan overtuigd dat "oorspronkelijke" ecosystemen zich enerzijds kenmerken door een hoge graad van complexiteit en soortendiversiteit, en anderzijds door hoge waarden van ecosystemfuncties gerelateerd aan watervasthoudend vermogen en bodembescherming. Het is dus essentieel, zowel vanuit het natuurbeschermings- als vanuit het landbouw-oogpunt, dat het aantastingsproces gestopt wordt en de natuurlijke, oorspronkelijke vegetatie hersteld wordt in een bepaalde staat met een acceptabele biodiversiteit en ecosysteem-functies. De meeste kennis van bos-herstel in de tropen is opgedaan in tropische laaglanden en vochtige berggebieden. Droge berggebieden zijn wat dit betreft nagenoeg onontgonnen.

Secundaire successie (vegetatieontwikkeling na een verstoring) verloopt vaak te langzaam of volgt een ongewenste richting als gevolg van abiotische of biotische barrières, zoals sterk schommelende temperaturen en vochtigheid van zowel de bodem als de lucht. Daarnaast is er in de meeste door de mens verlaten velden een gebrek aan inkomende zaden: veel boomsoorten uit aangrenzend natuurlijk bos in de tropen verspreiden hun zaden slechts over een afstand van ongeveer 10 meter het ontboste terrein in. Daar komt nog bij dat zaailingen vaak concurrentie ondervinden met exotische weide-grassen om licht, water en nutriënten.

Ecologische restauratie, gedefinieerd als "het proces van het begeleiden van het herstel van een gedegradeerd, beschadigd of vernietigd ecosysteem", kan op verschillende manieren ten uitvoer worden gebracht. Dit kan variëren van het direct herstellen van een – van tevoren gedefinieerd – oorspronkelijk ecosysteem met een bepaalde soortensamenstelling tot het tegenhouden van het degradatieproces en het initiëren van het herstelproces in de richting van een "origineel" systeem. Het succes van deze laatste benadering hangt dan af van het daaropvolgende natuurlijke herstelproces (bodenvorming, vegetatiesuccessie). De keuze van methoden van restauratie of rehabilitatie hangt – naast de gewenste eigenschappen van het ecosysteem – voornamelijk af van de mate van degradatie van het gebied en kan bijvoorbeeld gericht zijn op het opheffen van de oorzaak van verstoring, het herstellen van bepaalde bodemeigenschappen of het bevorderen van kolonisatie door gewenste soorten. Er is nog weinig ervaring met de aanplant van inheemse soorten, ofschoon er wel een aantal experimenten zijn begonnen, voornamelijk in tropische laaglandgebieden. Uit onderzoek in vooral Mediterrane gebieden is gebleken dat struiken, bijvoorbeeld door het geven van schaduw of het plaatselijk verrijken van de bodem, de ontwikkeling van andere soorten positief kunnen beïnvloeden; dit verschijnsel wordt facilitatie genoemd.

Dit proefschrift doet verslag van een experiment waarmee een begin is gemaakt met restauratie van het inheemse droge "dwergbos" van de vallei van de rivier de Checua, aan de noordrand van de hoogvlakte van Bogotá, Colombia. Het experiment is gebaseerd op het idee dat men vegetatieontwikkeling zou kunnen versnellen door middel van het aanplanten van struiken of bomen die relatief snel een gesloten kronendak vormen. Tijdens de uitvoering van dit experiment heb ik basale kennis vergaard over habitateisen van een aantal belangrijke en gewenste inheemse soorten, habitatkenmerken van vegetatietypen en enkele aspecten van zaadverspreiding van plantensoorten. De belangrijkste onderzoeksvragen waren:

- Welke vegetatietypen zijn er aanwezig in het onderzoeksgebied en welke lijnen van vegetatieontwikkeling kunnen we verwachten?
- Is zaadverspreiding een beperkende factor voor de ontwikkeling van herstellende struwelen en dwergbos?
- Hoe is de ontwikkeling van aangeplante pionier- en laatsuccessionele soorten in jonge, open vegetatietypen?
- Kan de natuurlijke vegetatiesuccessie versneld worden door aanplant van inheemse struik- en boomsoorten?
- Hoe is de ontwikkeling van aangeplante pionier- en laatsuccessionele soorten in een bos van de uitheemse boomsoort *Acacia decurrens*?
- Biedt de aanplant van inheemse soorten perspectieven voor het omvormen van aangeplante bossen met uitheemse soorten naar een natuurlijke inheemse vegetatie?

