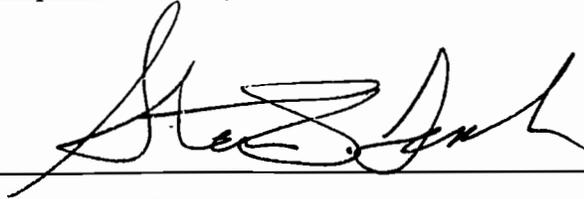


AN ABSTRACT OF THE THESIS OF

Susan Stevens Hummel for the degree of Doctor of Philosophy in Forest Resources presented on June 6, 1997. Title: Stand Development of *Cordia alliodora* (Boraginaceae), a Neotropical Secondary Forest Tree in Northern Costa Rica (1992-1996).

Abstract approved: _____



Steven D. Tesch

Cordia alliodora is used for reforestation programs and farm income in northern Costa Rica. This study investigated: 1) responses of *C. alliodora* associated with stand density, or trees/ha (TPH), and 2) plant diversity and biomass in the understory of *C. alliodora* plantations. Three Nelder plots, 31 temporary plots and 6 plantations in northern Costa Rica were measured between 1992-1996. The plots included monocultures of *C. alliodora* (MONO) as well as polycultures of *C. alliodora* (POLY) planted with crops, pasture or other trees. Plot measurements included: tree height (HT), age (AGE), breast height diameter (DBH), height-to-crown (HToCR), and crown diameter (CD), site soil texture and pH. Understory measurements included the number of total plant species (SR) and aboveground biomass (UBIO).

The HT of *C. alliodora* was related to AGE and DBH, but not to TPH. DBH was directly related to AGE and CD, and decreased with increasing TPH. The HToCR and volume/ha of *C. alliodora* were significantly associated with TPH, AGE and whether the plot was a MONO or POLY. The ratio of CD/DBH was related to AGE and with MONO or POLY, but not with TPH. Preliminary density-management diagrams constructed from study data illustrate that for trees of a given age, volume is directly related to TPH. These results suggest that the yield of *C. alliodora* can be influenced via stand density management.

In 1992, there was no significant difference in UBIO between MONO and POLY (79.75 kg ha⁻¹ and 54.27 kg ha⁻¹, respectively). The UBIO in MONO was

significantly greater in 1996 than in 1992. In contrast, UBIO in POLY was significantly less in 1996 than in 1992. By 1996, the UBIO between MONO versus POLY was significantly different. From 1992 to 1996, SR in the MONO and POLY plantations decreased from 109 to 20. Total SR during early stand development of *C. alliodora* plantations was as high as secondary succession on similar sites in northern Costa Rica.

It is not possible to maximize individual tree growth and stand growth of *C. alliodora* simultaneously. Optimal stand density will depend on site objectives for wood volume and understory production.

Stand Development of *Cordia alliodora* (Boraginaceae),
a Neotropical Secondary Forest Tree in Northern Costa Rica
(1992-1996)

by

Susan Stevens Hummel

A THESIS

submitted to

Oregon State University

in partial fulfilment of
the requirements for the
degree of

Doctor of Philosophy

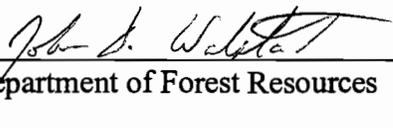
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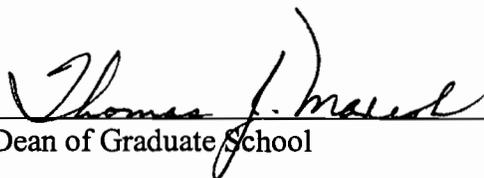
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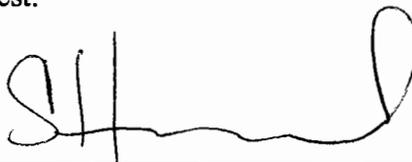


Head of Department of Forest Resources



Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.



Susan Stevens Hummel, Author

ACKNOWLEDGMENT

Many people have contributed to my education. This thesis results, in part, from the financial, logistical, and emotional support of the following individuals and organizations in Costa Rica and in Oregon.

The Organización para Estudios Tropicales (OET) awarded a predoctoral fellowship that paid for my travel to Costa Rica, and my residence at La Selva Biological Station in 1996. Dr. Jack Ewel motivated me to develop a research project that used the experimental installation of Huertos, and has offered encouragement since 1991. The staff and researchers associated with Huertos helped me with fieldwork, collected data and improved my Spanish. When I ventured outside of the boundaries of La Selva, landowners such as Don Isaias Alvarádo, Don Wilfrido Rodriguez Quesada and Doña Maria Nieves provided needed access to stands of *Cordia alliodora*. The staff of OET in San José and in Durham, N.C. arranged all details related to La Selva, my rental car and my visits to CATIE.

At Oregon State University I was encouraged to land on my feet and find my path. My advisor, Dr. Steve Tesch, and my doctoral committee, Dr. Sandra Brown, Dr. William Krueger, Dr. Susan G. Stafford, and Dr. John C. Tappeiner II, demanded my best efforts and offered constructive criticism and compassion.

The taxpayers of Oregon supported my primary, secondary and graduate education. I am indebted to teachers in Clackamas County and to the Multnomah County ESD “outdoor school” program. When Governor Tom McCall addressed my grammar school, his message reinforced what I learned first at home: live in the land, revere its bounty and leave it better than when I arrive. My family and friends remind me to look to the future but to take each day at a time. Rainer S. Hummel sweetens the challenges of life.

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DEDICATION

If you live your life in widening rings, this thesis is dedicated to you.

Stand Development of *Cordia alliodora* (Boraginaceae),
a Neotropical Secondary Forest Tree
in Northern Costa Rica (1992-1996)

1.0 Introduction

Temperature and moisture conditions in humid tropical forests contribute to rapid tree growth. Tropical land managers have a short time in which to influence stand development, so information about key components of stand structure is vital (Evans 1982). Despite the need, the autecology and density-yield relations of tropical trees have not been widely investigated. A lack of silvicultural information on commercially valuable native tree species is a current obstacle to sustainable tropical forest management (Butterfield 1994). Native trees that offer large potential financial and ecological benefits are a prudent choice for preliminary studies on species autecology and stand development. The neotropical secondary forest tree *Cordia alliodora* is one promising example.

The present study investigates responses of *C. alliodora* associated with different tree densities. Silvicultural principles of size-density and growth-growing stock relations are expected to extend to *C. alliodora*. If this hypothesis is correct, techniques developed in temperate regions can be used to investigate and manage this valuable native tree in the Atlantic lowlands of northern Costa Rica.

The puzzle of sustaining forests may be simplified as scientists identify fundamental principles that are consistent within temperate, tropical and boreal forest ecosystems. Sustainable forest use is essential if humans desire future benefits from forested ecosystems.

1.1 Objectives of this research

This study investigates individual tree and stand responses of *C. alliodora* associated with tree density at sites throughout the Atlantic lowlands of northern Costa Rica. The parameters investigated are 1) height increment, 2) diameter increment, 3) total height, 4) total diameter, 5) crown diameter/stem diameter ratio

(K/d ratio), 6) height-to-live-crown and 7) yield/ha. These parameters are important elements of stand structure and growth, and quantifying relationships among them is one objective of this study. Another objective is to describe the development and potential yield of stands dominated by *C. alliodora* spaced at different intervals. Monocultures of trees, as well as polycultural stands of *C. alliodora* grown together with commercial agricultural crops, pasture grass or different tree species are included.

As *C. alliodora* is a popular tree in agroforestry systems in northern Costa Rica, one other important component of stand structure is the understory. In polycultural systems, the productivity and composition of the understory plant community can be as important as wood volume/ha. The biomass of the understory may also be a measure of the efficiency of resource use by the overstory trees. This study extends the individual tree and stand study to include an investigation of understory plant diversity and biomass for both monocultures and polycultures over a four-year period.

The implications of extending size-density theory to *C. alliodora* include more than management of the species. Biometric methods developed for temperate forest trees are not commonly used to investigate tropical species. Combined with the difficulties of obtaining height measurements in tropical forests, a lack of height-diameter equations has led to tropical growth models that only use diameter as a predictive variable (eg. Condit et al. 1993). Vanclay (1995) provides a detailed summary of the approaches used to model growth in tropical forests, and concedes that height measurements are so “difficult and inaccurate” as to be unsuitable for prediction. Diameter is only one dimension of growth, however. Improved methods that relate diameter and height over a range of stand conditions will clarify how above-ground biomass in tropical forest stands changes with time. Extending the geographic range in which principles of size-density and growth-growing stock relations apply will also address the challenge identified by Drew & Flewelling (1979):

The relationship between density and yield will not be resolved until a general framework relating these variables has been developed and conceptualized in a manner that allows ideas and experimental evidence to be transferred from *one experiment to another, from one region to another and even from one species to another.*

(italics added for emphasis)

Information about stand development patterns in tropical forests is necessary for silvicultural practices that sustain the function and productivity of an ecosystem. Sustainable practices require more than autecological information, however. Silvicultural practices affect, and are affected by, human land-use activities. We influence the composition and structure of forest stands by harvesting timber and non-timber products. The value of specific autecological information will vary according to the social, economic, environmental and political landscape in which tropical trees grow.

This chapter provides background for the present study. An overview of issues in tropical forestry first describes the need for, and potential application of, studies on the autecology and stand development of native trees. Second, the discipline of silviculture is introduced as a framework through which to address key needs in tropical forestry. Subsequent sections discuss the potential to study *C. alliodora* in the Atlantic lowlands of northern Costa Rica. An overview of forestry in Costa Rica is followed by pertinent information on *C. alliodora* resulting from earlier studies.

Subsequent chapters proceed from studies at the tree, stand and understory levels to a final synthesis on the relevance of study results to regional silvicultural practices. Chapter Two gives results from an enquiry into competition-density effects in *C. alliodora* at the tree level. Chapter Three builds on tree-level relationships to investigate responses of *C. alliodora* to density at the stand level. Chapter Four identifies changes in the understory plant community associated with four years of stand development following plantation establishment. Chapter Five

considers study results from all three levels, within the context of managing *C. alliodora* in Atlantic lowland Costa Rica. The final objective of the investigation is to suggest silvicultural systems that may contribute to sustainable land-use practices in the study region.

1.2 Key issues in tropical forestry and the need for autecological research

Forests presently cover 27 % of global land area, or an estimated 3,443 million ha (FAO 1995). The less-developed countries of Africa, the Americas and Asia contain 78 % of the global human population, 58 % of total global forest resources, and are located primarily in tropical regions (FAO 1995). During 1980-1990, 163 million ha of forest were converted to a different land use, and 94 % of this conversion was in tropical regions. Concurrent with the net reduction in forest area, world demand for forest products increased by over one billion cubic meters (m^3) during the same decade. Global demand for timber is projected to increase from 1599 million m^3 of roundwood in 1990 to 2674 million m^3 in 2010. Fuelwood demands for the same period are estimated to increase from 1830 m^3 to 2395 m^3 (FAO 1995). The high rate of net primary productivity in tropical secondary forests suggests that these forests will have a key role in supporting this projected average annual increase of over 86 million m^3 yr^{-1} .

Secondary forests in the tropics account for about 40 % of total forest area and are increasing by about 9 million ha yr^{-1} (Brown and Lugo 1990). Intensification of secondary and plantation forest management is vital to meet future wood demands, and to reduce pressure on mature forest conversion (Ewel 1979). The majority of tropical secondary forest is in the Americas, where mature forest is often converted for agricultural activities. The region in the present study is one such example. Plantation export crops, subsistence farms, conservation areas, government settlement programs and expatriate cattle ranches create a land-use mosaic in northern Costa Rica that is typical for the region.

The management of tropical forests where people are resident must differ from management in expanses of uninhabited forest. Different site objectives

include planting trees to earn income, to restore ecosystem function and productivity on degraded sites, or to increase carbon storage. *C. alliodora* may provide benefits for each of these distinct goals. In order to evaluate the potential role of *C. alliodora* in sustainable land-use systems, more information about stand development, species autecology, nutrient requirements and response to silvicultural treatment is needed. Only then will informed decisions be made about the value and cost of regenerating and managing *C. alliodora* to meet different objectives.

There is compelling evidence that tropical secondary forests are valuable sinks of atmospheric carbon. Prior to the Industrial Revolution, the flux of carbon (C) from changes in tropical land use was approximately 0.06 Pg yr^{-1} . By 1990, Brown et al. (1993) estimate the C source from tropical lands increased to $1.7 \pm 0.5 \text{ Pg yr}^{-1}$. If mature forests continue to be converted to alternate land uses at current rates, 41-77 Pg of carbon could be released over the next 60 years and by the year 2050, atmospheric CO_2 concentration will be approximately 2.5 times the pre-industrial level of 280 ppm. Managing secondary forest and establishing plantations could reduce carbon emissions by 20 %. The carbon benefit of total productivity is an abstract concept to many landowners, however. It is academic to expect people to view trees as carbon rather than sources of timber and non-timber benefits, such as fuelwood and fodder. Instead, the incentive to maintain forestland will come from productivity and the timing of income received. If secondary forests are going to contribute to mitigating atmospheric carbon, landowners and forest users must support practices that contribute to this goal. The same is true for site restoration projects. A tree such as *C. alliodora*, which is locally prized for timber and income, may provide desired incentives.

1.3 A silvicultural framework for addressing tropical forestry issues

Many of the key challenges faced by tropical countries arise from human use of natural resources. To meet increasing human demands for food and fuel,

secondary tropical forest land must be managed in a sustained and productive manner. The discipline of silviculture is concerned with investigating and managing forest ecosystem productivity to support human demands. Silvicultural practices require information about the ecological and economic conditions that influence the growth of trees. Such conditions include site characteristics and species autecology as well as the human cultural practices which favor the establishment and growth of some species over others. Whether a silvicultural system is sustainable depends on whether the ecological and social components are integrated, and are grounded on fundamental biological principles.

In addition to individual tree characteristics, silvicultural decisions require an understanding of forest stand dynamics. Oliver and Larson (1990) observe that the study of stand dynamics occupies a conceptual position between physiology and ecosystem studies, since

Physiological processes act on individual trees. The trees in turn, interact with other trees and create particular stand development patterns. Stand development proceeds along various paths which lead to *limited numbers of successional patterns*, ecosystem behaviors, and biomass productivity pathways.
(italics added for emphasis)

If general patterns of stand development exist, it is reasonable to hypothesize that some of these patterns will be manifest in tropical as well as temperate forests. The current study tests this hypothesis of universal silvicultural principles contributing to regional silvicultural practices by investigating *C. alliodora* in northern Costa Rica.

1.3.1. Principles of silviculture

All biotic populations reach a level where the additional growth of some individuals is made possible only via the associated mortality of others (Harper 1977). This principle of self-thinning populations underlies the theory of size-

density relationships in all plant communities, such as forest trees. Individual tree volume has been directly related to the number of trees per ha for many temperate forest species (Reineke 1933, Drew & Flewelling 1979). Growth rates and trees per ha exhibit characteristic patterns associated with different stages of stand development and levels of growing stock (Oliver & Larsen 1990). These two key biological concepts, size-density and growth-growing stock relationships, underlie silvicultural practices.

The concept of size-density is based on work by Yoda et al. (1963), who showed that both the rate of growth and the mortality of individual plants in a population are correlated (Harper 1977). The -1.5 slope for the log of mean weight of survivors versus the log of density of survivors indicates that while the number of individuals present in a population is decreasing, the weight of the whole population increases. In other words, the rate of growth of individuals more than compensates for the decrease in total number. This “-3/2 power law” for size-density relationships has important implications for the management of trees.

The -3/2 power law was used by Reineke (1933) to investigate the relationship between basal area and trees per acre. Reineke found that over a range of tree species the maximum density line was approximately -1.6. Reineke demonstrated that for a given stand, the trees per acre for any given species could be estimated via the diameter of the tree of average basal area, or the quadratic mean diameter. He developed a relative density index based on a quadratic mean diameter of 10 inches. The position of the maximum density line varies by species while the slope remains consistent with the -3/2 “self-thinning” line. The self-thinning line for *C. alliodora* has not been reported in the literature but should be consistent with observations made on other plant species.

While size-density relations describe the trees per unit area associated with an average diameter, growth-growing stock relations describe the expected rate of growth associated with a given level of trees per unit area and stage of stand development. Langsaeter’s curve illustrates the trade-off between individual tree growth (size-density) and stand growth (growing stock), or between annual growth

increment and total cubic foot volume stocking. Both size-density and growth-growing stock relationships assume even-aged, homogeneous stands. The interaction between the two concepts is valuable for developing density management prescriptions for different desired future conditions. Rather than relying on subjective assessments, prescriptions are able to incorporate ecological principles about tree size and growth and stand density to achieve different target stand goals with minimum intervention. Long (1985) suggests that key stages in stand development can be expressed as a percentage of maximum density (100%). For conifers, Long identifies: the lower limit of self-thinning (60%), lower limit of full site occupancy (35%) and onset of competition (25%). This study will investigate the appropriateness of these relative density values to describe key stages in stand development for the tropical deciduous hardwood species *C. alliodora*.

The two most important factors contributing to stand productivity are site quality and stand density. The latter is the only one able to be directly influenced via management and is therefore the subject of this study. The former, however, has important implications for whether and how a particular species will grow on a given site. This is an obvious but critical consideration when planning reforestation.

The quality of a site is a combination of many physical and biological factors which Daniel et al. (1979) remind us are functions of geologic history, physiography, macroclimate and successional development. Site productivity accretes slowly as soils develop or are deposited, yet can be degraded via untimely or sustained human intervention (Ellison 1949, Brown and Lugo 1994). Species that ameliorate physical and chemical erosion will have an increasingly important role in managed forests and reforestation projects.

There are direct and indirect methods for determining site-quality. The direct method used by European foresters was as difficult for North Americans to apply forty years ago as it is for Central Americans today. This is because the most precision is obtained by growing a fully-stocked stand of a desired species for

a specific period of time (Daniel et al. 1979), which obviously will not produce guidelines for neotropical forest managers for decades. Site index is one indirect measure of site quality. An adequate interpretation of site index measurements for any species requires an awareness of the effects of density on height growth (Daniel et al. 1979). An investigation of site index and density effects associated with *C. alliodora* was contemplated thirty years ago by Tschinkel (1966):

Many of the techniques based on annual growth rings in the temperate zones could probably be applied to *C. alliodora*, i.e. determination of site index, studies of tree form as effected (sic) by stocking or of response to release.

1.3.2. Silvicultural practices and stand density

An understanding of how individual species respond to density is essential for effective management. The basic biological relationships expressed during tree growth can be translated into local silvicultural practices only with specific and local knowledge. Since local conditions are dynamic, activities to affect future outcomes necessarily must be based on consistent biological principles and non-subjective interpretation and application.

To avoid the subjectivity and site-dependent nature of absolute measures of density, relative density indices such as the stand density index (SDI) were constructed to be independent of site, age and management objectives. Drew and Flewelling (1979) developed density management diagrams, based on the SDI concept, which illustrate volume and diameter associated with different levels of trees per area. The diagrams help managers recognize how a stand is stocked relative to a stand of maximum stocking in order to evaluate the timing, intensity and need for treatments (Oliver and Larsen 1990). Assessments that are independent from age and site can improve temporal and spatial management. Long (1985) observed that a stand density that is ideal given a particular set of management objectives can be projected forward or backward to different stages of stand development via density management diagrams.

1.4 Tropical forestry issues in Costa Rica

Costa Rica provides an opportunity with which to investigate the potential role of silviculture in addressing tropical forestry issues. Key issues concerning forest conversion for agriculture, reforestation efforts, conservation reserves, uncertain domestic timber supply and foreign debt are all current topics in national debate.

The distinctive physical geography of Costa Rica results in many ecological habitat types or Holdridge life-zones (Holdridge et al. 1971), despite a total land area of only 50,700 km². The country is located between latitudes 11° 13'N and 8°N, and longitudes 82° 33'W and 85° 58'W in Central America. A volcanic ridge of mountains runs from the NW border with Nicaragua to the SE border with Panama. Costa Rica is thus split by a high 'cordillera' which slopes west to the Pacific Ocean and east to the Caribbean Sea.

Life zone diversity is exemplified by the tropical forest formations in Costa Rica, which include: (lowland) dry, moist and wet forests, premontane moist forest, premontane wet forest, premontane rain forest, lower montane moist forest, lower montane wet forest, lower montane rain forest, montane wet forest, montane rainforest, and subalpine rain páramo. The distinction among forest formations is based on seasonal variation and distribution in mean annual biotemperature and rainfall. *C. alliodora* grows on both the Pacific and Atlantic slopes of Costa Rica in lowland dry and moist forest, premontane moist forest and premontane wet forest life zones.

