Downloaded from UvA-DARE, the institutional repository of the University of Amsterdam (UvA)
http://dare.uva.nl/document/220975

File ID	220975
Filename	7: Synthesis

SOURCE (OR PART OF THE FOLLOWING SOURCE):

Type	Dissertation
Title	Flora and dynamics of an upland and a floodplain forest in Peña Roja, Colombian Amazonia = Flora y dinámica de bosques de tierra firme y de várzea en Peña Roja, Amazonia colombiana
Author	A.C. Londoño Vega
Faculty	Faculty of Science
Year	2011
Pages	243
ISBN	978-90-76894-97-3

FULL BIBLIOGRAPHIC DETAILS:
http://dare.uva.nl/record/381330

Copyright

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other then for strictly personal, individual use.

UvA-DARE is a service provided by the library of the University of Amsterdam (http://dare.uva.nl)

7

Synthesis

Ana Catalina Londoño Vega

7.1 The dipterocarp species in the upland plot

The unexpected discovery of *Pseudomonotes tropenbosii* as the second species of the dipterocarp family in the Neotropics illustrates the poor knowledge of the flora of Colombian Amazonian up to the mid eighties of the past century. Currently this situation has changed, not in the least because of the continuing botanical inventories carried out by the Herbario Amazónico of the SINCHI institute (http://www.sinchi.org.co/herbariov). For example, the number of species registered in this herbarium increased from less than 500 in 1985 to well over 6000 in 2009. The discovery of *Pseudomonotes tropenbosii* was narrowly related to the establishment of the permanent plots. Almost two years before the installment of the upland plot, a sterile specimen of the species had been collected in a temporary 0.1-ha plot as part of the ecological mapping project (Brand et al. 1542, collected on September 25 1986 in plot 51, located at the same site approximately 250 m from the permanent plot; Joost Duivenvoorden, personal communication; Duivenvoorden and Lips 1993, 1995; http://www.sinchi.org.co/herbariov/detalle.php?=SID&ejemplar=6216). This specimen remained unidentified at that time. However, as a consequence of the repeated visits to the permanent plot the species was eventually encountered in fertile condition and recognized as a member of the Dipterocarpaceae family.

The dominance of *Pseudomonotes tropenbosii* in the upland plot is intriguing. Local dominance of tree species in upper Amazonia tends to be correlated with wide regional distributions (Pitman et al. 2001). Indeed, the species has been spotted at other locations in the Middle Caquetá area: near Araracuara by Hans Vester (Londoño et al. 1995), corroborated by a collection of Dairon Cárdenas (7335, http://www.sinchi.org.co/herbariov/detalle.php?=SID&ejemplar=26196).

Since the publication of *Pseudomonotes tropenbosii*, studies have confirmed its taxonomic position. On the basis of wood anatomy, Morton (1995) confirmed the close affinity of *Pseudomonotes* to the genera *Monotes* (30 species in Africa and Madagascar) and *Marquesia* (three species in Africa) of the subfamily Monotoideae. Subsequent phylogenic analyses on the basis of *rbc*L sequences of 15 genera belonging to eight families, including the *rbc*L sequence of *Pseudomonotes* (Morton et al.

1999) supported the placement of *Pseudomonotes* in the subfamily Monotoideae of the Dipterocarpaceae. In one single most parsimonious tree the monophyletic Dipterocarpaceae clade formed a clade sister to the genus *Sarcolaena* (Sarcolaenaceae) while *Monotes* and *Pseudomonotes* formed one group, which was sister to the monophyletic clade of *Pakaraimaea* and the Asiatic dipterocarp species. Another molecular analyses of the *rbc*L gene comprising 35 species from 20 genera (excluding *Pseudomonotes*) confirmed the phylogenetic placement of members of the Dipterocarpaceae, including *Monotes* and *Pakaraimaea*, into a monophyletic group related to the Sarcolaenaceae and allied to Malvales (Dayanandan et al. 1999).