Het veldwerkgebied was een droge intramontane vallei in de Oostelijke Cordillera van de Colombiaanse Andes, tussen 2550 en 2950 meter boven zeeniveau, aan de rand van de hoogvlakte van Bogotá. Deze hoogvlakte is één van de dichtst bevolkte en meest intensief bebouwde streken van de Colombiaanse Andes. Het veldwerkgebied is een mozaïek van graslanden, struwelen, aangeplant *Acacia* bos en fragmenten van dwergbos. Door sterke erosie zijn kloven van enkele meters diepte een algemeen beeld. Het droge *Condalia* dwergbos, endemisch voor dit gebied, werd beschouwd als het "originele" ecosysteem van de streek. In de jaren 80 van de vorige eeuw zijn de *Acacia* bossen aangeplant om de bodems te beschermen. Er is thans echter nauwelijks sprake van ontwikkeling van een ondergroei, en mede hierdoor heeft dit aangeplante bos een lage ecologische functionaliteit vergeleken met het oorspronkelijke dwergbos.

Resultaten van dit onderzoek

In Hoofdstuk 2 wordt een onderzoek naar vegetatie patronen in het Checua gebied behandeld, dat als basis diende voor het restauratie-experiment. Met behulp van gegevens van de omgeving en de verstoringsgeschiedenis werden mogelijke patronen van vegetatiesuccessie bestudeerd. Daartoe werden er 101 vegetatieopnamen gemaakt in graslanden, struiklanden en dwergbos. Deze opnamen werden met behulp van een kwantitatieve klassificatiemethode ingedeeld in twee typen graslanden, drie typen struweel en één type dwergbos. De

droge graslanden in de lagere delen van het gebied hadden een lage vegetatiebedekking en werden gekenmerkt door relatief veel (éénjarige) kruiden van de composietenfamilie. De wat nattere graslanden van de heuveltoppen, daarentegen, bestonden uit relatief veel uitheemse grassoorten en andere grasachtige kruiden. In de jonge struwelen overheersden *Baccharis macrantha* en *Dodonaea viscosa*. Dwergbossen werden, vergeleken met andere struwelen, voornamelijk op steile, rotsachtige hellingen gevonden, hetgeen waarschijnlijk verklaard kan worden door de lage waarde van deze plekken voor boeren waardoor het kappen van het dwergbos niet interessant is. Op die gedeelten waar de bodem sterk geërodeerd was zodat oude, uitgespoelde kleilagen konden dagzomen, domineerden *Dalea coerulea* en *Baccharis macrantha* de struiklaag. De ondergroei hier was arm aan soorten en had een lage bedekking. De beschikbaarheid van nutriënten in de bodem was samen met organische stof sterk gerelateerd aan de soortensamenstelling op een bepaalde plek. De geërodeerde kleibodems zullen waarschijnlijk geen ontwikkeling van bergbos toelaten.