In response to high timber harvest levels during the 1970s, the Costa Rican government established a network of parks and conservation reserves. Sixty-six percent of existing forest is within national protected areas (Butterfield 1994). Forested areas outside of these reserves are subject to conversion for agriculture. As a consequence, areas in secondary forest are increasing, as are lands degraded by inappropriate management methods. The deforestation rates in Costa Rica are among the highest in the world (Sader and Joyce 1988, Harrison 1991). In 1943,

70-75 % of the land area was forested. In 1987 the Dirección General Forestal estimated the remaining forest cover to be 29 %.

Costa Rica is divided into eight forestry regions by the Dirección General Forestal. The northern region has the largest remaining area of unprotected forest. From 1988 through 1996, two reforestation incentive programs were targeted at small landholders. Shelhas et al. (1994) observed that the programs sought to ensure an adequate supply of national timber, as well as to reduce the degradation of marginal lands by erosion. The incentive programs were canceled in early 1996 due to shortages of government funds. By 1993 an external audit found that only 17% of reforested stands nationwide could produce quality timber and 21% were judged a complete loss for timber production (Shelhas et al. 1997).

At the outset of the incentive programs, few officially approved species were native to the region. One of the approved native species most popular with northern farmers was *C. alliodora*. In 1989, *C. alliodora* comprised 69% of the total incentive plantings in northern Costa Rica (Butterfield 1994). Despite the adoption of *C. alliodora* as an official species for reforestation projects in northern Costa Rica, no site classification information existed to guide site selection, initial spacing or silvicultural treatments. The evaluation of plantation performance is hampered by a lack of quantitative data.

Due to the success of exotic species in plantations (Bethel 1989) and a perception that native species were comparatively slow-growing and thus not cost-effective, few trials of native species were initiated prior to 1980. As awareness increased that native species might make ecological and economic contributions to reforestation objectives (Montagnini and Sancho, 1990), more studies were initiated and are summarized by Butterfield (1994). One of the native trees included in species trials, reforestation projects and agroforestry programs was *C. alliodora*. Once highly touted as a valuable, fast-growing tree capable of being grown in monocultures, *C. alliodora* has lost popularity in recent years. This is due in part to erratic performance of monospecific plantations and a lack of quantitative information on site selection and competition-density relations.

1.5 A potential role for *Cordia alliodora*?

C. alliodora is a useful species with which to investigate the potential role of native trees in addressing tropical forestry issues. *C. alliodora* has several attributes that make it able to be investigated with methods developed for temperate forest trees. Some attributes, such as regeneration in even-aged stands, meet the basic assumptions required for many biometric calculations. Unlike many tropical trees, *C. alliodora* has distinct seasonal rings that make age estimates possible (Tschinkel 1966). A number of stands with different densities, ages and site conditions exist in northern Costa Rica as a legacy from past management efforts. These stands make possible an investigation into competition-density effects for the species.

C. alliodora is desirable as well as feasible to investigate. The tree is valued and appreciated in countries throughout its range from Mexico to Argentina. Improving the regenerative success and timber value of *C. alliodora* through silvicultural practices may enhance the income received by farmers and thus provide incentives to maintain more land under tree cover. Results of this investigation into *C. alliodora* may also facilitate congeneric studies. The genera *Cordia* consists of over 350 species and many others also have potential commercial value (Record and Mell 1924).

1.5.1. The contribution of previous studies

C. alliodora is native to the American tropics and subtropics; it has also been reported indigenous on all islands in the Caribbean except Jamaica (Johnson & Morales 1972). The tree is a generalist, as indicated by a wide geographic range and occurrence in several Holdridge life zones. Observations about *C. alliodora* have been recorded by foresters and scientists since the 1920s. Early observations of the tree by British colonial foresters were anecdotal rather than empirical (Marshall 1939), yet provided a basis for subsequent experimentation both within the range and elsewhere in Africa and the South Pacific (Hudson 1984, Neil 1988 and Salah 1989).

C. alliodora is a light-demanding, early-successional tree. Results from physiological and agroforestry studies dominate the published literature on *C. alliodora* (Greaves and McCarter 1988). Information is available on tree reproductive biology (Opler et al. 1975), wood properties (Howe 1974), root system development and nutritional demands (Haggar and Ewel 1995), and water relations (Oberbauer 1985). Individual tree volume tables and form equations are published for *C. alliodora* grown in the open or as part of an agroforestry system (McCaffrey 1968, CATIE 1994, Somarriba 1990), but not for plantation-grown trees. Little quantitative information is available about tree growth and yield associated with density, tree form and yield in monocultural plantations, causes of mortality, and tree longevity. Many historical anecdotes, such as non-density dependent self-pruning and regeneration in pasture conditions, are recalled in contemporary literature without further scientific enquiry.

By the late 1970s, an accumulation of general information about *C. alliodora* suggested it to be a promising tree for agroforestry and reforestation projects (FAO 1977). To obtain more specific information about the species, a program of international provenance trials was initiated by the Commonwealth Forestry Institute. Results from this program provide the basis for most silvicultural information about *C. alliodora* published in English (Hazlett 1989). The Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) in Costa Rica also has a network of provenance trials throughout the country. Despite decades of interest in *C. alliodora*, silvicultural data are incomplete because of:

- research on the productivity of associated crops (cacao, coffee) to the detriment of tree performance measurements in agroforestry systems;
- a forestry emphasis on high-yielding exotic tree species rather than on native species, and
- a lack of operational tests of experimental results from native tree research.

Contemporary research on *C. alliodora* is a legacy of species autecology combined with historical management practices. *C. alliodora* persists for decades on alluvial or other fertile sites. Land settlement patterns predictably include converting such land to agricultural productivity. The Costa Rican Atlantic lowlands are one example; traditional management practices include retaining remnant *C. alliodora* when clearing forest to establish coffee plantations or cattle pasture. In the former the trees provide vital shade while in the latter they serve as assets which are easily converted to cash. These previously managed sites often became the basis for subsequent research on *C. alliodora*. Although *C. alliodora* supposedly regenerates naturally in pastures and abandoned agricultural fields, no studies have systematically investigated regeneration in pastures or with different levels of grass competition. Trees observed in pastures may instead represent remnants of previous forest stands (Opler and Janzen 1983).

The growth of *C. alliodora* associated with density has not been systematically investigated across a range of sites, ages, stand conditions and densities. Most available data results from agroforestry studies and are narrow in range. Somarriba and Beer (1987), for example, concluded that *C. alliodora* illustrates a sensitivity to density based on comparing projected yields for two 7-year old stands with 708 and 1238 trees ha⁻¹.

1.5.2. Biotic and abiotic environment of *C. alliodora*

The optimal conditions for growth of *C. alliodora* occur in regions characterized by 2000-5000 mm of annual rainfall (Johnson and Morales 1972). These conditions exist in the tropical moist forest, tropical premontane moist forest and tropical premontane wet forest life zones of Central America and northwestern South America (Holdridge 1971). In Central America the tree is also common in the tropical dry forest life zone, which receives 1000-2000 mm of annual rainfall. Budowski (1965) contends that in the drier formations *C. alliodora* reproduces well and thus may be considered part of the climax.

C. alliodora is a deciduous hardwood, which means it has 1) seasonal rings (Tschinkel 1966) and, 2) a different expected growth rate and form than non-deciduous species. (Hibbs 1996). Hardwoods often attain maximum height in 50-100 yr, while conifers continue growing. Consequently, hardwoods tend to be shorter and have lower stem volumes. The merchantable log length for hardwoods usually is at crown base due to branch knots and decurrent branching; this is true for *C. alliodora*.

The tiered, pagodal crown architecture of *C. alliodora* contributes to rapid canopy and root-system closure in one-year old plantations, as well as to high aboveground productivity (Haggard and Ewel 1995). Haggard and Ewel (1995) demonstrated that *C. alliodora* invested early in aboveground biomass, which enabled it to capture a site. Conversely, low observed allocation of biomass to roots may be the reason *C. alliodora* is susceptible to herbaceous weed competition.

The physical and chemical soil properties preferred by *C. alliodora* reportedly vary by elevation. The tree grows over a range of altitudes, from near sea-level in Puerto Rico to 2000 m in the Columbian highlands. Liegel and Stead (1990) reported common distribution below 500 m while McCaffrey (1968) identified an upper altitude limit of 600 m in Costa Rica. *C. alliodora* grows in flat coastal lowlands with deep infertile soils and low organic matter (Surinam) as well as in mountainous uplands characterized by deep volcanic soils high in organic matter (Columbia). Opler et al. (1975) claimed it occurred most frequently in non-riparian forests or at forest edges. Johnson and Morales (1972) suggested that acceptable growth of *C. alliodora* occurred under a wide range of soil conditions, including sites with: calcareous soils; moist, well-drained soils; loose soils derived from diorite and shales, deep clays and poor, rocky soils. Liegel and Stead (1990) insisted the tree was intolerant of poor drainage or dry rocky sites.

The anecdotal and empirical evidence concerning soil and nutrient requirements for *C. alliodora* is confused. It is unclear whether distribution is more dependent on soil characteristics or on site history. Liegel and Stead (1990)

reported that it was not exacting in nutrient requirements and adapted well to degraded and abandoned areas once used for row crops, pasture or shifting cultivation. However, preliminary evidence from long-term studies in Costa Rica suggest *C. alliodora* was extremely demanding in macronutrients such as nitrogen and phosphorus (Bergmann et al. 1994, Haggard and Ewel 1995) and ceased to establish on sites subject to leaching or to compacted soils.

Numerous articles suggest that *C. alliodora* colonizes agricultural lands (Johnson & Morales 1972, Hazlett 1989, Somarriba, 1990) because mature trees are commonly observed at pasture margins. Representation in the smaller diameter classes is poor however, indicating that regeneration is affected by agricultural land use. McCaffrey (1968) suggested that soil disturbance and minimal competition from grass were essential for establishment. Salas and Franco (1978) concluded that the initial development of *C. alliodora* was influenced more by the physical than by the chemical properties of the soil. Soil drainage and rooting depth were of particular importance. Bergmann et al. (1994) concluded that slope position and thickness of the A-horizon were both significantly associated with tree growth and nutritional status. The patterns included poor growth and chlorotic leaves on trees on slopes and high growth and lack of chlorosis on trees in the plateaus and slope-base positions. The Bergmann et al. (1994) study in northern Costa Rica is one of the few publications on growth of *C. alliodora* based on monocultural plantations rather than agroforestry plots. Giraldo et al. (1981) investigated chemical and physical soil properties associated with *C. alliodora* and reported no significant correlation between site index (dominant height at 50 yr) and any of 12 physical soil properties measured. Out of nineteen chemical soil properties, significant correlations existed only with pH and cation exchange capacity. Soil texture influences other physical and chemical properties of soils such as bulk density, water-holding capacity, permeability, and cation exchange capacity.

1.5.3. Management of *C. alliodora* in northern Costa Rica

Landowners who manage *C. alliodora* in northern Costa Rica have a variety of objectives. Traditional management methods include 1) clearing secondary forest and retaining a *C. alliodora* overstory to provide shade for cacao and coffee crops, 2) planting *C. alliodora* in monocultures to reforest degraded sites and obtain income, 3) planting *C. alliodora* in association with agricultural crops such as bananas to provide income at varied intervals, and 4) clearing forest to plant pasture grasses and leaving *C. alliodora* to provide shade for livestock and future timber income. The timing and type of treatments and harvest will differ among these four methods.

Regeneration of *C. alliodora* is secured either via bare-root seedlings or natural regeneration. Seedlings are obtained from local nurseries. International aid organizations, such as the U.S. Agency for International Development (and the German counterpart, GTZ) are involved in projects designed to improve the quality and the timing of root stock. Natural regeneration is most prolific if understory crops are cleared just prior to seed dispersal late in the dry season. Despite an abundance of *C. alliodora* seed in litterfall traps in secondary forest near La Tirimbina in northern Costa Rica, no regeneration occurs in experimentally-created overstory gaps (Guariguata, 1996, personal communication).

The recovery rate for merchantable timber ranges from approximately 30 % to 50 % of harvested stemwood (Somarriba 1990). Forked stems, large branches and rotted heartwood (Johnson & Morales 1972) contribute to merchantability reductions. The basic unit of scaling *C. alliodora* is the *vara*, which is equivalent to 34 commercial inches. Lengths of four *varas* are the standard against which logs are graded. Published nominal stumpage prices for *C. alliodora* in 1993 were 36.7 colones/pulgada (1\$= appx. 150 colones, 1 pulgada=11/12 board foot) (Howard 1995). Current prices for *C. alliodora* are 46 colones at the mill and 55-70 colones at a lumberyard in the capital city of San José. The annual rate of increase in stumpage price for *C. alliodora* for the decade ending in 1993 was 28.4 %. In a more recent period, the stumpage value for *C. alliodora* increased 60.9 %.

Schelhas (1994) reported that landholders receive just 4.6 % of the production cost of finished lumber. Incentives for managing *C. alliodora* must extend throughout the regeneration and harvest process.

1.6 Where do we go from here?

The objective of this study is to investigate individual tree and stand responses of *C. alliodora* associated with tree density. If the hypothesis is true that size-density relations in *C. alliodora* are consistent with fundamental principles of tree growth, the question then becomes: “How do study results contribute to designing sustainable silvicultural practices for *C. alliodora* in Atlantic lowland Costa Rica”? Answers to these questions, basic and applied in nature, are the combined goal of this study. The following three chapters investigate distinct elements of stand development in *C. alliodora*. Recommendations for activities and future research needs are included in the final chapter together with a summary of study results.

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2.0 Competition-density relations in *Cordia alliodora* plantations and Nelder plots in northern Costa Rica

2.1 Abstract

Cordia alliodora is a secondary forest species used for reforestation programs and farm income in tropical America. To investigate the growth of *C. alliodora* associated with tree density, 3 permanent Nelder plots and 31 temporary 0.09 ha plots in northern Costa Rica, representing a range of densities (100 to 195,883 trees per ha (TPH)), ages (1-45 yr) and elevation (30-430 m), were measured between 1993-1996. Tree height (HT), age (AGE), diameter at breast height (DBH), height-to-crown (HToCR), crown diameter (CD), site soil texture and pH were analyzed with regression techniques.

The HT of *C. alliodora* was significantly associated with AGE and DBH, but was not with TPH. The DBH was significantly associated with AGE and CD; the DBH decreased with increasing TPH. The HToCR and volume/ha of *C. alliodora* were significantly associated with TPH, AGE and whether the plot was a *C. alliodora* monoculture (MONO) or a polyculture of trees and crops (POLY). The ratio of CD/DBH was significantly associated with AGE and with MONO or POLY, but not with TPH.

2.2 Introduction

National reforestation incentive funds were available for farmers in northern Costa Rica who planted *Cordia alliodora* between 1986 -1996 (Butterfield 1994, Schelhas 1994). Quantitative information on tree and stand response associated with different densities was not available to guide initial spacing of *C. alliodora*. This study investigates growth patterns in *C. alliodora* under different levels of intra-and inter-specific competition. Since silvicultural prescriptions are based on species-specific knowledge about the physiological responses of trees to competition (Daniel et al. 1979, Drew & Flewelling 1979), results from this study

may be useful for future establishment of *C. alliodora* below 500 m elevation in the Atlantic lowlands of northern Costa Rica.

The native range of *C. alliodora* is from 25°N (Mexico) to 25°S (Argentina) latitudes in the American neotropics. There are over a dozen common names for *C. alliodora* (Appendix A); in Costa Rica the tree is called 'laurel'. *C. alliodora* is prized for timber and used by farmers to provide overstory shade to cash crops such as cacao and coffee (Record and Mell 1924, Somarriba and Beer 1987). Early observations of *C. alliodora* by British colonial foresters stimulated interest and provided a basis for subsequent experimentation with the tree both within the native range, and elsewhere in Africa and the South Pacific (Marshall 1939, Hudson 1984, Neil 1988, and Salah 1989). By the late 1970s, an accumulation of general information about *C. alliodora* suggested it to be a promising tree for agroforestry and reforestation projects (FAO 1977).

Despite improved knowledge about reproductive biology (Opler et al. 1975), wood properties (Howe 1974), root system development and nutritional demands (Haggard and Ewel 1995), and performance in agroforestry systems (Somarriba and Beer 1987), little quantitative information is available about tree growth associated with intraspecific competition, stand dynamics, causes of mortality and longevity. The latter areas require investigation if silvicultural practices for *C. alliodora* are to be improved. The paucity of autecological studies appears due to two key factors: 1) research on the productivity of associated agricultural crops to the detriment of tree performance measurements in agroforestry systems, and 2) lack of operational tests of experimental results.

2.3 Objectives

The objective of this study was to quantify relationships among important elements of stand structure for *C. alliodora*. I investigated relationships between 1) trees per ha, total height and diameter, and height and diameter growth, 2) age and height, 3) age and diameter, 4) height and diameter, 5) crown diameter and stem diameter (K/d ratio), 6) K/d ratio and trees per ha, and 7) K/d ratio and age.

2.4 Site description

The study is comprised of two types of sites: 1) Nelder density plots and 2) secondary forest stands or plantations.

2.4.1. Nelder plots

This study made use of Nelder density plots planted at La Selva Biological Station (La Selva) in 1991 (Nelder, 1962). La Selva (10°26'N, 84°00'W) is located in the Atlantic lowlands of Costa Rica. A recent book about La Selva included chapters that described soil types (Sollins et al. 1994), climate (Sanford et al. 1994), vegetation dynamics (Denslow and Hartshorn 1994) and land use history (Butterfield 1994), both within and adjacent to La Selva. The station is within the tropical moist forest life zone (Holdridge 1971) and receives an average of 4000 mm of rainfall per year.

The Nelder plots are part of a long-term experiment (Huertos) which is located on an alluvial floodplain. The site was previously occupied by an abandoned 30-year old cacao plantation with an overstory dominated by *C. alliodora*. The soils have been classified as mixed isohypothermic, possibly andic, fluventic dystropepts (Haggar and Ewel 1994). The complete project design is provided by Haggar and Ewel (1994, 1995). Prior to installation of the Nelder plots, overstory trees were harvested and the residual slash burned.

The characteristics of a Nelder plot are not the same as operational planting conditions. The planting space within a Nelder plot is a polygon rather than a rectangle or square as is common for plantation-grown trees. Planting densities in a Nelder plot are also higher than in operational plantings, and should be supplemented with data from sites which represent actual stand conditions. The Nelder data provides insight into patterns of growth in *C. alliodora*, while data from farms may identify whether the patterns hold true under conditions of interest to landowners.

2.4.2. Forest stands and plantations

A range of stand conditions, ages and tree densities were desired for the on-farm sites. All possible combinations of age (1-10 yr, 11-20 yr and over 21 yr), density categories (1-300 TPH, 301-1000 TPH and over 1000 TPH), and site types (monocultures or polycultures) were sought to complete a three-dimensional sampling matrix. Some categories were unavailable to sample (for example, no monocultures were available over 21 yr and 1000 TPH). All sample stands were located in the Atlantic lowlands of northern Costa Rica (10°15' N -11°00' E and 84°00' E-85°00' E). The stands ranged from 30-430 m in elevation, from 3-45 years in age and had soil pH that varied from 4.3 to 6.98. Tree densities ranged from 100 to 4011 TPH. The region is within the tropical moist forest life zone (Holdridge 1971) and receives 2500-3500 mm of rainfall per year. The sites included monocultures and polycultures dominated by *C. alliodora* which were either planted experimentally or regenerated naturally. The polycultures included *C. alliodora* managed together with: 1) pasture, 2) perennial crops, 3) other tree species. In all polycultures *C. alliodora* was the dominant tree. Sixteen of the stands were within the original boundaries and subsequent annexes of La Selva. The La Selva sites have been protected from harvesting since 1955 and thus included the oldest stands in the study. The other fifteen sites were located on private farms in the 'cantons' (roughly equivalent to counties) of Sarapiquí and San Carlos. The farm sites included monocultures of *C. alliodora* planted since 1989 as part of a national reforestation program, as well as 12-25 year old stands managed for income. Although the farm sites lacked the detailed history and replication available for the Huertos Nelder plots, they provided a sample of the economic and environmental conditions under which *C. alliodora* is actively managed

2.5 Methods and analyses

The response of *C. alliodora* to competition was investigated over a gradient of planting density, or trees per ha. Growth data from the Nelder plots

(1993-96) were used to evaluate the relationship between density and 1) total height and height growth and 2) total diameter and diameter growth. The Nelder plot study is concerned only with intraspecific competition. Data from the temporary plots installed in 31 forest stands in 1996 were used to evaluate the relationships between density and 1) total height, 2) diameter, and 3) K/d ratio, and between age and 1) total height, 2) dbh, and 3) K/d ratio. The forest stand study does not contain any periodic growth data. Competitive effects may be intra- or inter-specific, depending on whether the site is a monoculture or a polyculture.