7.2 Architectural analysis

Studies on forest architecture in Colombia are still scarce. Previous work in the Colombian Amazonia focused on secondary forests, which are less species rich and arguably less complex in structure than the forests in the two permanent plots. Architectural analysis of the forest as a whole depends on the presence of (woody) individuals in different stage of development (Hallé et al. 1978; Édelin 1991). Such situations are hard to encounter in the old growth or mature forests, where – contrary to secondary forests – most (woody) species are represented by only a few individuals (Appendix 3). This high diversity has two consequences. First, adequate architectural analyses by means of observations along transects of all species requires extension of the transects to areas outside the permanent plots, enhancing the chance that the forest changes in species composition and structure, for example due to changing environmental conditions. Secondly, transects to be used in the architectural analyses likely contain quite different assemblages of species. One single transect, or a low number of transects, may not give a balanced and representative view on the structure and architectural development of the forest. In all cases, substantial field efforts are required to render representative information about the forest architecture in the plots that can be fruitfully compared to plot variation in the demographic variables of mortality, recruitment and growth.

The above considerations led to the selection of the three species of Myristicaceae (*Iryanthera tricornis*, *Osteophloeum platyspermum* and

Virola pavonis) as feasible subjects for a case study of architectural analysis in old-growth forests. Myristicaceae is a family of trees, which tend to occur in relatively large abundances, widespread in upper Amazonia. The three selected species, which were represented by all regeneration stages in the plots, shared several important architectural characteristics. They showed a growth according to Massart's Model (Hallé et al. 1978), just as other species of Myristicacea (*V. michelii* and *V. surinamensis*) (Drénou 1994; Loubry 1994; Loup 1994), during which three orders of axes were reached. In early and mature stages of development the three species shared plagiotropy and radial symmetry in their branches, and showed capacity to reiterate adaptively and in response to damage. Thus, the architectural analysis suggested that the growth plan of these species would contribute to their ability to maintain healthy populations in the forest, from the understory to the upper canopy.

Both architectural analysis and demographic analysis of forest in permanent plots yield important information. Mortality and recruitment represent simple binary responses of plant individuals to a dynamically changing environment. However, plant responses are far more diverse, and comprise gradual changes in growth and development, reproductive performance, resource use efficiency, strength in competition with other plants, and ability to cope with herbivores and pathogens. The importance of architectural analysis lies in the large amount of information, which is derived from observational studies on plant individuals in all stages of structural development. The case-study of the three understory tree species of Myristicaceae shows the large potential of architectural analysis to build hypotheses why species might be adapted to particular conditions of forest development, especially regarding abundant canopy or subcanopy species.

7.3 Composition and dynamics in an upland and a floodplain plots

Because the comparative study of the composition and dynamics of the forests only included two plots, there were no means to generalize the conclusions on the basis of statistical tests. However, the results can be evaluated in the light of recently published paradigms of Amazonian forest assemblage. Two of these (upper Amazonian forest-landscape patterns and forest trends in Amazonia as a whole) are highlighted here.

The higher species richness in the upland plot compared to floodplain plot and the low overlap in species composition between the two plots fitted well into the general scheme of upper Amazonian forest-landscape associations (Duivenvoorden and Duque 2010). These forest-landscape associations have two explanations, which take place simultaneously but which rely on principally different processes. The first explanation emphasizes niche-filling mechanisms: species tend to show higher abundances in those environments where they have a competitive advantage over other species, for example because of species-specific adaptations related to limited resource availability or to species-specific abilities to overcome disturbances. This explanation tends to emphasize the role of the environment in explaining differences in community assemblage. During and shortly after the installment of the two plots it was already known that they differed strongly in soils and decomposition of organic matter. In the upland plot, soil nutrient availability and decomposition rates were among the lowest levels for mesic upland sites in Amazonia (Duivenvoorden and Lips 1995). In sharp contrast, the soils from the floodplain were less nutrient-poor and decomposition rates were higher, because the parent material was much younger and enriched through the occasional sedimentation during flooding by the Caquetá River. The results from the permanent plot study in this dissertation suggest that the two forests also differ substantially regarding forest dynamics (mortality, recruitment and modes of death). In the upland plot the tree turnover was relatively slow (comparatively a low mortality and recruitment) and trees tended to die in upright position yielding a low spatial spread of canopy disturbances. In the floodplain plot trees died quicker, grew faster, and tree uprooting was more common leading to more widespread disturbances of the forest structure through the entire plot. Clearly these differences agree with the between-plot differences in decomposition rates and soil nutrient availability of the plots (Duivenvoorden and Lips 1995). They also line up with results from analyses of forest dynamics along gradients of soils and forest productivity in the tropical forests worldwide (Malhi et al. 2006).