In Hoofdstuk 3 wordt de positie in de vegetatieontwikkeling behandeld van de negen houtige soorten die gebruikt zijn in het aanplantexperiment: *Baccharis macrantha*, *Dalea coerulea*, *Dodonaea viscosa*, *Condalia thomasiana*, *Croton bogotanus*, *Duranta mutisii*, *Hesperomeles goudo-tiana*, *Myrsine guianensis* en *Xylosma spiculifera*. Deze positie werd bepaald aan de hand van de structuur, diversiteit en verstoring van de vegetatie waar deze soorten in aangetroffen waren. De verstoringsgeschiedenis werd afgeleid van een serie luchtfoto's van het gebied, genomen van 1941 tot 1991. De soorten vertoonden alle een duidelijke samenhang met de structuur en diversiteit van de vegetatie. *Baccharis macrantha* en *Dalea coerulea* werden vaak gevonden op plekken waar veel begrazing had plaatsgehad, in tegenstelling tot de zeven andere soorten. Daarnaast bleken de gehalten aan klei, basen en organisch materiaal van de bodem een belangrijke factor voor het al of niet voorkomen van de soorten. De aanvankelijke indeling van de negen soorten in pionier- of laatsuccessionele soorten kon hierdoor aangepast worden. *B. macrantha* is een echte pionier, terwijl *D. viscosa* een pionier is die lang standhoudt in oudere vegetaties. *D. coerulea* is een pionier op de geërodeerde kleibodems en blijft ook dominant in latere vegetatiestadia. De overige zes soorten zijn duidelijk laatsuccessioneel, met enkele nuanceverschillen.

Hoofdstuk 4 gaat over bodemzaadbanken in vijf vegetatietypen: graslanden, lage struwelen, hoge struwelen, dwergbos en aangeplant *Acacia* bos. De zaden zijn in een kwekerij opgekweekt uit bodemmonsters van 0-5 en 5-10 cm diepte. Er zijn 22429 gekiemde zaden geteld van in totaal 110 soorten, welke naar groeivorm en positie in de vegetatieontwikkeling ingedeeld werden. Zaden van laatsuccessionele struiken en boompjes zijn nauwelijks aangetroffen in pioniervegetaties; hier zou kunstmatige toevoeging van zaden de vegetatieontwikkeling kunnen versnellen. In graslanden was *Baccharis macrantha*, een belangrijke pioniersoort, de enige algemene houtige soort in de zaadbank. Pionierstruiken zouden belangrijk kunnen zijn in het ontwikkelingsproces dat uiteindelijk leidt tot dwergbos, en ze verdienen daardoor de aandacht in beschermingsbeleid voor aangetaste gebieden van de Checuaastreek.

In Hoofdstuk 5 worden de resultaten van een aanplantexperiment met inheemse boom- en struiksoorten gepresenteerd. We verwachtten dat aanplant van pionier-struiken het meest succesvol zou zijn in open graslanden, en dat laatsuccessionele soorten succesvoller zouden zijn in struwelen. Ook evalueerden we het effect van het plaatsen van stenen rondom de individuele zaailingen en het toedienen van kunstmest op overleving en groei van die zaailingen. Daarnaast verwachtten we dat de natuurlijke successie van de vegetatie waarin de aanplant werd uitgevoerd, versneld zou verlopen als gevolg van een kronendakontwikkeling van de aangeplante struiken en boompjes. De soorten werden in mengsels van pionier- en laatsuccessionele soorten aangeplant in zowel graslanden als struwelen. De ontwikkeling van de zaailingen is gevolgd van 2000 tot 2004. De overleving was laag bij een aantal soorten, waarschijnlijk door periodieke droogte en nachtvorst. De groei was over het algemeen erg laag: pionierstruiken werden gemiddeld ongeveer 1 meter hoog, terwijl de laatsuccessionele soorten nauwelijks groeiden. We concludeerden dat pionierstruiken inderdaad succesvoller waren in graslanden dan in struwelen. De laatsuccessionele soorten hadden een hogere overleving in de graslanden, maar de groei was hoger in de struwelen. De plaatsing van stenen zorgde bij de meeste soorten voor meer overlevende individuen, terwijl de kunstmest de groei van de laatsuccessionele soorten bevorderde. Een kronendak met een substantiële bedekking werd alleen gevormd in graslanden waarin pionierstruiken waren aangeplant; de verandering in de soortensamenstelling van de vegetatie was echter niet anders dan daar waar geen soorten waren aangeplant. De veranderingen in die vegetatiesamenstelling waren dus geen gevolg van aanplant. De totale kruidenbedekking was echter wel meer toegenomen in de vegetatie met aanplant. Natuurlijke successie zou dus versneld kunnen worden door aanplant, maar er is meer tijd nodig om de successie als gevolg van de aanplant te kunnen meten. Het bij elkaar planten van pioniersoorten en soorten van latere successiestadia in aanplantexperimenten is in ieder geval aanbevelingswaardig.