2.5.1. Nelder study

A Nelder plot design is based on a series of concentric circles with spokes radiating out from the center (Nelder, 1962). Variations on the design exist; the La Selva Nelder plots are characterized by equal angles between spokes and equal distance between arcs. This design means that the planting area per tree increases logarithmically in size with increasing plot radius. *C. alliodora* occupies a quarter of each Huertos Nelder plot, or five spokes and eleven arcs. The quarter Nelder plot is replicated three times. Measurements in the Nelder plots were made annually beginning in 1992 and include height and diameter at breast height (dbh).

To regress the response variables against density, I first calculated: 1) the growing space available to each tree in an arc, and 2) the equivalent tree density per hectare represented by each arc. The area of each arc was calculated by subtracting the radius of the inner circle from the radius of the outer circle and multiplying by pi ($\pi*[R_2^2 - R_1^2]$). The area per arc was then divided by forty (the number of trees planted in each arc) to determine plot area per tree in m^2 . The per tree area was then divided into 10^4 to identify the per hectare planting equivalent (density). The central and the outer arcs as well as the outer four spokes function as buffers and were excluded from analysis. The 1992-93 data were excluded from analysis because the measurement protocol was inconsistent. The remaining 9 arcs on the central spoke are equivalent to planting densities for *C. alliodora* of 1118, 2086,

4448, 8,929, 17716, 36233, 70364, 142857, and 195883 trees per ha. These density values were regressed against height and diameter measurements for 1994-1996 to evaluate the response of *C. alliodora* associated with intraspecific competition.

2.5.2 Stand study

I chose the sample stands from the available range of densities, ages, and site conditions in which *C. alliodora* grows in San Carlos and Sarapiquí, Costa Rica. Permission to measure private stands was secured via personal introductions by a Sarapiquí extension forester and by a letter from the Organization for Tropical Studies (Appendix B).

A temporary 30 m x 30 m square plot was located randomly within each strata, based on compass coordinates. The plot size was based on pre-study sampling and estimates of variability within different size classes of *C. alliodora*. This plot area (0.09 ha) is consistent with guidelines discussed by Curtis (1983) and Van Deusen and Bayle (1991).

In each plot two 20 g soil samples were collected for pH and texture analysis. A soil spade was used to take samples from a depth of approximately 8 cm. One sample was taken near to, and the other sample taken distant from, the base of a *C. alliodora* tree. Both samples were packaged in sterile soil bags. A field test of soil texture was made using the technique described by Thien (1979). Soil pH analyses were done in the La Selva laboratory using a Corning pH meter 245 and the 'method for soil pH in water' described in Black (1965).

Tree and plot measurements were made with a clinometer, steel combination Spencer/diameter tape, and compass. Diameters for all plot trees were measured at breast height (1.37m) (n=1030 in the monocultures and n=1151 in the polycultures). Height measurements were taken for a sample of trees from each 3 cm diameter class (n=180). The dominant and co-dominant trees were used to evaluate the relationship between height and density. On a subset of trees measured for height, crown dimensions were measured, including height-to-crown-base and crown diameter (n=121). The lowest whorl with >75 % live foliage was selected

for the crown base (González and Fisher 1994). All the measurements were not obtainable in all stands. Crown diameter is the average of four quadrant measurements obtained from compass directions and 90° clinometer readings, multiplied by 2. A summary of collected data, including the range of measured values and sample size per variable per site, is presented in Appendix C.

All data were analyzed using SAS® 6.11 (SAS 1988) and Excel software. Standard preliminary statistical methods such as checking residuals, confirming assumptions of normality and testing for influential points were used to verify the suitability of model techniques.

2.6 Results

The 31 stands I sampled included a range of ages (3-45 yr), tree densities (100-4011 trees per ha), and soil characteristics (Table 2.1 and Table 2.2). In the polycultures, *C. alliodora* was grown together with cacao, coffee, bananas, perennial monocots and other tree species.

Regression results for 1) the Nelder plot study and 2) the stand study are provided in Table 2.3 and 2.4, respectively. These tables suggest that: 1) the total diameter and the diameter increment of *C. alliodora* are significantly associated with tree density and 2) neither total height nor the K/d ratio of *C. alliodora* is significantly associated with tree density. Tree age is significantly associated with total height, diameter and the K/d ratio.

2.6.1. Nelder study

In the Nelder study, total height in young *C. alliodora* is not significantly associated with density in 1995 and 1996 (p-values= 0.49 and 0.26, respectively). Height growth of *C. alliodora* is not associated with density in 1995-1996 (p=0.52). In the 1993-94 and 1994-95 growth periods, evidence suggests that height increment may be significantly associated with density (p-values= 0.007 and 0.038, respectively) (Table 2.3).

The diameter growth increment in 1994-95 and total diameter in 1996 are significantly associated with density in *C. alliodora* (p-values= 0.04 and 0.001, respectively) (Table 2.3). The log-log relationship between diameter and trees per ha for *C. alliodora* grown in the Nelder plots is linear and negative, as illustrated in Figure 2.1.

2.6.2. Stand study

In the stand study, no significant relationship exists between: 1) height and trees per ha ($p=0.27$) (Figure 2.2), or 2) K/d ratio and trees per ha ($p=0.26$) (Table 2.4). The relationship is significant between: 1) height and age ($p=0.001$) (Figure 2.3), 2) height and diameter ($p=0.0001$) (Figure 2.4), 3) diameter and trees per ha ($p=0.0006$) (Figure 2.5), 4) diameter and age ($p=0.0001$) (Figure 2.6), 5) crown diameter and bole diameter (K/d ratio) ($p=0.0001$) (Figure 2.7), 5) K/d ratio and age ($p=0.01$) (Figure 2.8) and crown diameter and trees per ha ($p=0.0018$).

The K/d ratio is significantly associated age, as well as with whether the *C. alliodora* tree is growing in a monoculture or whether it is growing with other species in a polyculture ($p\text{-value}=0.0053$, $R^2=0.49$). The equation to predict the K/d ratio in a polyculture is: $K/d = 0.53 - 0.29 (AGE^{1/2}) - 0.39 (\log TPH)$. In a monoculture of *C. alliodora*, the equation is $K/d = 0.53 - 0.29 (AGE^{1/2}) - 0.052 (\log TPH)$. Older trees exhibit lower K/d ratios than do younger trees (Figure 2.8). The mean K/d ratio of *C. alliodora* is 0.245.

Table 2.1 General characteristics of the sample polycultural stands in San Carlos and Sarapiquí, Costa Rica (1996)

Site	Location	Age	Trees/ha	Soil pH	Soil texture†	Associated crop
1	La Selva/ Huertos	5	1988	6.92	CL	Euterpe* Heleconia
2	Huertos	5	2898	6.58	CL	Euterpe, Heleconia
3	Venezia	15	165	4.9	L	coffee**
4	Huertos	5	2897	6.6	CL	Euterpe Heleconia
5	La Selva	5	4008	6.79	SL	HYAL*** CEOD Euterpe Heleconia
6	La Selva	5	3664	6.98	SL	HYAL CEOD Euterpe Heleconia
7	Horquetas	8	522	5.1	SC	roble****
8	Flamenia	3	333	5.84	CL	bananas
10	La Selva/ Holdridge	45	433	5.04	L	cacao
11	La Selva/ Chanchera	35	267	4.9	CL	cacao
12	Chilamate	25	556	4.9	SL	cacao
13	Zapote	4	856	6.01	CL	
14	La Selva Las Vegas 2	34	200	6.85	CL	cacao
15	Tirimбина	17	100	4.95	CL	cacao
16	4 Rios	15	144	4.94	CL	pasture

†Soil texture: C=clay, L=loam, S=sand and combinations thereof (after Thien, 1979)

**Euterpe macrospadix* and *E. oleracea* plus *Heleconia imbricata*

***Coffea arabica*

****Hyeronima alchorneoides*, *Cedrela odorata*, plus * (above)

*****Tabebuia rosea*

Table 2.2 General characteristics of the sample monocultural stands in San Carlos and Sarapiquí, Costa Rica (1996)

Site	Location	Age	Trees/ha	Soil pH	Soil † texture
17	Isla Grande	13	356	6.01	L
18	Cabinas Laureles	11	367	6.51	CL
19	San Ramon 1	13	122	4.84	SCL
20	San Ramon 2	15	133	4.95	SC
22	La Selva/ La Flamenia	3	246	5.25	L
23	La Selva/ Arboleda	35	587	6.4	L
24	La Selva/ Huertos	5	1797	6.9	CL
25	La Selva/ Huertos	5	2085	6.6	CL
26	La Selva/ Huertos	5	2243	6.6	CL
27	Tres Rosales 1	4	566	6.11	C
28	Tres Rosales 2	4	666	4.30	SCL
29	Zapote 1	8	143	6.61	SCL
30	Zapote 2	8	145	6.29	C
31	La Unión	4	1932	5.53	L

†Soil texture: C=clay, L=loam, S=sand and combinations thereof (after Thien, 1979)

Table 2.3 Summary of simple linear regressions of total height, height growth, total diameter and diameter growth in *C. alliodora* on density (TPH) in Nelder plots in northern Costa Rica

response variable	intercept	SE intercept	slope	SE (slope)	p-value (significance of density)	R ²	n
total height (1996)	8.80	0.59	-0.36	0.29	0.26	0.14	11
total height (1995)	8.74	0.48	-0.18	0.25	0.49	0.04	11
height growth (1995-96)	7.58	0.32	-0.2	0.29	0.52	0.09	7
height growth (1994-95)	8.49	0.27	-0.70	0.29	0.038	0.39	11
height growth (1993-94)	8.94	0.27	-0.85	0.20	0.0007	0.55	17
total diameter (1996)	11.49	0.42	-1.67	0.2	0.0001	0.9	9
diameter growth (1995-96)	7.03	0.35	-0.46	0.24	0.19	0.64	4
diameter growth (1994-95)	7.99	0.30	-0.72	0.0	0.04	0.39	11

Table 2.4 Summary results of linear regression of height, dbh, crown diameter (CD) and CD/dbh (K/d) ratio on TPH and of height, dbh and K/d ratio in *C. alliodora* on tree age in stands in northern Costa Rica

response variable	independent variable	p-value	R ²	n
height	age	0.001	0.40	179
height	dbh	0.0001	0.75	179
height	TPH	0.27	0.02	71
dbh	age	0.0001	0.47	179
dbh	TPH	0.0006	0.06	178
dbh	CD	0.0001	0.74	121
K/d	age	0.01	0.05	121
K/d	TPH	0.26	0.01	121
CD	TPH	0.0018	0.08	121

Figure 2.1: Log-log relationship between diameter at breast height (DBH) and density (TPH) for *Cordia alliodora* in Nelder plots in northern Costa Rica

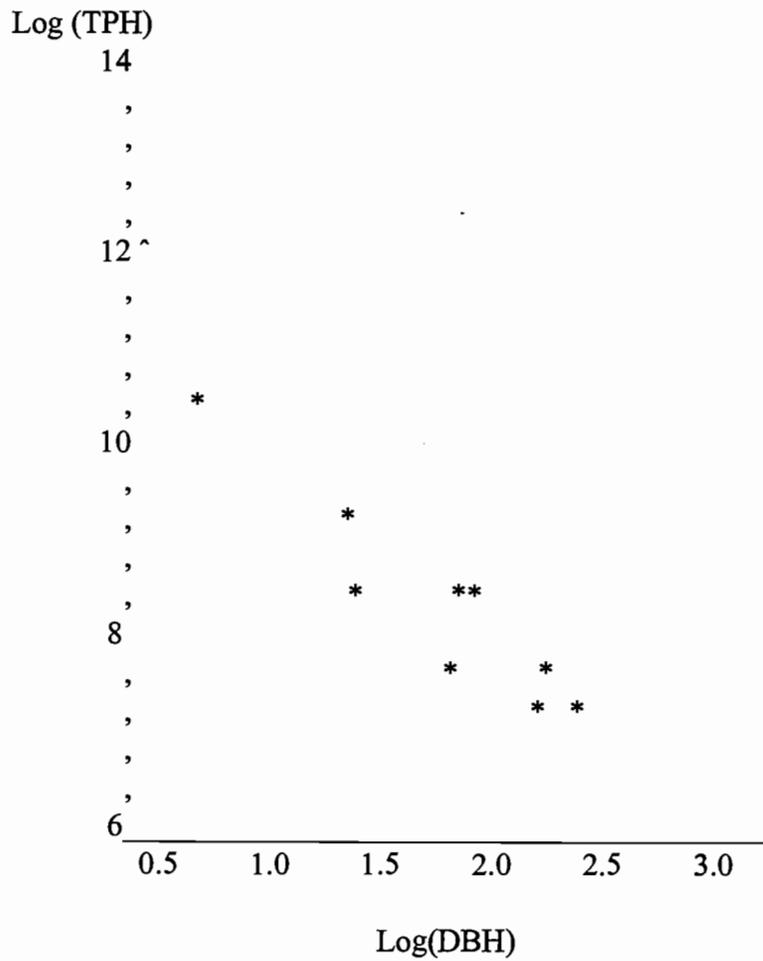


Figure 2.2 The relationship between trees/ha (TPH) and total height (HT) in *C. alliodora* trees in northern Costa Rica

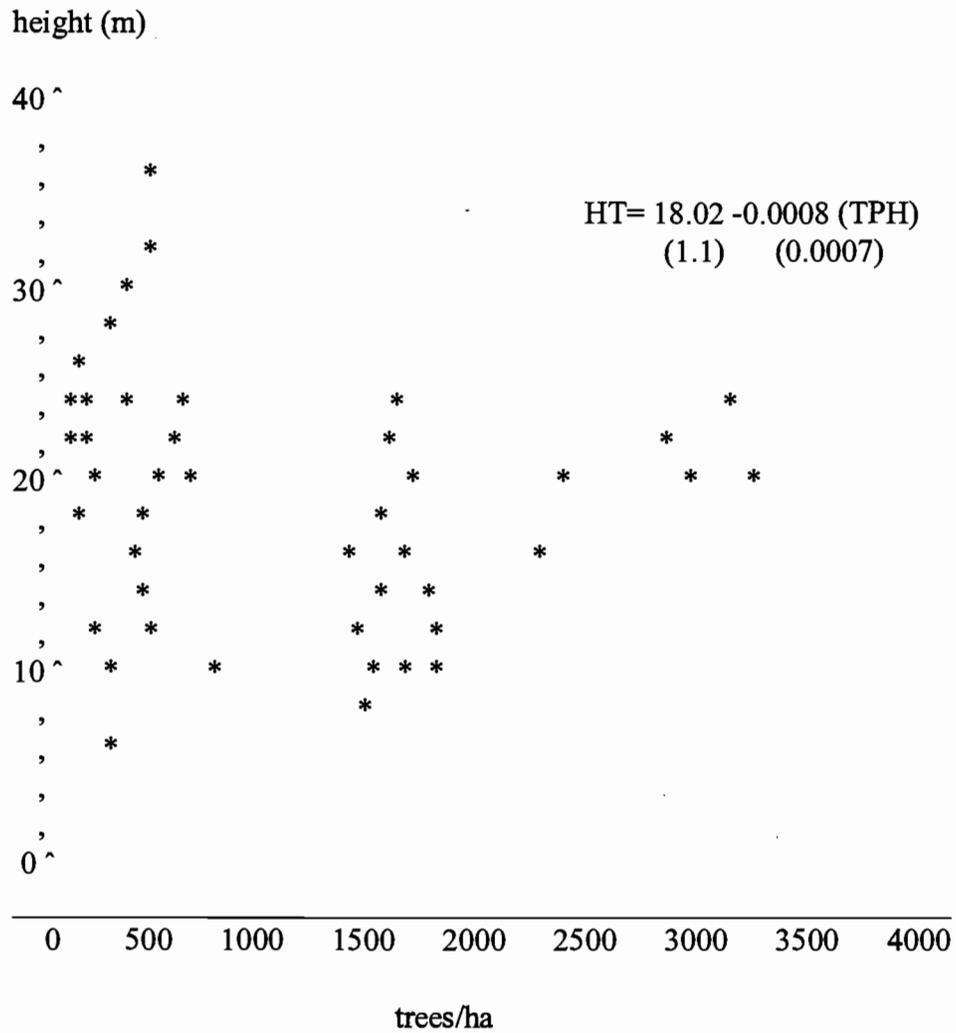


Figure 2.3 The relationship between total height (in meters) and tree age (in years) for *C. alliodora* in Atlantic Costa Rica

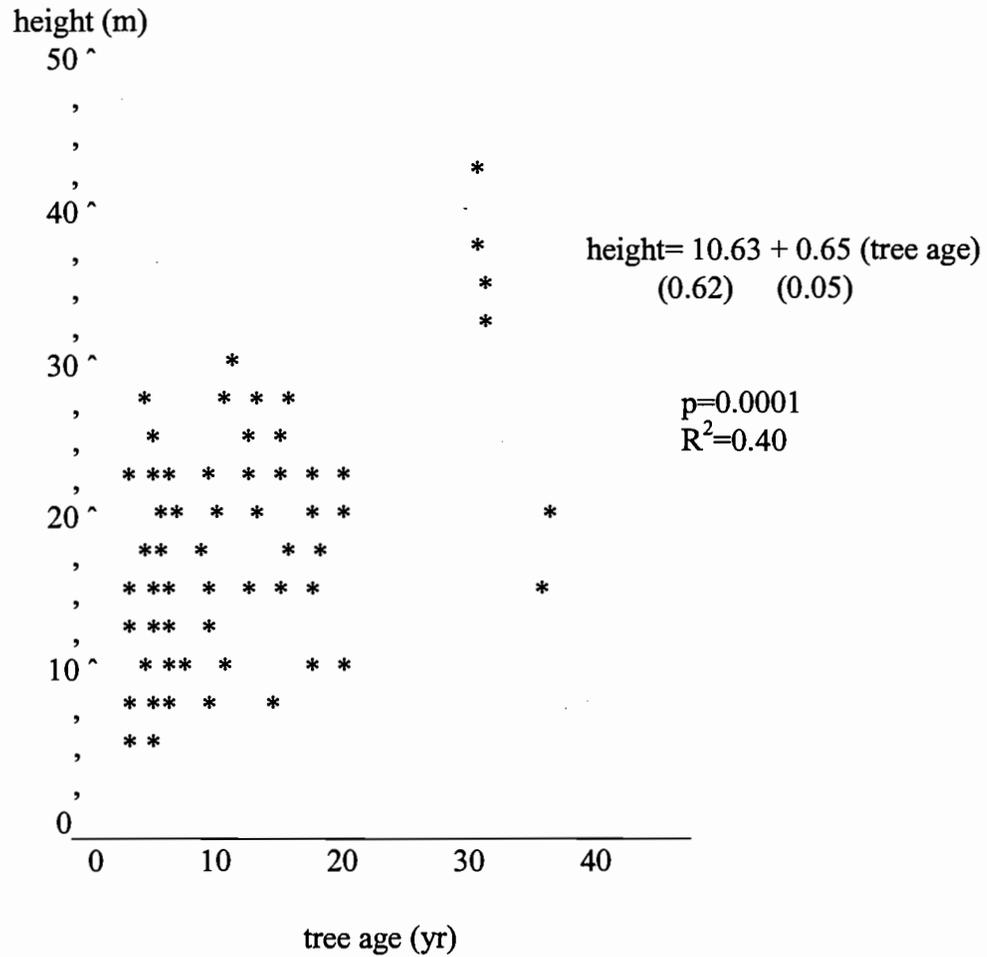


Figure 2.4 The relationship of total height (in m) to diameter (in cm) for *C. alliodora* in northern Costa Rica