The second mechanism to explain the divergent between-plot patterns in species richness and composition is by random walk processes modulated through seed dispersal (Hubbell 2001). This explanation emphasizes that

forest communities are assembled by means of species immigrating from surrounding species pools. Contrary to the upland plot that is located in the Tertiary Sedimentary Plain, which is of Miocene to Pliocene age (Duivenvoorden and Lips 1995), the floodplains of the Caquetá River originated in the Lateglacial and Holocene (van der Hammen et al. 1992ab). Given the long duration of the reproductive cycle of tree species and the potentially slow migration rates of trees, it is not inconceivable that time has been insufficient for many species to reach the floodplains, explaining the lower species richness. The total species pool of the flora of the Middle Caquetá area includes several thousands of species (Sánchez 1997), a number exceeding the number of species that can inhabit one single plot. Therefore, random walk processes of species migration always yield differences in species assemblages between any pair of plots, potentially explaining the divergent species composition between the upland and floodplain plot.

Regarding forest trends in Amazonia as a whole, recent publications drew attention to a wide-scale trend of wood density (Baker et al. 2004), biomass (Baker et al. 2004; Malhi et al. 2006), tree mortality (Phillips et al. 2004) and tree species alpha diversity (ter Steege et al. 2006) along a gradient from the (north)east (Surinam, Guyana) to upper Amazonia. Because of the main geological configuration of Amazonia, where highly weathered outcrops of the Guiana Shield are mostly found in the northeast and less weathered basin infills along the Andes in the west, this trend can be associated to a gradient in soil nutrient richness and productivity. This, low diversity forests associated to low levels of forest dynamics (low mortality, low productivity) are found in the northeast on very poor soils developed on top of the highly weathered craton. On the other hand, high diversity forests show higher mortality (and high wood productivity) and are found on richer soils on geologically younger, less weathered sediments along the Andes. How do the results of the two permanent plots fit into this trend?

As far as the link between soil and forest dynamics is concerned the results for the permanent plots corresponded well to the wide-scale Amazonian trend: in the upland plot where soil nutrient availability and decomposition rates were far below those in the floodplain plot, tree turnover was lower. However regarding the mortality rates in the upland plot and the between-

plot diversity patterns the results of the permanent plots survey deviated from the Pan-Amazonian trends. The tree mortality rates in the upland plot were among the lowest recorded for Amazonian as a whole, and clearly far lower than would be expected purely because of the location of this plot in upper Amazonia. The species richness in the upland plot was higher than that of the floodplain plot, even though its tree turnover was lower. This suggests that particular conditions of occasional flooding and the presence of poorly drained soils in Holocene to Lateglacial floodplains together with the associated assemblage of tree species give rise to a high level of forest dynamics relative to tree diversity. In general, the results from the two permanent plots indicate that it is hazardous to apply insights based on regional studies to local situations without proper knowledge of the local physiography and terrain conditions.

7.4 Conclusions and recommendations

For two compelling reasons it is highly recommended to continue the monitoring of the forests in the permanent plots near Peña Roja. The first is that the upland plot represents the type locality of *Pseudomonotes tropenbosii*. Adequate maintenance of the plot will help preserving the habitat of this species, which represents one of the two species of Dipterocarpaceae in the Neotropics. The second important reason is that the two plots represent the oldest permanent plots in Colombian Amazonia. Insights in forest dynamics yield crucial information regarding the maintenance of forest diversity and the longer the time range in the records the more reliable the information.

In addition, and parallel to the monitoring studies in the two permanent plots, several lines of research need to be further developed to deepen our insight how and why Amazonian forests vary regarding diversity and species composition. Studies that experimentally test the link between seed dispersal and species composition are highly needed. Likewise, the habitat effect on plant diversity and species composition needs experimental confirmation, for example by means of transplantation trials. In these studies all relevant life-stages from different habits should be incorporated.