De ontwikkeling van zaailingen van zeven soorten (een deel van de negen soorten uit Hoofdstuk 3 en 5) aangeplant in *Acacia* bos wordt behandeld in Hoofdstuk 6. Een zogenaamd “katalytisch effect” van exotische boomplantages op het herstel van natuurlijke vegetatie – door het dempen van schommelingen in temperatuur en vochtigheid – is gesuggereerd en aangetoond door verschillende onderzoekers. Of een boomaanplant daadwerkelijk een katalytisch effect heeft hangt af van het beheer van het bos (verstoring en beschadiging), de aangeplante soorten (eventueel allelopatisch effect), nabijheid van natuurlijke vegetatie (zaadbronnen), degradatie van de plek (bodemgesteldheid), en begrazing. Er zijn dan ook veel voorbeelden van een gestagneerde ontwikkeling in de ondergroei van dergelijke aangeplante bossen in de tropen. We onderzochten de mogelijkheden voor omvorming van *Acacia* bossen naar “natuurlijk” *Condalia* dwergbos, door middel van aanplant van de inheemse houtige soorten in de ondergroei. De overleving en groei werd vergeleken met die van geplante soorten in open vegetatie (Hoofdstuk 5). Daarnaast onderzochten we het effect van verschillen in standplaats van de proefvlakken in het bos en van het toedienen van kunstmest op overleving en groei. Laatsuccessionele soorten hadden een veel hogere

overleving in de *Acacia* bossen dan pioniersoorten en deden het beter in deze bossen dan in de open vegetatietypen. Het aanplanten van laatsuccessionele soorten biedt dan ook goede vooruitzichten voor de omvorming van *Acacia* bossen, hoewel er nog aanvullende experimenten nodig zijn om noodzakelijke kennis aan te vullen.

Conclusies en aanbevelingen

Ondanks dat er in de eerste vier jaar van dit aanplantexperiment geen vegetatiesuccessie van betekenis is opgetreden, zou de aanplant van houtige soorten in de toekomst wel tot versnelde successie kunnen leiden. De opgetreden successie is waarschijnlijk niet het gevolg van een eventueel door de geplante zaailingen gevormd kronendak, maar eerder van het uitsluiten van grazers. Verscheidene proefvlakken in struwelen kwamen in 2004 relatief sterk overeen met die in *Condalia* dwergbossen wat betreft de floristische samenstelling. De vegetatiestructuur van deze proefvlakken echter was duidelijk er één van open en laag struweel. Andere eigenschappen van de vegetatie in de experimentele proefvlakken (structuur en diversiteit) veranderden over het algemeen ook weinig over de periode 2000 tot 2004. De enige statistisch aantoonbare respons op de aanplant was een toename in de totale kruidenbedekking in de graslanden waarin pioniersoorten waren aangeplant. Ik verwacht echter dat gedurende de komende jaren sterkere veranderingen zullen optreden in de proefvlakken met aanplant in vergelijking tot die waarin geen aanplant heeft plaatsgehad, in ieder geval in de graslanden. Op het moment van de laatste waarneming lag de bedekkingsgraad van de aangeplante pionierstruiken tussen de 10 en 20 % en bovendien werd die bedekking pas kort daarvoor bereikt. Hierdoor was het faciliterende effect van de aangeplante struiken waarschijnlijk nog zwak. Het volgen van de ontwikkelingen van microklimaat en soortsvervanging is nodig om hier goed gefundeerde uitspraken over te kunnen doen.