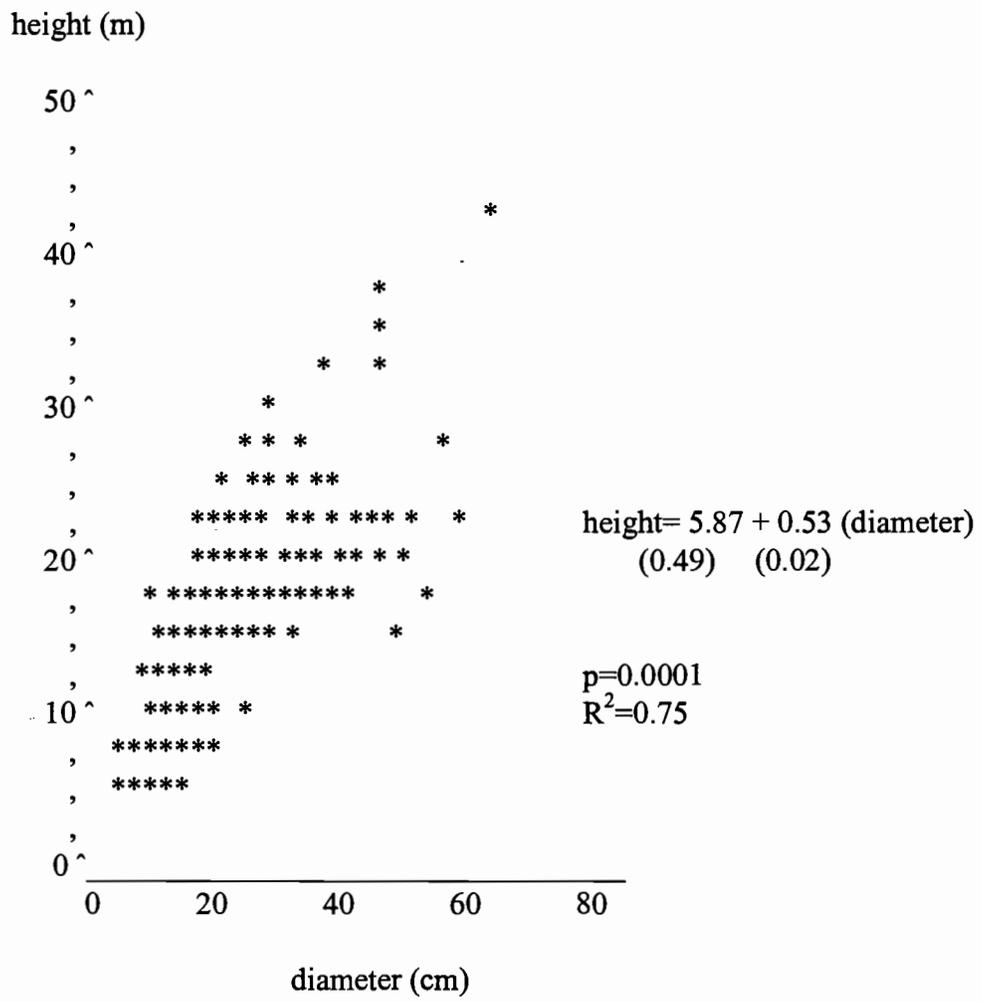


Figure 2.5 The relationship between trees per ha and diameter for *C. alliodora* in northern Costa Rica

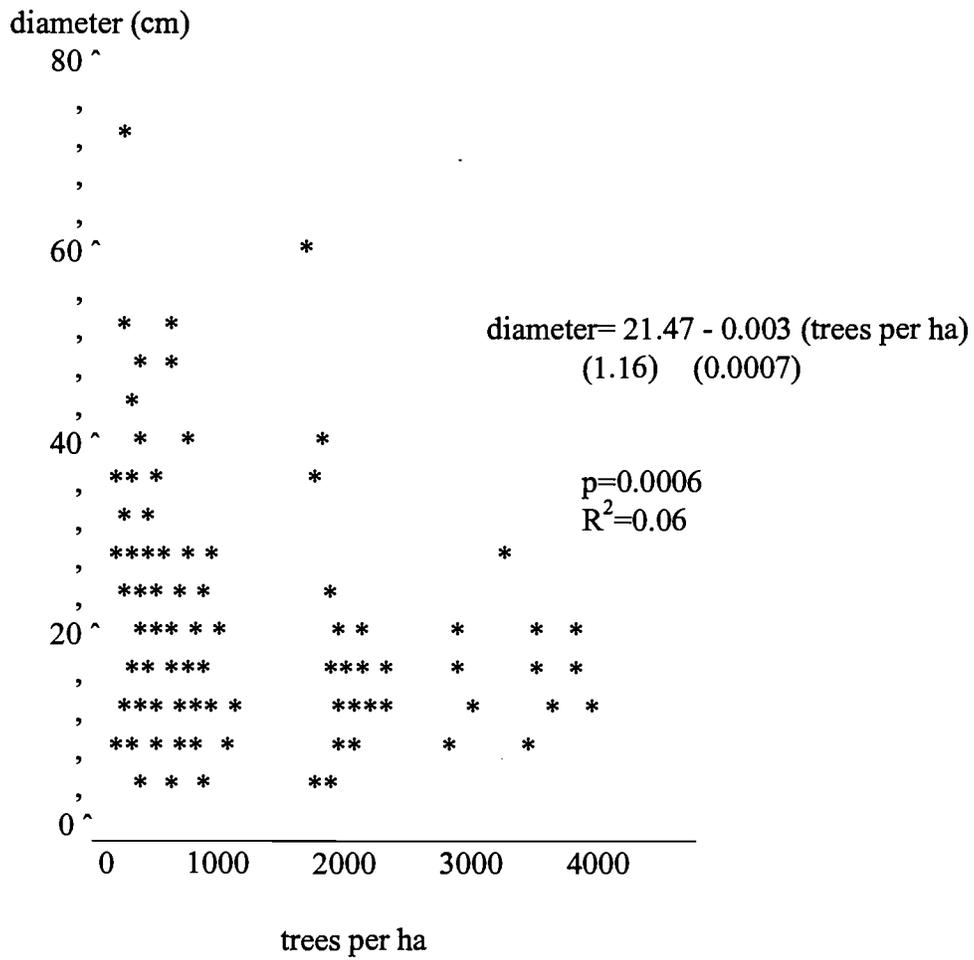


Figure 2.6 The relationship between tree age (AGE) and diameter (DBH) for *C. alliodora* in northern Costa Rica

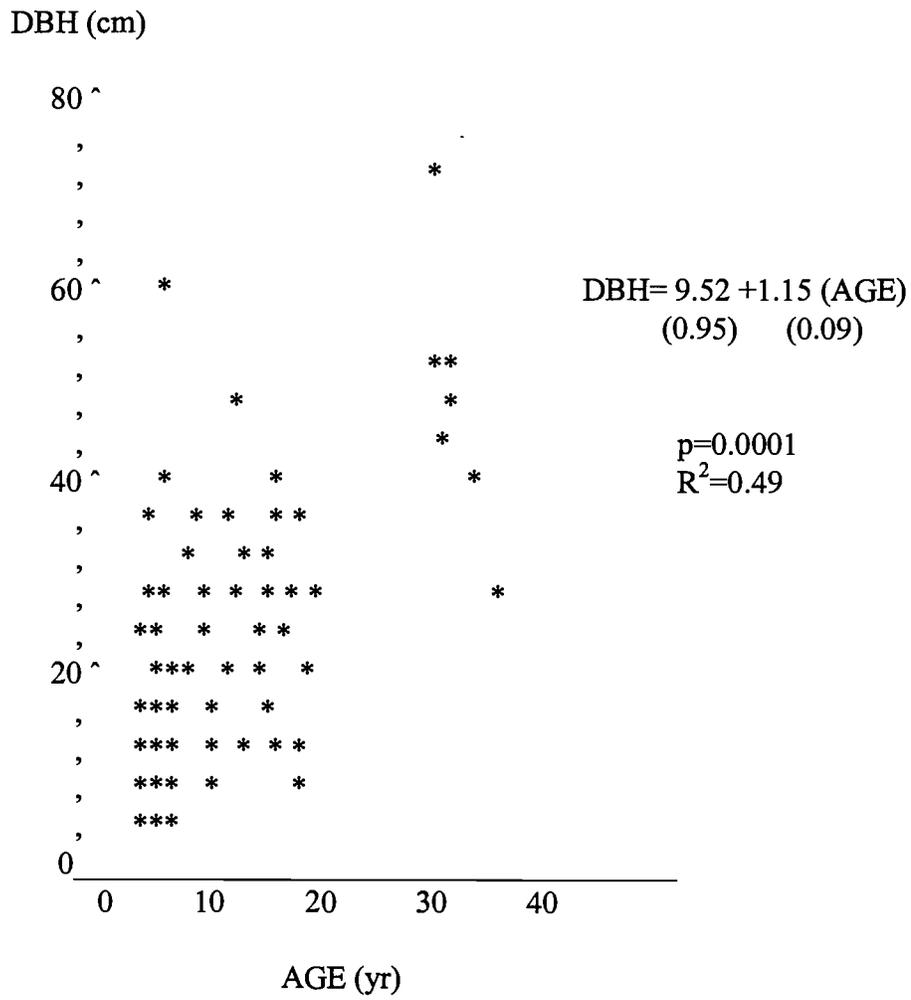


Figure 2.7: Relationship between the crown diameter (in m) and stem diameter (in cm) for *C. alliodora* in northern Costa Rica

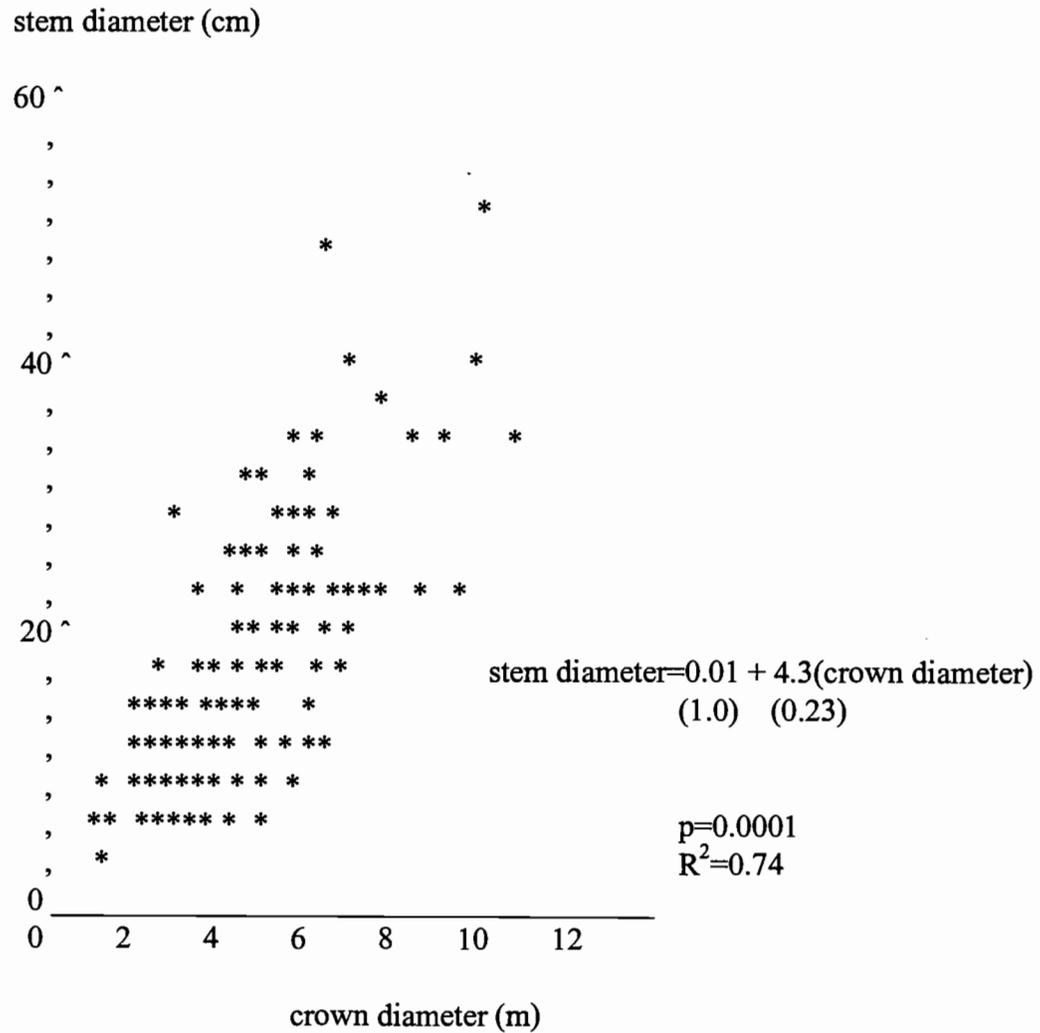
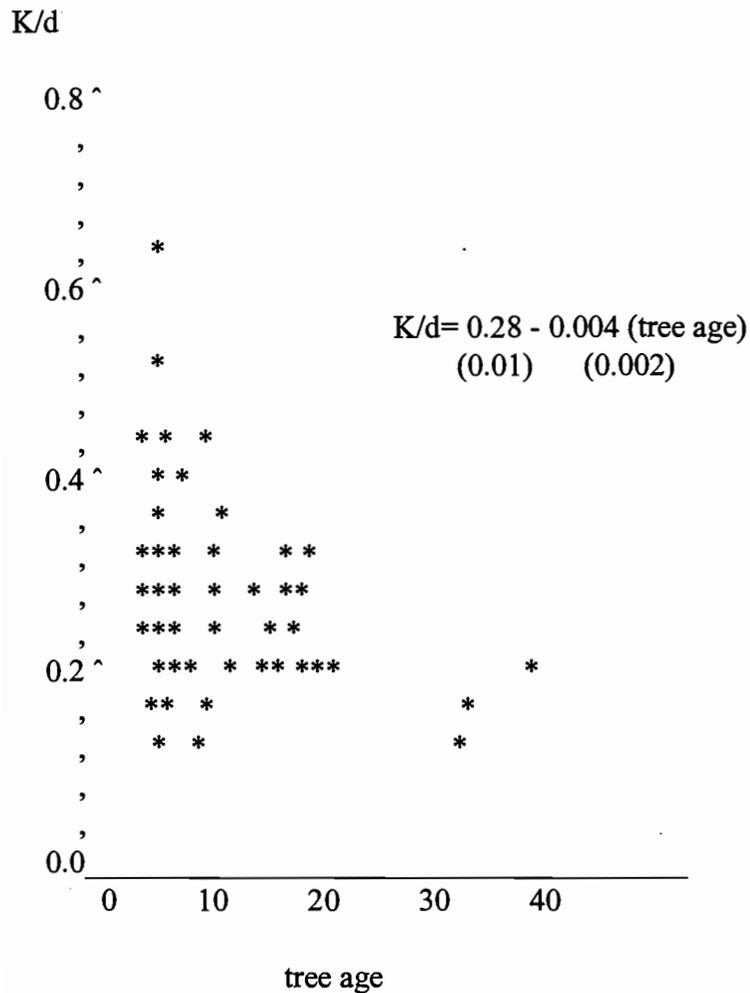


Figure 2.8: Relationship between crown diameter (m)/stem diameter (cm) ratio (K/d) and tree age in *C. alliodora* in northern Costa Rica



2.7 Discussion

Individual tree growth patterns in *C. alliodora* appear to be consistent with principles of size-density theory. The response of *C. alliodora* associated with intraspecific competition in Nelder plots has not previously been reported. Schlönvoigt (1993) used the Nelder spacing design to investigate interspecific competition between *C. alliodora*, *Eucalyptus deglupta*, *Zea mays* and *Manihot esculenta*. In 1984, *C. alliodora* was included among 12 promising fuelwood species in Nelder plots established by CATIE in Costa Rica. Butterfield (1994)

noted that data from these earlier Nelder plots were never analyzed and have since been lost. At a conference on plantation forests in the neotropics held in Puerto Rico in 1986, an abstract was submitted for a study on "Spacing Experiments using Forest Trees". The author intended to assess the "initial behavior of 28 forest species planted at different spacings in six sites in Costa Rica" (Torres 1986). *C. alliodora* was included in the study, but no record of published results exists. The Nelder design originated in agricultural research but has been used to investigate height pattern formation in *Pinus sylvestris* (Galinski et al. 1994), diameter increment and mortality in *Alnus rubra* (Knowe and Hibbs 1996), inter- and intra-specific competition in *P. menziesii* and *A. rubra*, (Cole and Newton 1986) and herbaceous understory development associated with *Eucalyptus grandis* (Cameron et al. 1989).

According to silvicultural theory, height growth is relatively unaffected by competition (Daniel et al. 1979) unless basal area diminishes with an increasing number of trees. While height growth is relatively unaffected by density, diameter growth decreases with increasing density (Drew and Flewelling 1979). In the Nelder study, total height and height increment for the most recent year in the study (1995-96) suggest that these parameters were not associated with density for *C. alliodora*. Although in 1993-1995 height increment was associated with density, this may be because the planting densities in the Nelder plots are extreme or because the sample size was small. Future studies designed explicitly to test the height response of *C. alliodora* associated with interspecific competition will clarify patterns of height growth over a range of tree ages. *C. alliodora* may exhibit a non-random height pattern formation, as was identified by Galinski et al. (1994) for *Pinus sylvestris*.

Consistent with size-density theory and the $-3/2$ power-law, the log relationship between diameter and trees per ha for *C. alliodora* was linear and negative. Long (1985) observed that the relationship is independent of both age and site quality and provides an excellent basis from which to develop an understanding of the competitive interactions between individuals in a population.

Implications of the relationship between dbh and trees per ha will be investigated further in Chapter 3.

Results from this study suggest that the K/d ratio in *C. alliodora* does not vary significantly with density. This result is consistent with Dawkins' (1963) study of eighteen other tree species in the African, American and Asian tropics. In the Dawkins' study, the K/d ratio was consistent within species regardless of site, age or density. Although Curtin (1964) found that other species exhibited more variation in the K/d ratio, he confirmed a strong correlation between the crown diameter and breast height bole diameter for any given species. For *C. alliodora*, evidence suggests that the K/d ratio varies with tree age.

Philip (1994) observed that interest in the K/d relationship is based on the implication that a rigid K/d ratio limits the basal area and number of trees of a certain mean diameter for any given species. For example, Dawkins (1963) suggested that trees with a low K/d ratio are more suitable for pure even-aged plantations than those with higher ratios. The former could support higher basal area per unit area and thus higher volume per area growth rates. The mean K/d ratio of *C. alliodora* is 0.245, which places it among trees at the lower end of the spectrum and suggests it may be suited for monocultural stands.

2.8 Conclusion

Results from this study suggest that the growth of *C. alliodora* is consistent with silvicultural theory for both height and diameter. The results of this study are applicable only to *C. alliodora* growing in the low-elevation moist tropics of Atlantic Costa Rica. Given differences in the specific gravity of *C. alliodora* wood (Howe 1974) and in tree appearance (Opler and Janzen 1983) associated with drier climate zones, it is likely that growth patterns of the tree on dry sites will differ from patterns observed in the present study.

No volume tables exist for *C. alliodora* grown under conditions existing in the Nelder density plots, so patterns of volume increment were not analyzed directly. Volume is a function of diameter and height, however, and these

parameters appear to vary with density according to well-established principles of tree growth. The next chapter investigates how volume/ha in *C. alliodora* is associated with density.

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3.0 The volume and self-pruning habit of *Cordia alliodora* (Boraginaceae) associated with stand density in Atlantic lowland Costa Rica

3.1 Abstract

Cordia alliodora is a secondary forest species used for reforestation programs and farm income in tropical America. To investigate the volume/ha and self-pruning habit of *C. alliodora* associated with stand density, 31 temporary 0.09 hectare (ha) plots in northern Costa Rica, representing a range of densities (100 to 4011 trees per ha (TPH)), ages (3-45 years), elevations (30-430 m) and management types (monocultural and polycultural stands), were measured in 1996. Tree height (HT), age (AGE), diameter at breast height (DBH), height-to-crown (HToCR), crown diameter (CD), site soil texture and pH were analyzed with linear regression techniques.

Volume/ha and self-pruning of lower branches are both associated with density (TPH), age and management type. These results suggest that the volume/ha of merchantable *C. alliodora* (yield) can be influenced via stand density management. Preliminary density-management diagrams constructed from study data may guide silvicultural practices to increase the yield of *C. alliodora* on sites with similar soil conditions, annual mean rainfall and temperature.

3.2 Introduction

Global demand for timber is projected to increase from 1599 million cubic meters (m³) of roundwood in 1990 to 2674 million m³ in 2010. Fuelwood demands for the same period are estimated to increase from 1830 m³ to 2395 m³ (FAO 1995). Intensification of secondary and plantation forest management will help sustain this projected increase and reduce pressure on mature forest conversion. Tropical countries will have an expanded role in supplying wood products to both domestic and export markets.

The high rate of net primary productivity associated with tropical secondary forests is attractive to managers who seek short-rotation tree crops. Non-indigenous, or exotic, genera such as *Pinus* and *Eucalyptus* have been planted in the moist tropics since the 1980s, with good results in survival and yield (Evans 1982, Sawyer 1993). Some evidence suggests however, that tropical monocultures of exotics may result in decreased site productivity and wood production with each successive rotation (Evans 1982, Parrotta 1992). Monocultures of native tree species, or polycultures of trees and different guilds of crop species may mitigate reductions in site fertility associated with exotic monocultures (Haggar and Ewel 1994). Despite an increasing need, the autecology and density-yield relations of valuable native tropical species have not been widely investigated. The benefits and costs of exotic versus native species must be quantified in order to make informed decisions that meet site-specific objectives. The trade-offs in terms of time, yield, cost and benefit between exotic and native species are not yet sufficiently understood. Native species that offer high potential financial and ecological benefits are a prudent choice for preliminary studies on the potential yield of tropical trees. The neotropical forest tree *Cordia alliodora* is one promising example.

3.3 Background

3.3.1. Characteristics of *Cordia alliodora*

C. alliodora is a deciduous, early-successional secondary forest species. The native range of *C. alliodora* is from 25° N (Mexico) to 25° S (Argentina) latitudes in the American neotropics. The tree is prized for structural and decorative timber and is used by farmers to provide overstory shade to cash crops such as cacao and coffee (Record and Mell 1924, Somarriba and Beer 1987). *C. alliodora* may also contribute to long-term site productivity via seasonal inputs of nitrogen-rich litterfall (Glover and Beer, 1984). Results from physiological and agroforestry studies dominate the published literature on *C. alliodora* (Greaves and

McCarter 1988). Information is available on tree reproductive biology (Opler et al. 1975), wood properties (Howe 1974), root system development, and nutritional demands (Haggard and Ewel 1995). Individual tree volume tables and form factor equations are published for *C. alliodora* grown in the open or as part of an agroforestry system (McCaffrey 1968, Somarriba 1990, CATIE 1994), but not for plantation-grown trees. Little quantitative information is available about tree growth and yield associated with density, tree form and yield in monocultural plantations, causes of mortality, and tree longevity.

The form of *C. alliodora* is an important determinant of merchantable volume, or yield. As is common in hardwoods, *C. alliodora* trees often fork at or below the base of the live crown, which limits the merchantable log length (Johnson & Morales 1972). The recovery rate for *C. alliodora* ranges from approximately 30-50 % of stemwood volume (Somarriba 1990). In non-forked trees, the portion of the stem within the crown is less valuable due to branch size and knots. The height-to-live-crown is a measure of self-pruning, and is also a key component of yield. No published studies have systematically investigated how the height-to-live-crown in *C. alliodora* is associated with stand characteristics.

The lack of designed experiments on crown characteristics in *C. alliodora* is probably due to observations and anecdotes that the tree is self-pruning regardless of density (Somarriba and Beer, 1987). Johnson and Morales (1972) claimed that the effect of spacing on tree form was not important and that rapid self-pruning of the crown occurred on open-grown trees. Trees in pastures do often display straight boles and small crowns despite low densities. It is possible however, that these trees are remnants from cleared forest stands and were established at higher densities than is evident to casual observation. Given the history of forest clearing in northern Costa Rica (Sader and Joyce 1988, Harrison 1991), the preference of farmers to leave *C. alliodora* for timber income (Kapp and Beer 1995), and the rapid rate of vegetative decomposition, the chance that branch pruning actually occurred under conditions of higher density is plausible (Opler and Janzen 1993).

If the height-to-live-crown in *C. alliodora* is associated with stand density,

the length of merchantable stemwood can be influenced by initial tree spacing or by pruning. Density management may thus increase the yield of *C. alliodora* and provide financial incentives for improved management.

3.3.2 The need for density-yield information on *C. alliodora* in northern Costa Rica

To encourage establishment and management of trees, two national reforestation incentive programs were available to landholders in Costa Rica during 1988-1996. Program objectives were to ensure an adequate future national supply of timber and to reduce soil erosion and land degradation (Shelhas et al. 1994). Farmers in northern Costa Rica who planted *C. alliodora* were eligible for reforestation funds, and in 1989 *C. alliodora* comprised 69 % of the total incentive plantings in the region (Butterfield 1994). Despite a need generated by the incentive program, quantitative information on stand response associated with different densities of *C. alliodora* is not available for the region. The current lack of density-yield information hampers the evaluation of plantation performance as well as the design of silvicultural treatments to enhance wood productivity.

3.4 Objectives

My first objective is to investigate whether 1) the volume/ha, and 2) the height-to-live-crown of *C. alliodora* are significantly associated with 1) the number of trees per ha (density) and 2) whether the stand is a monoculture or a polyculture (stand type). Volume/ha and height-to-live-crown are both key factors for yield/ha estimates of *C. alliodora*. If, as expected, volume/ha is significantly associated with density, my next objective is to prepare a variable-density yield table for *C. alliodora* based on study results and published conversion equations. If, as expected, evidence indicates that the HToCR of *C. alliodora* is also significantly associated with density and stand type, then density management may improve future conversion factors for the tree. My final objective is to construct preliminary

density management diagrams from study data to identify key stages of stand development and to guide silvicultural treatments for *C. alliodora* stands in northern Costa Rica.

3.5 Site description

The 31 stands in the study were located in the Atlantic lowlands of northern Costa Rica (10°15' N -11°00' E and 84°00' E-85°00' E). The stands ranged from 30-430 m in elevation, from 3-45 years in age and had soil pH that varied from 4.3 to 6.98. Tree densities ranged from 100 to 4011 TPH. The region is within the tropical moist forest life zone (Holdridge 1971) and receives 2500-3500 mm of rainfall per year. The stands included monocultures and polycultures dominated by *C. alliodora*, and were either planted experimentally or regenerated naturally. The polycultures included *C. alliodora* managed together with: 1) pasture, 2) perennial crops, 3) other tree species. In all polycultures *C. alliodora* was the dominant tree. Sixteen of the thirty-one stands were within the original boundaries and subsequent annexes of La Selva. The other fifteen sites were located on private farms in the 'cantons' (roughly equivalent to counties) of Sarapiquí and San Carlos. Table 3.1 and Table 3.2 provide descriptions of the polycultural and monocultural stands, respectively, including soil characteristics, location and stand age.

3.6 Methods

To determine whether 1) the volume/ha and 2) the height-to-live-crown of *C. alliodora* were significantly related to 1) density and 2) whether the stand was a monoculture or a polyculture (stand type), dimensions of *C. alliodora* trees were measured over a range of density, ages and stand types at sites throughout the Atlantic lowlands of Costa Rica.

All possible combinations of age (1-10 yr, 11-20 yr and over 21 yr), density categories (1-300 trees per ha, 301-1000 trees per ha, and over 1000 trees per ha), and stand types were sought to complete a three-dimensional sampling matrix.

Some categories were unavailable to sample (for example, no monocultures were available over 21 yr and 1000 TPH). Pre-study sampling, to estimate the variability in diameter size classes of *C. alliodora* and to calculate desired plot size, was done in young (5 yr) and old (35 yr+) stands.

The 31 stands sampled in 1996 were chosen from the available conditions in which *C. alliodora* was found in San Carlos and Sarapiquí, Costa Rica. Available stands were stratified according to age, density and whether they were monocultures or polycultures. A temporary 30 m x 30 m square plot was located randomly (via compass coordinates) within each stand. This plot area (0.09 ha) is consistent with guidelines discussed by Curtis (1983) and Van Deusen and Bayle (1991). In plantations, plots were installed at an angle to planted rows so as not to misrepresent available growing space. Permission to measure private stands was secured via personal introductions by a Sarapiquí extension forester and by a letter from the Organization for Tropical Studies (Appendix B).

In each plot two 20 g soil samples were collected for pH and texture analysis. A soil spade was used to take samples from a depth of approximately 8 cm. One sample was taken near to, and the other sample taken distant from, the base of a *C. alliodora* tree. Both samples were packaged in sterile soil bags. A field test of soil texture was made using the technique described by Thien (1979). Further analyses were completed in the La Selva laboratory with a Corning pH meter 245 according to Black's (1965) method for soil pH in water.

Tree and plot measurements were made with a clinometer, steel combination Spencer/diameter tape, and compass. Diameters for all plot trees were measured at dbh (1.37m) (n=2729). Diameters were recorded for other woody dicots over 15 cm. Height measurements were taken for a sample of trees from each 3 cm diameter class (n=180). A diameter class size of 3 cm was selected to be consistent with regional forestry practices in Costa Rica, and to ensure that total tree numbers in the larger diameter classes were congruent with anticipated rotation lengths. On a subset of trees measured for height, crown dimensions were measured, including height-to-crown-base (n=171) and crown diameter (n=121).

The lowest whorl with >75 % live foliage was selected for the crown base (González and Fisher 1994). Crown measurements were made late in the wet season (November and December) to ensure that the deciduous habit of *C. alliodora* did not affect measurements. Increment cores were taken from an average of 3 trees per plot; for stands of known planting date a core was taken to confirm the viability of the method. All the measurements were not obtainable in all stands. A summary of collected data, including the range of measured values per plot, is presented in Appendix C.

All data were analyzed using SAS[®] 6.11 (SAS 1988) and Excel software. Standard preliminary statistical methods such as checking residuals, confirming assumptions of normality and testing for influential points were used to verify the suitability of model techniques.

3.7 Analyses

3.7.1. Volume

Diameters of all *C. alliodora* plot trees and heights 1) measured directly (n=180) and 2) estimated using the equation presented in Chapter 2, were used in a double-entry volume equation (Somarriba and Beer, 1987) to calculate total overbark stemwood volume for each tree in all plots. The volume equation was developed for *C. alliodora* in Atlantic Costa Rica from trees in agroforestry plantings; no volume tables are published for *C. alliodora* grown in monocultures. The range of diameter data used in developing the volume equation (6-66 cm dbh) was appropriate for the range of study data. The smallest diameter class in the study (<6 cm) was excluded from volume calculations because it lies outside the range of data used in the volume equation, and because it consistently returned negative per tree volume estimates. Individual tree volumes were summed for each plot to obtain stand volume of *C. alliodora* (n=30), and multiplied by 11.1 for per/ha estimates. Stand volumes were regressed against trees per ha, age, soil texture and soil pH using linear regression procedures in SAS[®] and forward and stepwise variable selection methods.

3.7.2. Self-pruning

Height-to-live-crown values were calculated for measured trees (n= 171) and then mean height-to crown was calculated for each plot. Plot means were regressed against trees per ha, age, site-type (monospecific or polyculture) and interaction terms (sitetype*TPH, sitetype*AGE) using multiple linear regression techniques in SAS 6.11.

3.7.3. Density management diagram

The methods to construct a preliminary density management diagram for *C. alliodora* were based directly on the work of Drew and Flewelling (1979), Reineke (1933), Long (1985) and Dawkins (1963). The quadratic mean diameter of all *C. alliodora* trees and other woody stems >15cm was calculated for each plot according to methods in Husch, et al. (1972). Plot quadratic mean diameter was regressed against plot density (trees per ha). The maximum density line estimated for *C. alliodora* was based on the size-density equation in Drew and Flewelling (1979), on visual interpretation of Figure 3.1 and on the $-3/2$ power law of self-thinning populations. The estimate for the onset of competition was made using the crown dimension data (K/d ratio) discussed in Chapter 2, the method for crown closure described in Drew and Flewelling (1979), and the basal-area density equation of Dawkins (1963). The stand density index, or percent of maximum density, for each sample plot was calculated using the equation in Long (1985). Plot stand density index values were compared with the relative density values suggested by Long (1985) to evaluate key stages in the stand development of *C. alliodora*.

3.8 Results

The wood volume per ha and the height-to-live crown in *C. alliodora* were both associated with trees per ha, age and whether the stand was a monoculture or a polyculture. The preliminary density management diagram constructed from this

study is consistent with published information on stand conditions in *C. alliodora* and with relative density values identified by Long (1985).

3.8.1. Volume

The stemwood volume per ha of *C. alliodora* was significantly related to TPH and age but the relationship varied by whether the stand was a monoculture or was a polyculture ($p=0.0006$, $R^2=0.50$). Soil texture and soil pH values did not significantly influence volume/ha ($p=0.20$ and 0.83 , respectively).

The volume/ha of *C. alliodora* grown in a monoculture was higher than the volume/ha in a polyculture for any given age and TPH (Figure 3.1, data in Appendix D). Volume/ha of *C. alliodora* in a monoculture can be predicted by the equation (with standard errors of estimates in parentheses):

$$\text{volume}_M = \exp \left\{ 0.16 + 0.47(\ln(\text{TPH}) + 0.5(\text{age}^{1/2})) \right\}$$

(1.0) (0.18) (0.11)

when: volume = overbark volume of *C. alliodora*, $\text{m}^3 \text{ha}^{-1}$;
 $\ln(\text{TPH})$ = natural log of tree density ($\# \text{ha}^{-1}$);
 $\text{age}^{1/2}$ = square root of stand age (yr)

The volume/ha of *C. alliodora* grown in a polyculture can be predicted by the equation:

$$\text{volume}_P = \exp \left\{ -0.35 + 0.47(\ln(\text{TPH}) + 0.5(\text{age}^{1/2})) \right\}$$

(1.03) (0.18) (0.11)

when: volume = overbark volume of *C. alliodora*, $\text{m}^3 \text{ha}^{-1}$;
 $\ln(\text{TPH})$ = natural log of tree density ($\# \text{ha}^{-1}$);
 $\text{age}^{1/2}$ = square root of stand age (yr)

Table 3.1 General characteristics of the sample polycultural stands in San Carlos and Sarapiquí, Costa Rica (1996)

Site	Location	Age	Trees/ha	Soil pH	Soil texture†	Associated crop
1 (A)	La Selva/ Huertos	5	1988	6.92	CL	Euterpe* Heleconia
2 (B)	Huertos	5	2898	6.58	CL	Euterpe, Heleconia
3 (C)	Venezia	15	165	4.9	L	coffee**
4 (D)	Huertos	5	2897	6.6	CL	Euterpe Heleconia
5 (E)	La Selva	5	4008	6.79	SL	HYAL*** CEOD Euterpe Heleconia
6 (F)	La Selva	5	3664	6.98	SL	HYAL CEOD Euterpe Heleconia
7 (G)	Horquetas	8	522	5.1	SC	roble****
8 (H)	Flamenia	3	333	5.84	CL	bananas
10 (I)	La Selva/ Holdridge	45	433	5.04	L	cacao
11 (J)	La Selva/ Chanchera	35	267	4.9	CL	cacao
12 (K)	Chilamate	25	556	4.9	SL	cacao
13 (L)	Zapote	4	856	6.01	CL	
14 (M)	La Selva Las Vegas 2	34	200	6.85	CL	cacao
15 (N)	Tirimbina	17	100	4.95	CL	cacao
16 (O)	4 Rios	15	144	4.94	CL	pasture

†Soil texture: C=clay, L=loam, S=sand and combinations thereof (after Thien, 1979)

**Euterpe macrospadix* and *E. oleracea* plus *Heleconia imbricata*

***Coffea arabica*

****Hyeronima alchorneoides*, *Cedrela odorata*, plus * (above)

*****Tabebuia rosea*

Table 3.2 General characteristics of the sample monocultural stands in San Carlos and Sarapiquí, Costa Rica (1996)

Site	Location	Age	Trees/plot (<i>C. alliodora</i>)	Soil pH	Soil † texture
17 (P)	Isla Grande	13	356	6.01	L
18 (Q)	Cabinas Laureles	11	367	6.51	CL
19 (R)	San Ramon 1	13	122	4.84	SCL
20 (S)	San Ramon 2	15	133	4.95	SC
22 (T)	La Selva/ La Flamenia	3	246	5.25	L
23	La Selva/ Arboleda	35	587	6.4	L
24 (U)	La Selva/ Huertos	5	1797	6.9	CL
25 (V)	La Selva/ Huertos	5	2085	6.6	CL
26 (W)	La Selva/ Huertos	5	2243	6.6	CL
27 (X)	Tres Rosales 1	4	566	6.11	C
28 (Y)	Tres Rosales 2	4	666	4.30	SCL
29 (Z)	Zapote 1	8	143	6.61	SCL
30 (W)	Zapote 2	8	145	6.29	C
31	La Unión	4	1932	5.53	L

†Soil texture: C=clay, L=loam, S=sand and combinations thereof (after Thien 1979).

3.8.2. Self-pruning

The mean height-to-crown in *C. alliodora* is significantly associated with tree density, age and whether the tree is grown in a monoculture or a polyculture ($p=0.0001$, $R^2=0.82$). The equation to predict the mean height-to-crown for *C. alliodora* in a monoculture (with standard errors of estimates in parentheses) is:

$$\text{HtoCR}_M = \exp \left\{ 1.82 - 0.01(\log(\text{TPH})) + 0.36(\log(\text{age})) \right\}$$

(0.74) (0.09) (0.11)

when:

HtoCR_M = mean height-to-crown of *C. alliodora* grown in a monoculture (m)

TPH = trees per ha

age = stand age (yr)

The mean height-to-crown for *C. alliodora* grown in polycultures is lower than for trees in monospecific stands for the range of data in this study, and can be predicted with the equation:

$$\text{HtoCR}_P = \exp \left\{ -0.91 + 0.25(\log(\text{TPH})) + 0.78(\log(\text{age})) \right\}$$

(0.55) (0.06) (0.09)

when:

HtoCR_P = mean height-to-crown of *C. alliodora* grown in a polyculture (m)

TPH = trees per ha

age = stand age (yr)

3.8.3. Preliminary density-management diagram

The maximum density for *C. alliodora* was estimated to be 2000 trees per ha at a quadratic mean diameter of 25 cm. The onset of competition in *C. alliodora* is estimated to be at a relative density of 0.15 or approximately 300 trees per ha and a quadratic mean diameter of 12 cm. The preliminary density-management diagram constructed from study data illustrates that for *C. alliodora* of similar age, the natural log of individual tree volume is directly related to tree density (Figure 3.2).

Figure 3.1 Estimated volume (m^3/ha) of *Cordia alliodora* in monocultures and polycultures in northern Costa Rica