Afgezien van de omgevingsfactoren wordt de ontwikkeling van struwelen, dwergbos en ondergroei in het onderzoeksgebied gelimiteerd door een gebrek aan zaden. De tijdschaal waarover een "substantiële" vegetatieontwikkeling plaatsvindt hangt dus af van standplaatskenmerken en eigenschappen van plantesoorten (voortplantingsstrategie, demografie, ontwikkeling, kiemingseisen, etcetera). Een langdurige monitoring van de experimentele plots kan een beter beeld opleveren van de ontwikkeling van *Condalia* dwergbos uit gras- en struwelen, met of zonder aanplant. Tot nu toe hebben de meeste publikaties over aanplant van inheemse soorten zich gericht op de ontwikkeling van de aangeplante zaailingen. Voor zover ik weet waren er tot het moment van publikatie van dit proefschrift geen onderzoeksgegevens van monitoring aan de ontwikkeling van de vegetatie waarin die aanplant is uitgevoerd, los van die in dit proefschrift (Hoofdstuk 5).

De verschillen in overleving en groei tussen de verschillende struik- en boomsoorten kan waarschijnlijk worden verklaard door verschillen in strategieën van nutriëntenopname en fotosynthese. Hoewel het gevaarlijk is hier algemene uitspraken over te doen, kan men verwachten dat laatsuccessionele soorten eerder te lijden hebben van droogte (en een daarmee gepaard gaande lagere activiteit van fotosynthese) dan pioniersoorten die misschien

makkelijker nutriënten kunnen opnemen in lagere concentraties. Deze veronderstellingen zijn echter nog niet onderzocht voor de soorten van het *Condalia* dwergbos.

Restauratie-experimenten gebaseerd op successie: vervolgonderzoek

Baccharis macrantha – *Dodonaea viscosa* struwelen lijken een belangrijk stadium te zijn in de ontwikkelingsreeks naar *Condalia*-dwergbos. De twee soorten waaraan deze struwelen hun naam ontleen zouden een rol zouden moeten spelen in toekomstige aanplant-experimenten. Onder een zich relatief snel (in de orde van 5 jaar) ontwikkelend kronendak van pionierssoorten zouden aangeplante laatsuccessionele soorten zich kunnen handhaven om zich later verder te kunnen ontwikkelen als er gunstige veranderingen zijn opgetreden in het microklimaat.

Een beperking van de vegetatieontwikkeling door gebrek aan zaden zou gecompenseerd kunnen worden door het uitstrooien van zaden van gewenste (houtige) soorten. Dit biedt ook de gelegenheid de kiemingseisen van de dwergbossoorten nader te onderzoeken.

Het aanplanten van laatsuccessionele soorten biedt goede vooruitzichten voor de omvorming van *Acacia* bossen. Om te bepalen in welk ontwikkelingsstadium van de aangeplante inheemse soorten het kronendak van het *Acacia* bos zou moeten worden uitgedund of volledig verwijderd, en welk effect die activiteit heeft op de inheemse soorten, zijn meer experimenten nodig. *A. decurrens* is in staat op te slaan vanuit worteluitlopers. De complete verwijdering daarvan is waarschijnlijk een tijdrovende zaak. Ondanks de slechte reputatie van monocultures van *A. decurrens* denk ik dat we deze soort niet bij voorbaat moeten uitsluiten in aanplantexperimenten met inheemse soorten waarbij beoogd wordt de vegetatiesuccessie een “sprong” te laten maken. *A. decurrens* zou toegepast kunnen worden in de beginfase van de ontwikkeling van een zogenaamd “katalytisch” struweel, samen met *B. macrantha*, *D. viscosa* en enkele mid- en laatsuccessionele dwergbossoorten. De aanplant zou kunnen profiteren van de snelle kroonexpansie en (waarschijnlijk) de stikstoffixatiecapaciteit van *A. decurrens*. De groei en ontwikkeling van de *Acacia* boompjes zouden door middel van monitoring en onderhoudsprogramma's wel onder controle moeten blijven.

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Curriculum Vitae

Jeroen Groenendijk was born on June 26th 1972 in Nieuwkoop. His education started at the pre-school play group "De Ark". At the age of seven, he received the first prophecy of his future from his grandmother, who told him to be a "boswachter" (forester) when he'd grow up. During the writing stage of his PhD research (some years later), he repeatedly wondered why he did not follow his grandmother's advice in more detail.