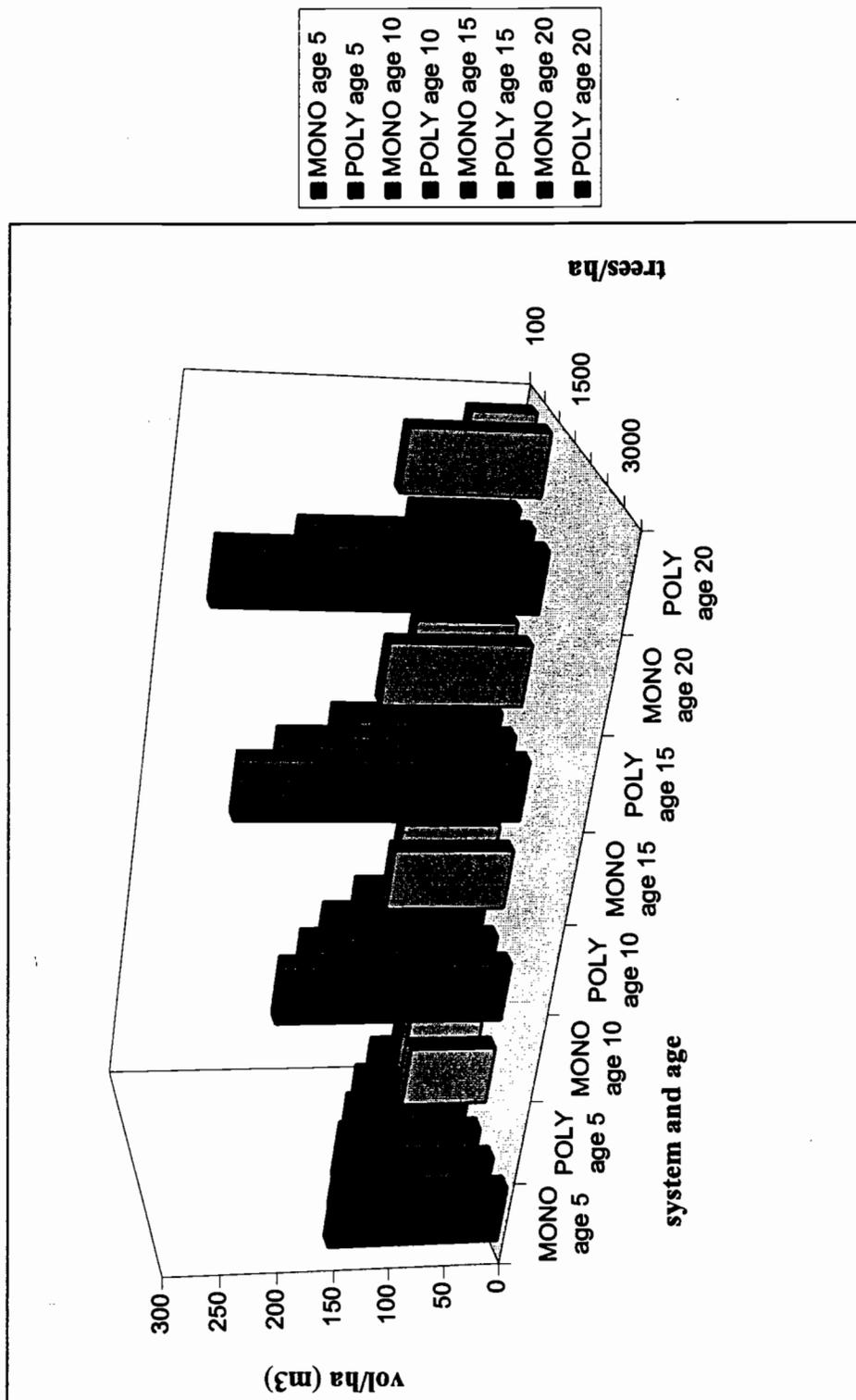
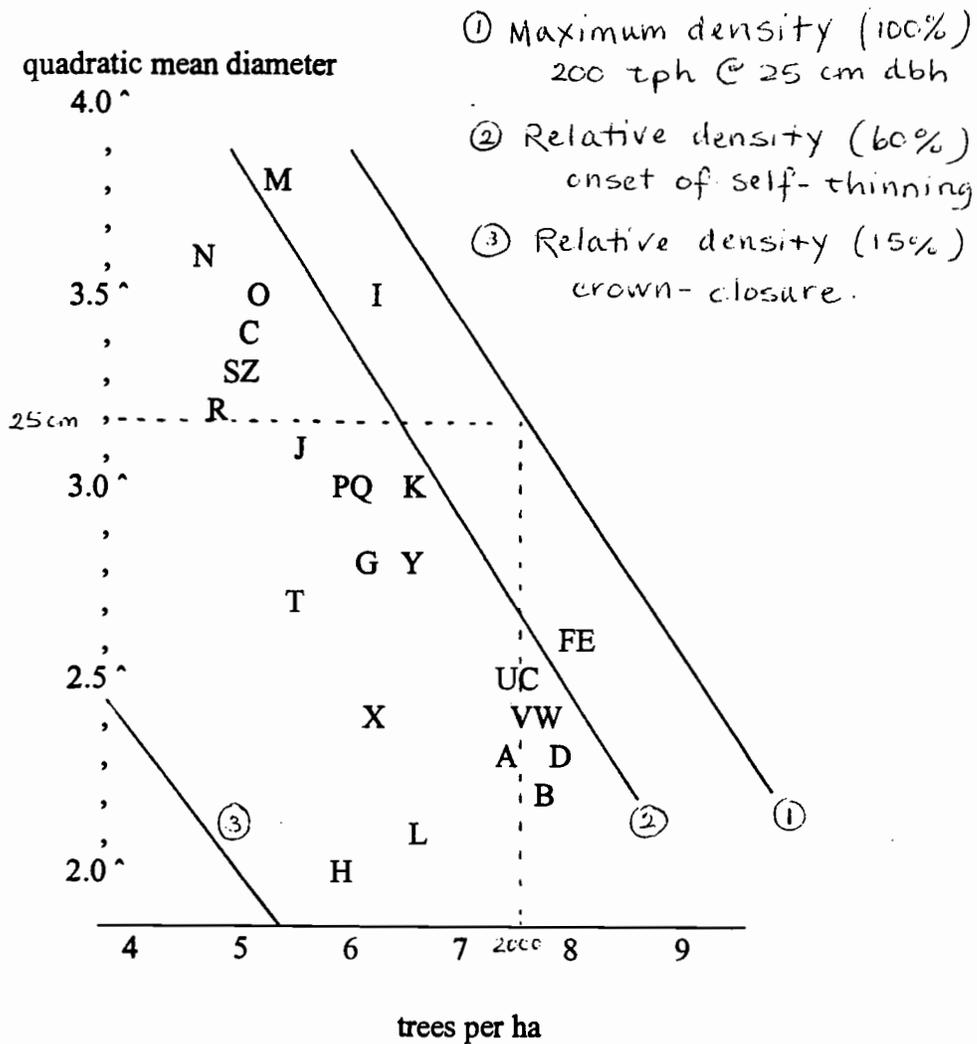


Figure 3.2 Preliminary density management diagram for *C. alliodora* in northern Costa Rica, based on the relationship between the log of quadratic mean diameter (QMD in cm) and the log of density (trees per ha)



The letter codes in the diagram correspond to the sites in the study (Table 3.1 and 3.2).

3.9 Discussion

This study suggests that the yield of *C. alliodora* can be influenced by stand density management. Both the volume/ha and the height-to-live-crown of *C. alliodora* were significantly associated with tree density, stand age and stand type.

The equations to estimate volume/ha of *C. alliodora* in the Atlantic lowlands of northern Costa Rica return values that are consistent with, or lower than other published values for the species (Table 3.3). One reason for my lower estimates may be that my sample stands were selected to represent a range of conditions, and not the best examples of management. The latter criteria is often used in agroforestry projects (e.g.: Somarriba and Beer 1987). The present study investigated the volume/ha of *C. alliodora* associated with a broader range of stand ages, densities and management types than has previously been reported.

Table 3.3 Estimated volume (m³/ha) of polycultures of *C. alliodora* based on age and trees per ha (TPH) from this study compared with reported volumes for the species grown in agroforestry plots

Source	TPH	Age	Reported (m ³ /ha)	Study estimate (m ³ /ha)
Mora	1238	7	48	75
Somarriba & Beer	1238	7	117	
Mora	708	7	74	58
Somarriba & Beer	708	7	67	
Rosero	228	15	162	63
Rosero	180	20	308	76
Rosero	120	20	271	62

Results from the equation to predict volume/ha of *C. alliodora* in monocultural stands are lower than published observations. No studies report on yield in monocultures in the Atlantic lowlands of Costa Rica. Salas and Valencia (1979), using the growth values from 8-year old monocultures in tropical Columbia, predicted volume/ha at a 20 yr rotation that were twice the prediction from this study ($250 \text{ m}^3 \text{ ha}^{-1}$ versus $132 \text{ m}^3 \text{ ha}^{-1}$). Neither study sampled enough older monocultural stands to extend predictions past age 15. The volume/ha of *C. alliodora* predicted for monocultural stands in Atlantic Costa Rica should be limited to stands aged 15 years and younger until current stands are old enough to modify the prediction equation.

The total volume/ha predicted by the equations can be used to calculate periodic annual increment (PAI) values for *C. alliodora*. The PAI associated with the monocultures are $3.8 \text{ m}^3 \text{ ha}^{-1}$ (age 5-10), $4.2 \text{ m}^3 \text{ ha}^{-1}$ (age 10-15), and $4.8 \text{ m}^3 \text{ ha}^{-1}$ (age 15-20). Values for *C. alliodora* polycultures (with corresponding stand ages), are 2.2, 2.4, and $3.0 \text{ m}^3 \text{ ha}^{-1}$.

The total volume/ha predicted by the equation for polycultural stands dominated by *C. alliodora* is a basis for estimating yield of the tree in the Atlantic lowlands of Costa Rica. Somarriba and Beer (1987) reported that the merchantable component of *C. alliodora* in agroforestry systems is 64 % of overbark volume. Together with estimated volumes/ha from this study, expected yields/ha for 100 TPH are: $20 \text{ m}^3 \text{ ha}^{-1}$ at age 10, $27 \text{ m}^3 \text{ ha}^{-1}$ at age 15, $37 \text{ m}^3 \text{ ha}^{-1}$ at age 20 and $48 \text{ m}^3 \text{ ha}^{-1}$ at age 25. To estimate the yield of *C. alliodora* grown in monospecific plantations, taper equations and individual tree volume tables for such conditions need to be developed.

The height-to-live-crown in *C. alliodora* is associated with tree density and whether the tree was grown in a monoculture or a polyculture. Results of this study suggest that initial low tree density of *C. alliodora* is associated with shorter merchantable stems and lower yields at any stage of stand age. To increase merchantable log length, landowners can maintain high initial tree densities or prune crop trees. High initial tree densities may also minimize the invasive

understory grasses that are reputed to affect adversely the establishment and growth of *C. alliodora*. Subsequent thinnings will make growing space available either for associated crops, for diameter growth on remaining trees, or a combination of the two.

Good comparisons exist between the relative density values associated with study plot conditions and their associated position on the preliminary density management diagram. Proposed relative density values for key stages in stand development in *C. alliodora* are: onset of competition (15 %) and the lower limit of self-thinning (50-60 %). The relative density of 15 % estimated for the onset of competition is equivalent to a stand basal area of $3.39 \text{ m}^2\text{ha}^{-1}$. This basal area value is consistent with the basal area of $3.27 \text{ m}^2\text{ha}^{-1}$ for *C. alliodora* at crown closure predicted by Dawkins (1963) basal-area density equation. By using the reported equation to predict volume/ha in a monoculture, the proposed 2000 trees per ha maximum for *C. alliodora* at a quadratic mean diameter of 25 cm is roughly equivalent to $400 \text{ m}^3\text{ha}^{-1}$ at age 20. This is consistent with the $380 \text{ m}^3\text{ha}^{-1}$ measured by Rosero and Gewald (1979) at the same age.

The preliminary density management diagram constructed from this study is consistent with published information on volume/ha and stand conditions in *C. alliodora*. Relative density values are consistent with the target zones identified by Long (1985). Beer et al. (1979) suggest that an optimal density for *C. alliodora* in agroforestry plantings is between 100 and 200 trees ha^{-1} depending whether it is in the mature or sapling stages, respectively. While densities over 100 mature trees per ha may adversely affect crop yields, the value of timber often offsets this limitation.

Foresters manipulate the density of a stand, initially and through subsequent thinnings, to promote various objectives. The value of a stand for timber can be enhanced by high initial densities to promote straight stems with small, shaded lower branches. As competition starts to reduce growth, removal of some trees will increase growing space to those remaining. Diameter (and volume growth) can then accrue on trees with the best form which in turn increases the value of wood

utilization per stem. Effects on yield associated with density and thinning are discussed comprehensively by Smith (1986).

The application of stand density concepts to *C. alliodora* will vary according to landowner objectives. Landowners who manage *C. alliodora* in northern Costa Rica have a variety of objectives. Traditional management methods include:

- 1) clearing secondary forest and retaining a *C. alliodora* overstory to provide shade for cacao and coffee crops,
- 2) planting *C. alliodora* in monocultures to reforest degraded sites and obtain income,
- 3) planting *C. alliodora* in association with agricultural crops such as bananas to provide income at varied intervals, and
- 4) clearing forest to plant pasture grasses and leaving *C. alliodora* to provide shade for livestock and future timber income.

The timing and type of silvicultural treatments designed to increase the value of *C. alliodora* will differ among these four methods. Results from this study suggest that although *C. alliodora* grown in polycultural stands had lower volume/ha and shorter log lengths than in monocultures, the yield can be increased by early density management.

3.10 Recommendations

This investigation into the yield of *C. alliodora* associated with density should be extended to drier sites within Costa Rica. *C. alliodora* grows in a range of climatic zones. How are the relationships identified in this study expressed under different environmental conditions? The wood density of *C. alliodora* varies with life zone in Costa Rica. Wood from the tropical dry forest and premontane moist forest sites has significantly higher densities than does wood from the tropical moist forest, premontane wet forest and tropical wet forest life zones (Howe 1974). This variation in wood density in *C. alliodora* contrasts with diffuse porous hardwoods in temperate regions where the relationship between wood

density and rate of growth are not significantly related. Devall et al. (1995) have demonstrated the seasonality of growth rings for *C. alliodora* in drier, seasonal forests of Panama. Such an investigation was anticipated thirty years ago by Tschinkel (1966):

Many of the techniques based on annual growth rings in the temperate zones could probably be applied to *C. alliodora*, i.e. determination of site index, studies of tree form as effected (sic) by stocking or of response to release. *Nevertheless, a tropical species that forms annual growth rings in one climatic region does not necessarily do so in another.* (italics added for emphasis)

Extending this investigation of density-yield relations in *C. alliodora* to drier sites may improve the silviculture of this important secondary forest species throughout its range in the American tropics.

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4.0 Biomass and diversity of understory plants in *Cordia alliodora* plantations in northern Costa Rica (1992-1996)

4.1 Abstract

The biomass and composition of the understory plant community associated with *Cordia alliodora* planted at 2 m x 2 m spacing are characterized for the first (1992) and fourth (1996) years after stand establishment. Three replicates each of *C. alliodora* monocultures and *C. alliodora* interplanted with perennial monocots (polycultures) comprise the study plantations, which are part of an experiment located in the La Selva Biological Station in northern Costa Rica. In 1992, there was no significant difference in the mean aboveground understory biomass between the monocultures of *C. alliodora* (79.75 kg ha⁻¹) and the polycultures of trees and monocots (54.27 kg ha⁻¹). The understory biomass in the monocultures was significantly greater in 1996 (169.18 kg ha⁻¹) than in 1992. In contrast, the understory biomass in the polycultures was significantly less in 1996 (1.16 kg ha⁻¹) than in 1992. By 1996, the understory biomass between the monocultures and the polycultures was significantly different ($p=0.005$, $R^2=0.78$, $LSD=52$ kg).

In 1992, the understory species with the highest relative dominance rank in both the monocultures and polycultures was the monocot *Tripogandra serrulata* while *Panicum polygonatum* was ranked second. In 1992, 109 plant species were present in the understory of the *C. alliodora* monocultures and polycultures. In 1996, the species with the highest relative dominance was *Paspalum conjugatum*, followed by *Tripogandra serrulata*, 20 species representing 15 families were present in the monocultures. Only two new species were recruited, and both were woody shrubs: *Nectandra membranacea* and *Vernonia patens*.

The understory plant community in tropical plantations may provide insight into resource-use efficiencies and assist in the design of silvicultural treatments to meet objectives such as stocking, site restoration and habitat, forage or crop production.

4.2 Introduction

Throughout the humid tropics, trees are being planted: 1) to yield biomass for fuel, fodder and timber, 2) to provide shade for crops in agroforestry projects, and 3) to restore or sustain site productivity (Evans 1982). The values attributed to tree planting include economic and environmental benefits. Tropical plantations are often economically viable in the short-term, but associated ecological effects are not well understood.

Some evidence suggests that tropical plantations may accumulate understory species as fast as secondary forests (Brown and Lugo 1994). Parotta (1992) advocates the use of tree plantations to recruit species diversity on degraded tropical sites. The composition, management and location of a plantation probably influences understory development and, in turn, management of the understory will vary according to stand objectives. Understory species, no matter how diverse, may not contribute to structural or functional objectives for the site. For example, weedy or exotic competitors may be undesirable.

Monocultural and polycultural plantations have different objectives and products. Polycultures are often chosen to provide periodic income from annual crops and wood products. Polycultures may improve resource partitioning (Haggar and Ewel 1994), mitigate reductions in site fertility associated with monocultures (Evans 1982) and minimize herbivory and pathogens (Perry 1994). In polycultures such as agroforestry systems, the productivity of understory agricultural crops can be as economically important as the tree crop. In contrast, monocultures are often preferred when timber yield is a primary objective. If understory plants compete with crop trees for site resources, the invaders may need to be controlled during plantation establishment.

Data on the understory component of stand development associated with different management methods are needed to improve: 1) the cost/benefit analyses of plantation establishment and 2) silvicultural systems. A qualitative and quantitative difference probably exists in plantation understories associated with: 1)

native versus exotic trees (Haggar et al. 1997), 2) trees with different canopy and root architecture and 3) monocultures versus polycultures. The present study investigates the latter. This paper details differences in the understory community associated with monocultural and polycultural plantations dominated by the neotropical timber tree *Cordia alliodora*.

4.3 Objectives

This study examines the biomass and composition of the understory plant community associated with one- and five-year old *C. alliodora* plantations in Atlantic lowland Costa Rica. Questions of importance include: 1) does plant species diversity differ in the understory of *C. alliodora* monocultures versus polycultures? 2) how does the composition of the plant community change between the first and fifth years after establishment within each plantation type? 3) is the aboveground biomass of understory plants associated with *C. alliodora* monocultures significantly different than the understory biomass associated with *C. alliodora* polycultures planted at a similar density? and 4) does the biomass of understory plants change significantly within five years following stand establishment?

4.4 Methods and analyses

4.4.1. Site description and experimental design

A sixteen-year experiment (Huertos) was established in 1991 at the La Selva Biological Station in northern Costa Rica (10 26 N, 83 59 W) in order to investigate the role of life-form diversity and stand-turnover time in determining the rate and sustainability of tropical plantation production. The history, setting and physical and biotic characteristics of La Selva are described by McDade and Hartshorn (1994). Accounts of human settlement and natural history in the region are given by Pierce (1992) and Young (1991).

The Huertos project is located on an alluvial floodplain at the confluence of two rivers. The site was previously occupied by an abandoned 30-year old cacao

plantation with an overstory dominated by *C. alliodora*. A description of the site soils, experimental design and initial hypotheses of Huertos are explained in Haggard and Ewel (1994). The site was selected due to uniform soil conditions and few abiotic constraints to growth. La Selva has an average annual precipitation of 4000 mm and a temperature of 24°C.

Three native tree species (*Cordia alliodora* (Boraginaceae); *Cedrela odorata* (Meliaceae); and *Hyeronima alchorneoides* (Euphorbiaceae)) comprise the Huertos experiment. Initial stand density for all plots was 2887 trees per hectare. Each species plot is replicated three times (50 m x 40 m units) and is subject to four treatments: three of which are tree monocultures with rotations of 1, 4 or 16 yr. The fourth treatment in each experiment involves the 16 yr rotation, in which the trees are interplanted with perennial monocots (*Euterpe macrospadix* and *E. oleracea*; plus *Heliconia imbricata*). Only the 16 yr rotation of *C. alliodora*, with and without monocots, was sampled for the present study.

4.4.2. Field sampling

At the time Huertos was installed in June 1991, subplots (2 m x 1.73 m plus 0.5 m buffer) were randomly established within the 16 yr treatment in each replicate; three subplots in the monoculture and three in the polyculture. The vegetation within these 54 fenced subplots was not cleared during subsequent weeding operations. The first sampling of aboveground understory biomass and plant species composition in the *C. alliodora* monocultures and polycultures was in March-May 1992. The exclosures were reestablished in August 1995. Sampling for the second period occurred in May 1996. To evaluate total aboveground understory biomass associated with each replicate, the 54 subplots were divided into eight microplots (0.5 m x 0.86 m). In each subplot, one randomly chosen microplot adjacent to each of a planted tree, a planted palm (if present), and no planting were sampled. Aboveground understory biomass from a total of 143 microplots was clipped, separated by species, oven dried at 70° C and weighed to 0.01 g.

To investigate species diversity in the *C. alliodora* plantations, voucher specimens were first collected on the perimeter of the Huertos subplots during February and March 1992. Species identifications were made with the assistance of the La Selva station naturalist, Orlando Vargas, and used to verify data collected from the Huertos subplots. Data were collected using a one-hundred point intercept grid sampling technique during March-May of 1992. At each point, a thin wire was inserted vertically. Recorded information included 1) the presence or absence of vegetative cover, 2) plant species touched by the wire and 3) the number of touches by the leaves of each species. Further details on the point-intercept sampling method are available in Ewel, et al. (1982). The point-intercept sampling was not repeated in 1996.

Data gathered in the subplots were used to calculate: 1) relative frequency (RF), relative abundance (RA), relative dominance (RD), and importance values (IV); and 2) species richness (SR). These composition and diversity indices either 1) describe one biotic element relative to all others, or 2) depict the total richness of a given component in a given ecosystem.

Relative frequency (RF) describes how often a species is encountered within a given area. In the present study, the RF for every species was calculated in each subplot by tallying the number of times a species was encountered in a 100-point sampling grid ($X/100$). Relative dominance (RD) refers to the biomass contribution of any particular species to the total biomass of all species. For each subplot, the aboveground biomass of each species was divided by the total subplot biomass. Subplot values were pooled within replicates and replicate results compared by monoculture and polyculture. Relative abundance (RA) describes how common a species is relative to other species. The total number of "touches" on a vertical tally wire during a 100-point sample grid was divided into the total touches for any given species (species X /total touches). The Importance Value (IV) of each species in a plant community is the sum of its RF, RA and RD, and thus ranges between 0-300 (Barbour 1987). Species with a similar IV might thus have very different values for RF, RD and RA. Species richness (SR) is the total number of species in

the plantation understory. Other richness values were tallied for the number of genera and families represented.

4.4.3. Data analyses

To compare the mean aboveground understory biomass values for the monocultures and the polycultures, I first: 1) computed the size of the microplot harvested for biomass estimates (0.45 m²), 2) multiplied the microplot area by 9 to determine the total subplot area harvested in each replicate (4.05 m²), 3) calculated the per/ha equivalent of biomass by dividing the harvest area into 10⁴ (2500 g), and 5) divided by 1000 to express biomass in kg.

Differences in the mean aboveground understory biomass between the *C. alliodora* monocultures and polycultures for both 1992 and 1996 were tested with linear regression and analysis of variance techniques in SAS® (1988). A Least Significant Difference (LSD) was calculated from Fisher's Protected LSD mean separation technique to compare the mean aboveground understory biomass between monocultures and polycultures and between years. Plots of residuals, predicted values and mean values by biomass, treatment and species were constructed from the data to confirm that assumptions of normality and constant variance were met. The first analysis compared the mean aboveground understory biomass in *C. alliodora* monocultures versus polycultures to determine whether a significant difference existed between plantation types in 1992 and in 1996. The second analysis examined trends in the mean aboveground understory biomass within plantation types between the sampling periods.

Descriptive information calculated for the understory community included: 1) the most dominant species (RD) within and between sampling periods, 2) the total number of species (SR), and 3) the recruitment of new species between sampling periods. Evaluation of RD was via ranking procedures in SAS. The species list (Appendix E) was used to calculate SR and check for new plants between 1992 and 1996.

4.5 Results

In 1992, there was no significant difference in the mean aboveground understory biomass between the monocultures of *C. alliodora* (79.75 kg ha⁻¹) and the polycultures of trees and monocots (54.27 kg ha⁻¹). The mean aboveground understory biomass in the monocultures was significantly greater in 1996 (169.18 kg ha⁻¹) than in 1992. In contrast, the mean aboveground understory biomass in the polycultures was significantly less in 1996 (1.16 kg ha⁻¹) than in 1992. By 1996, the mean aboveground understory biomass between the monocultures and the polycultures was significantly different (LSD=52 kg) (Table 4.1).

Table 4.1 Differences in mean aboveground plant biomass (kg ha⁻¹) in the understory of *C. alliodora* monocultures and polycultures between 1992 and 1996) (LSD=52 kg)

	1992	1996
monocultures	79.75	169.18
polycultures	54.27	1.16

In both *C. alliodora* monocultures and polycultures in 1992, the herb with the highest relative dominance was the monocot *Tripogandra serrulata* (Commelinaceae), followed by *Panicum polygonatum* (Poaceae) (Table 4.2).

Table 4.2 The relative abundance (RA), relative frequency (RF), relative dominance (RD) and importance value (IV) of plant species in the understory of *C. alliodora* monocultures in 1992 with IV>10

Species	RA	RF	RD	IV
<i>Panicum polygonatum</i>	21.73	19.38	19.62	60.73
<i>Paspalum conjugatum</i>	17.81	13.78	16.90	48.49
<i>Tripogandra serrulata</i>	11.70	12.16	22.12	45.98
<i>Piper auritum</i>	11.08	11.77	12.31	35.16
<i>Panicum trichiodes</i>	6.18	5.92	3.75	15.85
<i>Hamelia patens</i>	5.48	3.90	1.70	11.08

Table 4.3 The relative abundance (RA), relative frequency (RF), relative dominance (RD) and importance value (IV) of plant species in the understory of *C. alliodora* polycultures in 1992 with IV>10

Species (family)	RA	RF	RD	IV
<i>Tripogandra serrulata</i>	12.02	15.63	24.09	51.74
<i>Panicum polygonatum</i>	11.74	11.60	17.34	40.67
<i>Cyperaceae sp.</i>	14.37	10.38	12.57	37.32
<i>Piper auritum</i>	9.50	11.66	13.08	34.24
<i>Melamponium sp.</i>	14.23	7.24	6.85	28.32
<i>Paspalum conjugatum</i>	7.43	5.89	5.45	18.77
<i>Neurolana lobata</i>	2.73	1.54	7.76	12.03

In 1992, 109 plant species were present in understory of the *C. alliodora* monocultures and polycultures. These 109 species represent 100 genera from 46 families. In 1996, diversity data were not tabulated for the polycultures, which had a scant understory. In the monocultures, the number of species with a RD>10 decreased from the earlier sampling period (Table 4.4) In the monocultures in 1986, 20 species representing 15 families were present (Appendix E), including two new species which were both woody shrubs: *Nectandra membranacea* (Lauraceae) and *Vernonia patens* (Asteraceae).

Table 4.4 The relative abundance (RD) of plant species in the understory of 3 *C. alliodora* monocultures in 1996 with RD>10

Replicate	species	RD
1	<i>Tripogandra serrulata</i>	35.39
	<i>Paspalum conjugatum</i>	25.17
	<i>Panicum polygonatum</i>	18.29
2	<i>Paspalum conjugatum</i>	83.14
3	<i>Paspalum conjugatum</i>	84.64
	<i>Tripogandra serrulata</i>	

4.6 Discussion

The data for 1992 were collected when the trees were only 1 m in height and crown closure had not yet occurred. Because competition for site resources was low, significant differences in understory biomass were not found, as expected between the monoculture and the polyculture in the first year. In contrast, the data for 1996 was collected when the trees averaged 7 m in height. By 1996 the architecture of the mixed overstory in the polycultures cast the understory in deep shade but the distinctive, tiered leaf-display of *C. alliodora* permitted light-penetration in the monocultures. In 1996, understory biomass in the polycultures was thus expected to be lower than in the monocultures.

Results confirm that the mean aboveground understory biomass was lower in polycultural plantations dominated by *C. alliodora* than in monocultural plantations. The understory development in *C. alliodora* plantations interplanted with perennial monocots was significantly reduced in biomass by the fourth year after establishment. In contrast, the understory biomass of *C. alliodora* monocultures increased during early stand development. The relatively abundant invasive plant community in the monocultures suggests that non-captured site resources were available for understory establishment. If recruitment of

understory species or biomass acquisition is a site objective, a polyculture overstory consisting of *C. alliodora* interplanted with perennial monocots is not a good species choice.

The implication of my results for *C. alliodora* monocultures is that control of understory vegetation after establishment may be important for tree growth. Except for the experimental plots, the monocultural stands in my study were routinely weeded following establishment. Future studies, which compare tree growth in unweeded monocultures to tree growth in weeded stands, will help clarify the potential impact of herbaceous competition in the first years following establishment.

Does plantation establishment negatively impact the rate of species acquisition? Some evidence suggests that tree plantations on degraded tropical sites may facilitate the recruitment of other woody species (Parotta 1992, Lugo et al. 1993, Haggard et al. 1997,). Results from this study confirm the trend of species recruitment under *C. alliodora* plantations established on fertile sites in Atlantic lowland Costa Rica. Species recruitment in the *C. alliodora* plantations was greater than, or equal to, species recruitment in a nearby clearcut that underwent succession for a 3 yr period (Hunter 1989) (Table 4.5).

Table 4.5 Comparison between total species richness (SR) in 1 and 5 yr-old *C. alliodora* monocultures and polycultures and in secondary forest succession after a clearcut in Atlantic Costa Rica

	time since treatment	SR
monoculture	9 mo	49
	4 yr	20
polyculture	9 mo	58
	4 yr	*
secondary succession**	8 mo	30
	4 yr	15

*missing data

**Hunter 1989

4.7 Recommendations

The results of this study describe the plant community in the understory of *C. alliodora* plantations established at 2 m x 2 m spacing on fertile alluvial soils in northern Costa Rica. Sampling techniques which estimate below-ground understory biomass will improve the interpretation of system response and resource capture. The design of the present study does not address the origins of the understory community. The seed source may be: site residual, dispersed from the surrounding secondary forest, inadvertently introduced via humans or dispersed via birds and animals from a non-proximate location. Future studies that clarify the source, diversity, biomass and composition of the understory in tropical plantations will improve understanding of nutrient-use efficiency, productivity and successional dynamics in simplified tropical ecosystems such tree plantations.

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5.0 *Cordia alliodora* silviculture within the land-use mosaic of northern Costa Rica

5.1 Introduction

This chapter summarizes the results of my investigation into development patterns in *C. alliodora* stands in Atlantic lowland Costa Rica. The theoretical and practical implications of study results are considered; recommendations for future activities are given. A brief review of land-use issues in the study area first establishes the context for forest research and management. New information on stand development is discussed relative to the traditional land-uses within which *C. alliodora* is valued. How can the results of this investigation improve silvicultural practices for *C. alliodora*? What is the potential role for *C. alliodora* in sustainable land-use systems in northern Costa Rica? What key pieces of information will refine our answers to these questions?

5.2 The regional land-use context

Simplified ecosystems, such as agricultural lands and secondary forests, are part of landscape dynamics in tropical regions throughout the world. Most tropical secondary forest land is in Latin America, where past forest clearing was primarily associated with agricultural activities rather than with timber export (Schelhas 1994.) A lack of autecological information for commercially valuable trees, such as *C. alliodora*, is an obstacle to sustainable forest management. In addition to autecological information, silvicultural systems must consider the social, economic and political context in which trees grow. Information that improves the regenerative success or yield of a species may be useless if the tree is not valuable relative to competing land-uses.

Land-use objectives are determined by multiple-stakeholders, and are influenced by the political, cultural and physical environments in which they are established. This study does not address what specific mix of forested, agricultural

and urbanized lands is appropriate for sustaining economic and ecosystem values in Atlantic lowland Costa Rica. International scientists can contribute useful information to a local dialogue, but decisions must be made by residents.

All Central American countries have unique features related to geography, ethnic and cultural issues and land tenure. Each country faces development challenges that include:

- servicing foreign debt;
- improving transportation and communication infrastructures;
- maintaining sufficient employment; and
- providing affordable basic human needs (Colchester & Lohmann 1993).

Political and economic objectives have individually and collectively influenced the patterns of land use throughout the region.

This study was conducted in northern Costa Rica, which provides one example of land-use pressures, forest management challenges, and economic conditions within Central America. Study results are only applicable locally, although they may offer insight elsewhere in the region. The silvicultural options for *C. alliodora* depend on site-specific histories, needs and objectives. Stand development patterns in *C. alliodora* will probably differ less throughout the range of the tree than will the cultural and political landscape. Given that forest and agricultural sector goals are clearly established, results from this study may be useful for evaluating the potential role of *C. alliodora* in meeting site-specific objectives in Atlantic lowland Costa Rica.

Costa Rica has a history of political stability, educational achievement, and economic prosperity. This has specific implications for research, management, and potential changes in agricultural and forestry practices. Scientists and extension foresters are able to live and travel within remote areas with minimal discomfort and fear of hostilities. Public literacy rates over 80 % facilitate communication and extension activities throughout rural areas.

This study focused in the tropical lowlands of Atlantic Costa Rica, in the region surrounding the La Selva Biological Station. This region is characterized by a mosaic of forest conservation areas and land colonization projects. Key land-use issues in the study area include: (Schelhas 1994, McDade 1994, pers. obs.)

- the conversion of land from forest to agriculture on the borders of Braulio Carrillo National Park;
- sustaining small subsistence farms;
- absentee ownership of large land tracts devoted to Brahma cattle and banana plantations;
- increasing numbers of landless foreign and non-local workers seeking employment, and
- government-sponsored agricultural settlements.

Colonization in the area has been increasing steadily since the 1970s; over 40 % of land in the Sarapiquí canton is occupied by government settlement projects (Butterfield 1994). The increase in population is associated with the success of export agriculture elsewhere in the country, and has been encouraged by national laws that permit acquisition of land via occupation. Smallholder farms (5-50 ha), cattle ranches (>100 ha) and commercial export-crop plantations now dominate the agricultural landscape. The cattle ranchers bought land from smallholders whose land was unprofitable for agriculture (McDade 1994). Government land policies are, ironically, now dismantling unproductive cattle ranches and offering parcels to smallholders (Butterfield 1994). Developing sustainable systems for smallholders that combine agricultural and forestry crops is a key challenge in the region.

Diversification of crops and land-uses in the study area has increased in the past decade, as transportation networks improve access to markets. Many crops were chosen based on market value rather than on demonstrated adaptability and productivity in the tropical lowlands (Montagnini 1994). For the region to be economically and ecologically viable, it is necessary to stabilize productive land

areas devoted to farming and forestry objectives. On lands designated for production, sustainable agricultural and forestry systems may enhance local income and encourage long-term management. A key challenge in developing sustainable, simplified ecosystems is ensuring that ecosystem functions are maintained while human demands are satisfied. Simplified systems will also provide an opportunity for controlled studies on ecological interactions and sustainability that are more difficult in complex, mature tropical forests (Opler and Jansen 1983).

C. alliodora may be a suitable component of simplified ecosystems in northern Costa Rica. The requirements of the tree for high-light environments and fertile sites suggest it can fill various niches within a farm/forestry land-use mosaic. It is a native species with high commercial value and is already popular among landowners. Sustainable systems that are a modification of existing practices stand more chance of being adopted than new methods and species. The results of this enquiry will facilitate the evaluation of systems in which *C. alliodora* is presently regenerated or cultivated and may improve the design and management of such systems in the future.

5.3 A potential role for *C. alliodora* in the study area?

This section considers the land-uses within which *C. alliodora* is currently present in northern Costa Rica and, given the results of this study, discusses the silvicultural methods that may be appropriate. This includes a consideration of the site objectives and trade-offs that might be associated with different establishment and treatment alternatives.

5.3.1. Contribution of study results

This study investigated the response of *C. alliodora* to density at the individual tree and stand level. Changes in the aboveground biomass and composition of native understory plants were also documented for plantations of *C. alliodora* established at 2 m x 2 m initial spacing. Results from this study suggest that the relationship of height and diameter growth to tree density in *C. alliodora* is

consistent with silvicultural theory. Height was not significantly associated with tree density (TPH), but diameter decreased with increasing density. The crown of *C. alliodora* responded to density differently in diameter (horizontally) than it did in height (vertically). The ratio of the crown diameter to stem diameter at breast height (K/d ratio) was not related to tree density at any given age. The K/d ratio in *C. alliodora* was significantly associated with tree age; older trees exhibited lower K/d ratios than did younger trees. The height-to-live-crown base was directly associated with tree density, tree age and whether the *C. alliodora* stand was a monoculture or a polyculture. The mean height-to-crown of *C. alliodora* in polycultures was lower than for trees in monospecific stands for the range of age and density data in this study.

Volume per hectare in *C. alliodora* was significantly associated with tree density, age and whether the plantation was a monoculture or a polyculture comprised of trees and other crops. For example, at age 5, a monoculture with 500 TPH and no understory will have an estimated $67 \text{ m}^3 \text{ ha}^{-1}$, while a polyculture with the same age and TPH will have only $40 \text{ m}^3 \text{ ha}^{-1}$. By year 10, on 100 TPH, the monocultures will accrue an estimated $106 \text{ m}^3 \text{ ha}^{-1}$ while the polycultures will have only $63 \text{ m}^3 \text{ ha}^{-1}$. Results from this study suggest that the yield and form of *C. alliodora* associated with polycultures will be better with high initial density and subsequent thinning to favor crop trees than if initial density is equal to final tree spacing. Alternatively, pruning may be required if trees are established at low initial densities.

Four years after stand establishment, understory plant biomass of monocultural plantations was significantly higher than in polycultures of *C. alliodora* mixed with perennial monocots. In contrast, in 1992 there was no significant difference in understory plant biomass between the monocultures of *C. alliodora* and the polycultures. The understory plant biomass in the monocultures was significantly greater in 1996 than it was in the same stands in 1992. In contrast, the understory plant biomass in the polycultures was significantly less in 1996 than in 1992.

What are the implications of these study results for *C. alliodora* silviculture within the land-use mosaic of Atlantic lowland Costa Rica?

5.3.2. *C. alliodora* in the land-use mosaic of northern Costa Rica

Landowners who manage *C. alliodora* in the study region have various objectives and methods. Commonly observed methods include 1) clearing secondary forest and retaining a *C. alliodora* overstory to provide shade for cacao, coffee and other perennial crops, 2) planting *C. alliodora* in monocultures to reforest degraded sites and to obtain income, and 3) clearing forest to plant pasture grasses and leaving *C. alliodora* to provide shade for livestock and future timber income. Improved information about stand development patterns associated with *C. alliodora* will help clarify when and where these various methods may be appropriate within an overall land-use design. When a particular method is desirable for a given set of circumstances then information about spacing, growth habit and stand development can improve the type and timing of silvicultural treatments.

5.3.2.1. *C. alliodora* overstory with perennial crops

Retaining or planting an overstory of *C. alliodora* in cacao or coffee plantations is practiced throughout the study region. The benefits associated with this type of management include 1) periodic revenue from the understory crop and 2) improved tree form associated with inter- and intra-specific density when initial trees per ha exceed 400. Example stands from this study include Site 12 (cacao) and Site 15 (cacao). Trees spaced from 5-10 m were initially underplanted with cacao. For several decades, cacao was a viable and financially-attractive crop. Cacao became unproductive following infestation with the pod fungus *Monila rozeri* or was abandoned due to an unstable market. At Site 15, the cacao was removed when the *C. alliodora* trees were approximately 15-yr old. The resulting light environment was sufficient for natural regeneration of *C. alliodora* seedlings, as well as various native shrubs and herbs from the list in Appendix B.

Results of this study suggest that the initial 5 m spacing of the overstory trees contributed to an increase in height-to-crown relative to trees established at a wider spacing. Although not investigated, it is possible that the lateral influence of the cacao also contributed to lower branch pruning in the *C. alliodora* overstory. Cacao removal, coupled with selective thinning of poorly formed trees, will ensure that overstory trees add future diameter increment on well-formed stems. The trees have at least 10 additional years of growth to reach a typical rotation age of 25-30, at which time the diameter will average 45-55 cm. During this time, established seedlings can be selectively spaced for a future crop of *C. alliodora*, or eliminated in favor of an alternative understory crop such as black pepper (*Solanum nigrum*); coffee does not produce well below 500 m in elevation (Schelhas 1994). Kapp and Beer (1995) contend that in similar environmental conditions in southern Costa Rica, a potential commercial understory crop is a fruiting shrub, *Eugenia stipitata* or 'araza', introduced from Brazil. Future botanical investigations into native herb and shrub properties may identify alternative plants for understory regeneration and management.

In contrast to Site 15, the 25-year old stand at Chilamate (Site 12) still has a decadent cacao understory. The understory light environment is low and litterfall inputs high, which likely contribute to the rarity of herbaceous plants and non-existent regeneration of *C. alliodora*. Cacao removal and thinnings to increase tree growth should be timed to provide favorable conditions for a desired understory crop. The selection of an understory crop will depend, in part, on; 1) the desired basal area retained on the overstory trees, 2) the resulting light environment in the understory, 3) timing requirements for harvest income.

Results from this study suggest that a single-species overstory of *C. alliodora* may provide sufficient light for understory development. Light may not be the only limiting factor, however. Gerwing (1994) found that even with adequate light, the growth of two species of *Piperaceae* were impeded by root competition in *C. alliodora*. In this study, a mixture of *C. alliodora* planted with *Euterpe* palms in the overstory is associated with a significant reduction in

understory plant biomass over a four-year period. *Euterpe* palms may not be a good crop in association with *C. alliodora*; in study sites 1, 2 and 4, the palms appear to be outcompeting the trees for site resources by year six.

The sustained productivity of *C. alliodora* grown in association with perennial understory crops will depend on the initial spacing of the trees and on the crop variety, as well as the timing of subsequent thinning operations 1) to create favorable conditions for establishment of the desired crops or tree regeneration, and 2) to capture mortality and redistribute growing space on desirable crop trees. The preliminary density management diagram developed from study data can 1) guide the timing and intensity of thinning to meet the latter objective and 2) help reduce the subjectivity in selective thinning (eg: Kapp and Beer 1995).

5.3.2.2. *C. alliodora* monocultures

The site fertility requirements of *C. alliodora* suggest that high-density monocultural plantations will only be feasible for wealthy landowners who can afford the opportunity costs associated with 25-30 year rotations. Site 31 offers a good example of a landowner who can afford the labor and land costs associated with a *C. alliodora* monoculture on fertile soils. The landowner, Don Wilfrido Rodriguez Quesada, has a personal preference for native tree species. For landowners who elect to establish and manage monocultural plantations, the costs and benefits associated with exotic species will often be considered.

The mean annual increment predicted by this study for *C. alliodora* in monocultures is $6.3 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ for 100 TPH at a rotation age of 30. Kapp and Beer (1995) report mean annual increment for *C. alliodora* in monocultures of $12 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$; the rotation length is estimated to be between 25-30 yr. In contrast, the mean annual increment and rotation lengths for exotic genera that are popular for plantation establishment in Costa Rica are presented in Table 5.1.