He rather consistently neglected biology during his primary and even secondary schools, copying country contours from the atlas, and calculating right triangles and other nerdy objects, respectively. Suddenly, the idea came to his mind that it would be interesting to dig up dinosaur bones, together with the desire to work in some remote tropical country. After the start of his biology study at the University of Amsterdam (in 1990), his attention was gradually drawn towards plant ecology. The first odours of the tropical rainforests were enjoyed among the pressed, dried, and brown plants of the herbarium of Utrecht University, from which he picked equally pressed, dry, and brown seeds to study them under the microscope. After that, he got the opportunity to do his MSc thesis work in the Colombian Amazon. He spent five months climbing emergent trees and making inventories of epiphytes. In June 1996, he obtained his MSc.

At the end of 1996, he left for Ecuador to participate in the Profafor/FACE research on the impact of pine plantations on soils and vegetation in the high Andes. He prepared a pilot study on population genetics and reproductive strategies of epiphytes in montane and lowland forests in Colombia, and meanwhile worked as a biology education assistant at a secondary school. In the beginning of 1999 he spent another four months in Colombia, visiting possible epiphyte fieldwork sites for a future project. At the end of 1999, he chose for the relative security of a temporal job, and for a move into applied vegetation ecology, by accepting the PhD research documented in this thesis.

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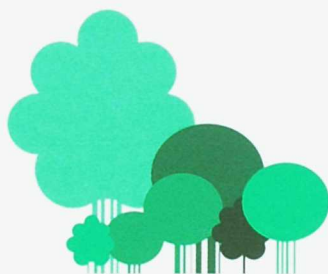
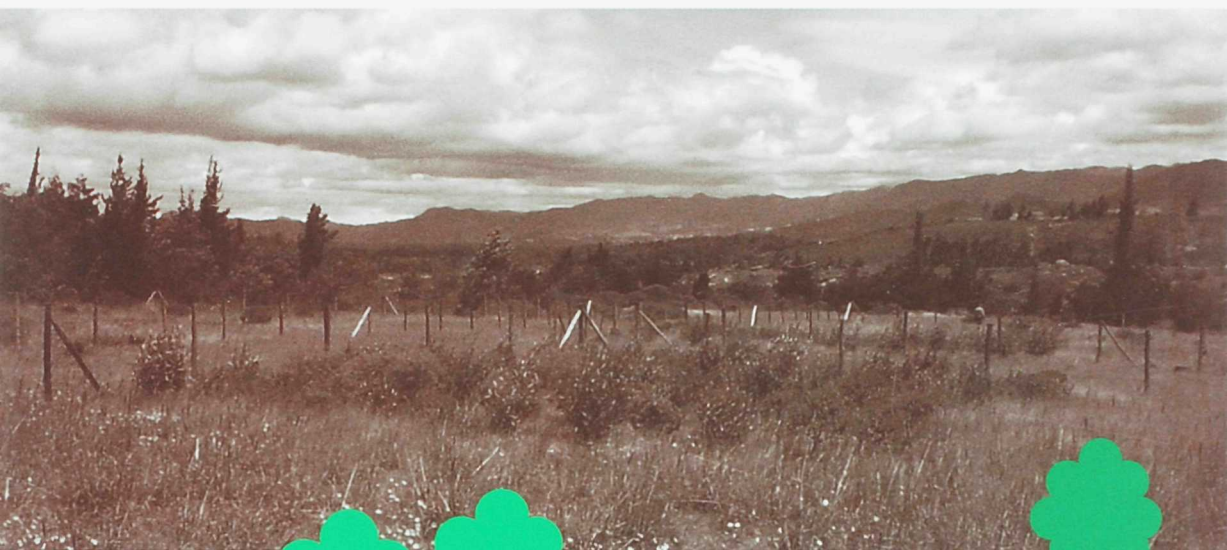
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