Table 5.1 Mean annual increment for some exotic tree species used for plantations in Costa Rica

Location	Species	Mean Annual Increment ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$)	Rotation (years)
Fiji	<i>Pinus caribaea</i>	15-20	15-17
Brazil	<i>Pinus caribaea</i>	20	16
Costa Rica	<i>Gmelina arborea</i>	11.8	-
Costa Rica	<i>Eucalyptus deglupta</i>	11.9	-

sources: Evans 1992

A species that requires minimum inputs of land, labor and capital to obtain a given return will generally be preferred by investors. Financial and environmental information will help improve the match of species to site conditions and objectives. Full accounting will only be possible when comparable information is available for a variety of species, including both native and non-native trees. Although the mean annual increment of *C. alliodora* was lower than that for many exotic species, other attributes may make the tree a good choice for specific sites.

The mean K/d ratio of *C. alliodora* was 0.245, and was not significantly associated with density. Interest in the K/d ratio is based on the implication that a rigid ratio limits the basal area and number of trees of a certain mean diameter for any given species (Philip 1994). Trees with a low K/d ratio, such as *C. alliodora*, are more suitable for even-aged plantations than those with higher ratios, since the former can support higher basal area per unit area (and thus higher volume per area growth rates) (Dawkins 1963).

To evaluate the potential value and sustainability of *C. alliodora* monocultures in the study region, further information is needed on:

- long-term site productivity and nutrient balances,
- volume tables and taper equations
- biotic and chemical defenses to herbivory and pathogens.

5.3.2.3. *C. alliodora* retained in cattle pasture

C. alliodora trees retained when forest is cleared for pastureland are generally of merchantable size and reasonable form. At what rate these remnant trees will increase in diameter following removal of other trees has not been investigated. Seedlings of *C. alliodora* were not present in the pasture sites included in this study, which include Site 19 and Site 20. The conventional wisdom that grass competition inhibits the early growth of *C. alliodora* needs to be investigated to evaluate the benefits associated with this method as well as the implications for sustained management.

5.4 Potential implications of study results

Results from this study suggest that in the design of sustainable land use systems, *C. alliodora* may be especially suitable in, 1) the margins of mature forestland, 2) mixtures with perennial crops, or 3) managed within secondary forest. *C. alliodora* may be a good component of “buffer zones” between conservation forests, annual agriculture and urban areas. The tree has a potential, but insufficiently investigated, role in monocultural plantations and pastures.

The results of this study have both theoretical and practical implications. The present study extends theories of size-density and growth-growing stock relations to the tropical secondary forest species *C. alliodora*. Study results also offer preliminary guidance for other investigations into key aspects of system productivity, such as non-tree biomass. This could help shorten the time needed to develop sustainable management practices for tropical secondary forest ecosystems.

Study results immediately contribute to information needs of extension foresters in the study region (Marota, 1996, personal communication). The *C. alliodora* plantations established with incentive program funds over the last decade are now in need of some silvicultural treatment to enhance stand value for timber production. When the incentive plantings were established, there was no clear sense of the desired future condition or a schedule of the type and timing of treatments needed to guide management decisions. The initial conditions, such as spacing and

site quality, of each stand dictate what options are available now. The preliminary density-management diagrams resulting from this study can help identify what these options are and how various treatments might move the stands toward a desired future condition.

Study results may also help educate landowners about principles of tree growth and encourage realistic, site-specific objectives. Although understood by extension foresters, the concept of thinning has not had widespread support from landowners or the agencies that provide management funds. This study provides tools that extension foresters can use to:

- communicate to landowners and funding agencies such as the U.S. Agency for International Development (FUNDECOR) the potential response associated with different levels of thinning,
- evaluate existing stand densities to prescribe silvicultural treatments and
- identify further areas for research and solicit assistance in the design and implementation of future experiments.

This study created educational tools such as cross-sectional bole segments or “galletas” that demonstrate clearly the growth response associated with thinning in 5-yr old *C. alliodora* plantations. More dramatically than words, the seasonal rings or “anillos” in the *C. alliodora* galletas reveal that increased growing space is associated with increased diameter increment.

Study results may also aid in the interpretation of other related investigations. For example, Kapp and Beer (1995) observed that *C. alliodora* grown with other species were taller in height than *C. alliodora* grown in monocultures. The investigators were uncertain whether the observed difference in height was due to differences in *C. alliodora* spacing, or whether some aspect or treatment of the associated crop was involved. If, as the present study supports, height growth in *C. alliodora* is not significantly associated with tree density, the latter explanation is most likely. Further studies on height growth could include a designed experiment to test the response of *C. alliodora* associated with fertilizer .

5.5 Recommendations for additional research on *C. alliodora*

This study contributed to information needs about the neotropical timber tree *C. alliodora*. In considering the implications of study results for the management of this tree some further gaps in information were identified. Some of the areas for further research are directly related to quantifying stand development and growth dynamics in *C. alliodora*, while others are less direct.

5.5.1. Future studies needed in stand development

A key limitation in the study analyses is a lack of individual tree volume tables for plantation-grown *C. alliodora*, for small stems and for stands in excess of 20 yr in age. Studies need to be undertaken that evaluate the height/diameter/stem taper relationship of *C. alliodora* grown in monocultures. This will enable a more accurate comparison of yield between *C. alliodora* and other species grown in plantations. An investigation into the wood quality associated with plantation trees will also improve comparisons with other management alternatives.

5.5.2. General studies on related topics

C. alliodora grows on both the Pacific and Atlantic slopes of Costa Rica in dry, moist, premontane moist and premontane wet life zones. The present study focused only on Atlantic moist and premontane moist forests. A comparison of size-density relations, tree form and seasonal growth in *C. alliodora* in other life zones is necessary. Opler and Janzen (1983) observed that *C. alliodora* reaches 30 m in height and 90 cm dbh in rainforest, but is small and bushy in deciduous forests. Devall et al (1995) demonstrated the seasonality of growth rings for *C. alliodora* in drier, seasonal forests of Panama. Extending this investigation of density-yield relations in *C. alliodora* to drier sites will help improve the silviculture of this important secondary forest species throughout its range in the American tropics.

Other aspects of *C. alliodora* that deserve further study include both ecological and economic concerns. How is *C. alliodora* associated with site

nitrogen availability? What mechanism influences the timing and duration of seasonal leaf loss? What chemical or biological defenses protect the tree against herbivory when in young, single-species' plantations and how long does the resistance persist? Economic questions relate to harvest and yield. Is the yield of *C. alliodora* associated with farm size and landowner characteristics as well as environmental variables (McCaffrey 1968). One innovative design encountered during my sampling was Site 7 (Isla Grande), where *C. alliodora* provided an overstory to another valuable timber species, roble (*Tabebuia rosea*). Planting designs that facilitate harvesting efficiency in two-story stands are needed, as well as further studies to quantify the optimal timing and intensity of silvicultural treatments associated with different understory crops.

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APPENDICES

Appendix A

Common names for *Cordia alliodora* within the native range of the tree

<u>location</u>	<u>name</u>
Central America & Ecuador	laurel, laurel blanco, laurel negro
Puerto Rico, Caribbean Islands	capá prieto
Trinidad & Tobago	cypre
Honduras	salmwood
Mexico & Honduras	bojón
Columbia	solera
Haiti	bois soumis
Venezuela	pardillo
Paraguay	peterbi
Peru	arbol del ajo

Appendix B

Letter of introduction from the Organization for Tropical Studies



Organización para Estudios Tropicales
Organization for Tropical Studies, Inc.

Estación Biológica La Selva
Nacional
Apartado 676-2050 San Pedro, Costa Rica
Tel.: (506) 710-1515 • Fax: (506) 710-1414
Internacional
Air Mail Incentive 341
P.O. Box 02-5635
Miami, FL 33152

17 de junio, 1996

A quien interese:

La portadora de esta carta, Susan Stevens, está realizando investigación de silvicultura del árbol Cordia alliodora (laurel). Ella está investigando diferencias en las tasas de crecimiento y formas con relación con las densidades de plantación del laurel. Para evaluar, estas diferencias, ellas debe medir el crecimiento del laurel en un ámbito de sitios que representan diferentes edades y densidades. Las mediciones se realizarán en muestras de 30 x 30 incluyen el diámetro altura y ancho de la copa de todos los árboles de laurel. No es necesario hacer ninguna anotación. Con el permiso del dueño de la finca, se tomará una parte del diámetro del centro para verificar la edad del árbol.

Los resultados de este estudio pueden ayudar en el establecimiento y manejo de laurel en el futuro. Cualquier ayuda que pueda proveerle a ella en identificar la localización de los árboles de laurel o darle permiso para medirlos será muy apreciada.

Muchas gracias por su atención al respecto,

Cynthia Echeverría

Cynthia Echeverría
Co-directora
Estación Biológica La Selva

Appendix C

Table of data collected or calculated from the study plots

Polycultures		age	dbh(range)	ht (range)	tot.BA/plo	BA/CoAl/plot	BA/CoAl/h	Vol/ha(m ³)/Co	meanHToC	QMD(cm)	SDI
Site#	TPH										
1	1988	5	2.1-24.4	2.1-19.48	1.47607	1.4760682	16.4	74.08967984	10.83375	10.25	477.39
2	2898	5	2.0-17.3	1.7-18.1	1.65329	1.6532874	18.36	99.96182345	10.46	8.96	561.16
3	165	15	13.0-41.1	14.1-21.9	0.98955	0.9895451	10.99	96.76128816	10.811429	28.98	209
4	2897	5	2-16.4	2.3-20.1	1.88895	1.8889467	20.98	143.2566074	12.24	9.6	626.43
5	4008	5	2.9-24.9	2.9-17.8	5.47357	2.26	25.11	153.0311303	8.1583333	13.9	1566.92
6	3664	5	2.5-28.0	3.5-24.5	4.84854	1.45	16.11	102.26	13.128	13.68	1398.34
7	522	8	9.5-27.5	10.9-19.5	1.05572	1.055715	11.73	83.4471447	11.9	16.73	274.51
8	333	3	1.5-11	1.7-6.9	0.1353	0.1353048	1.5	5.292461266	2.7425	7.58	49.34
10	433	45	11.0-53	35-38	3.09361	1.45	16.11	176.8321405	25.4	31.78	550.43
11	267	35	10.0-45	20-32	0.99795	0.47	5.22	101.7643974	30.25	23.01	233.82
12	556	25	10.2-49		1.73581	0.65	7.22	178.8221375	16.15	21.02	421.29
13	856	4	2.1-13.7	5.3-11.1	0.37764	0.37764	4.12	23.58847193	5.3953846	7.91	135.79
14	200	34	22.4-72	36-42.1	3.09094	2.1	23.33	389.7935834	28.36	48.77	544.85
15	100	17	10.5-48	8.3-24.1	0.91743	0.9174257	10.19	105.5933516	11.385	36.03	179.46
16	144	15	5.5-37	4.1-28	1.09881	0.89	9.89	119.4426861	15.683333	32.81	222.47
Monocultures											
17	356	13	28-45	9.6-23	1.05674	1.0567369	11.74	90.17001986	14.351667	20.5	259.15
18	367	11	21-38	22-27.2	1.01786	0.967	10.74	100.4479654	17.0425	19.82	253.12
19	122	13	15.3-31.1	14.5-25	0.54263	0.462	5.13	50.23884741	14.99	25.06	122.46
20	133	15	11.5-34	10.7-26.9	0.65838	0.6583812	7.31	68.07247248	13.283333	26.43	145.38
22	246	3	4.5-23	2.7-14.3	0.96272	0.954	10.6	69.32874807	7.2757143	15.21	111.08
23	587	35	10.5-55	14.4-35.8					19.35		
24	1797	5	2.5-23.5	3.2-17.1	1.74745	1.7474506	19.41	122.2662576	9.275	11.65	529.62
25	2085	5	2.5-20.7	4.5-18.9	1.71162	1.7116199	19.01	143.0946106	11.575	10.77	541.94
26	2243	5	3.3-25.4	3.7-18.3	2.12846	2.1284646	23.64	164.0274835	10.2	11.58	664.73
27	566	4	3.1-17.6	5.6-14	0.5345	0.52	5.77	37.74725883	7.7366667	11.23	157.3
28	666	4	4.5-26	12.7-19.4	1.38304	1.3830431	15.37	112.4747661	13.935	17.13	363.73
29	143	8	8-33.5	7.3-22.9	0.78589	0.7858909	8.73	34.6518725	12.411429	27.74	168.89
30	145	8	22-34	18.7-20.5	0.73184	0.7318357	8.14	70.20686997	14.063333	26.77	161.77
31	1932	4	4.2-5.8	4.9-26.1	2.03931	2.0393139	22.66	200.9084161	7.7819048	12.22	614.63

Appendix D

Estimated volume/ha (m³) for *C. alliodora* in
monocultures and polycultures in northern Costa Rica

Stand age	TPH	estimated volume	
		for monoculture	for polyculture
5	100	31	19
5	500	67	40
5	1000	92	55
5	1500	111	67
5	2000	128	77
5	2500	141	
5	3000	154	
10	100	50	30
10	500	106	63
10	1000	146	88
10	1500	176	106
10	2000	203	
15	100	71	42
15	500	151	90
15	1000	208	125
15	1500	251	
20	100	95	57
20	500	203	122
20	1000	281	
25	100	124	75
25	500	264	
30	100	157	94
40	100	240	144

Appendix E

List of plant species by family collected in the understory of *C. alliodora* monocultures and polycultures in 1992 at La Selva Biological Station, Costa Rica.

(Identification information in parentheses is the author specimen voucher number. The vouchers are catalogued in the La Selva herbarium.)

Acanthaceae:

Blechum brownei Juss. (Stevens #43)

Razisea spicata Oerst. (Stevens #50)

Amaranthaceae:

Iresine diffusa Humb. & Bonpl. ex Willd. (Stevens #32)

Cyathula achyranthoides (H.B.K.) Moq. (Stevens #34 & 86)

Cyathula prostata (L.) Blume (Stevens #59)

Alternanthera sp. (Stevens 113)

Amaryllidaceae:

Bomarea obovata (Stevens #12)

Araceae:

Xanthosoma sp. (Stevens #44)

Dieffenbachia sp. (Stevens 133)

Asteraceae:

Clibadium (Stevens #7)

Neurolana lobata (L.) R.Br. (Stevens #16)

Erechtites hiracifolia (L.) Raf. ex DC. (Stevens #23)

Eupathoryum sp. (Stevens #20)

Conyza bonariensis (L.) Cronq. (Stevens #33)

Pseudelephantopus (Stevens #37)

Mikania sp.(Stevens #60)

Eclipta prostrata L.(Stevens #62)

Chaptalia nutens (Stevens #70)

Hebeclenium macrophyllum (L.) DC. (Stevens #7)

Synedrella nodiflora (L.) J. Gaertn.(Stevens #73)

Lasianthaea fruticosa (L.) K.M. Becker (Stevens #28)

Melamponium sp. (Stevens #85)

Fleishmannia microstemon (Cass.) R. King & H. Robinson (#98)

Asclepiadaceae:

Matelea sp. (Stevens #88)

Begoniaceae:

Begonia semiovata Liebm. (Stevens #51)

Begonia fischeri Schrank (Stevens #53)

Campanulaceae:

Hippobroma longiflora (L.) G. Don (Stevens #8 & 19)

Caricaceae:

Carica papaya L.(Stevens #54)

Caryophyllaceae:

Drymaria cordata (L.) Willd. ex Roemer & Schultes (Stevens #64)

Cecropiaceae:

Cecropia obtusifolia Bertol. (Stevens 129)

Commelinaceae:

Tripogandra serrulata (Vahl) Handlos (Stevens #5)

Convolvulaceae:

Ipomea philomega (Vell.) House (Stevens #21)

Merrimia umbellata (L) Hall. f. (Stevens #46)

Ipomea alba (L.) (Stevens #77)

Costaceae:

Costus malortieanus Wendl. (Stevens #52)

Cucurbitaceae:

Frantzia villosa Wunderlin (Stevens #10)

Melothria pendula L. (Stevens 81) .

Psiguria sp. (Stevens #119)

Memordica charantia L. (Stevens 130)

Cyperaceae:

Cyperus tenuis Swartz (Stevens 39)

Cyperus sp (oderatus?) (57 &67)

Rhynchospora (Stevens 117)

Dichroma sp. (Stevens 100)

Euphorbiaceae:

Chamaesyce sp. (Stevens #47)

Acalypha diversifolia Jacq. (Stevens 124)

Fabaceae:

Mimosa pudica (Stevens 87)

Vigna sp (Stevens #109)

Desmodium sp. (Stevens 94)

Calpogonium coeruleum (Benth.) Sauvalle (Stevens #27 & 48)

(Stevens #38)

(Stevens #83)

Gesneriaceae:

Chrysothemis friedrichsthaliana (Hanst.) H.E.Moore (Stevens #9)

Episcia sp. (Stevens #116)

Haemodoraceae:

Xiphidium coeruleum Aubl. (Stevens 89)

Lamiaceae:

Hyptis sp. (Stevens #110)

Loasaceae:

Sclerothrix fasciculata Presl (Stevens 108)

Loganiaceae:

Spigelia humboldtiana Cham. & Schlecht. (Stevens #42)

Malvaceae:

Sida rhombifolia L. (Stevens 6 & 24)

Wissadula exselcior (Cav.) Presl. (Stevens #15)

Marantaceae:

Calathea marantifolia Standl. (Stevens 140)

Melastomataceae:

Conostegia subcrustulata (Beurl.) Tr. (Stevens #2)

Molluginaceae:

Mollugo verticillata L. (Stevens #65)

Myrsinaceae:

Auricularia nigropunctata (Oerst.) Lundell (Stevens #49)

Onagraceae:

Ludwigia (Stevens #78 & 82)

Oxalidaceae:

Oxalis sp.

Passifloraceae:

Passiflora lobata (Killip) J. MacDougal (Stevens 80)

Phytolaccaceae:

Phytolacca rivinoides Kunth & Bouch (Stevens #4)

Rivina humilis (L.) (Stevens #40 & 44)

Piperaceae:

Piper hispidum Sw. (Stevens #35)

Lepianthes peltata (L) Raf. (Stevens #45)

Peperomia pellucida (L.) H.B.K. (Stevens #56)

Piper phytolaccaefolium Opiz (Stevens #75 & 105)

Piper auritum H.B.K. (Stevens 95)

Poaceae:

Coix lachryma -jobi L. (Stevens #11)

Panicum trichiodes Sw. (Stevens #26)

Oplismenus burmannii (Retz.) P. Beauv. (Stevens #41)

Eleusine indica (L.) J. Gaertn. (Stevens #55)

Panicum polygonatum Schrader ex Schultes (Stevens #61)

Bracharia fasciculata (Sw.) Parodi (Stevens #79)

Paspalum conjugatum Bergius (Stevens #86 & 101)

Andropogon bicornis L. (Stevens 142)

Axonopus compressus (Sw.) P. Beauv.

Portulacaceae:

Portulaca oleracea L. (Stevens #22 & #90)

Pteridaceae:

Pityrogramma calomelanos (L.) Link (Stevens #63)

Rubiaceae:

Hamelia patens Jacq (Stevens #1)

Spermacoce assurgens (Stevens 36)

Manettia reclinata L. (Stevens 107)

Psychotria hebeclada DC. (Stevens 132)

Scrophulariaceae:

Stemodia verticillata (P.Mill.) Hassler (Stevens #66)

Mecardonia procumbens (P. Mill) Small (Stevens #84)

Lindernia sp. (Stevens #120)

Scoparia dulcis L. (Stevens 110 & 126)

Selaginellaceae:

Selaginella silvestris Aspl. (Stevens #111)

Solanaceae:

Browallia americana L. (Stevens #3)

Solanum americanum P. Mill (Stevens #13 & 14)

Solanum lancaeifolium Jacq (Stevens #17)

Solanum jamaicense P. Mill. (Stevens #71 & 123)

Lycianthes synanthera (Sendt.) Bitter (Stevens # 102)

Physalis pubescens L. (Stevens 138)

Cestrum racemosum Ruiz & Pavon

Thelypteridaceae:

Thelypteris torresiana (Gaud.) Alston (Stevens 74)

Umbelliferae:

Eryngium foetidum L. (Stevens #18)

Spananthe paniculata Jacq (Stevens #25)

Hydrocotyle sp. (Stevens 106)

Urticaceae:

Urera baccifera (L.) Gaud. (Stevens #29)

Phenax sonneratii (Poir.) Wedd. (Stevens #30)

Laportea aestuans (L.) Chew (Stevens #31)

Pilea microphylla (L.) Liebm. (Stevens 135)

Verbenaceae:

Lantana trifolia (Stevens # 96)

Vitaceae:

Cissus sp. (Stevens #103)

Zingiberaceae:

Hedychium coronarium Koenig (Stevens 130)