メヒルギ林の自己間引き過程と、それが地上部現存量動態と森林構造に及ぼす影響

メタデータ	言語: 出版者: 琉球大学 公開日: 2015-05-13 キーワード (Ja): キーワード (En): 作成者: Mouctar, Kamara, モクタール, カマラ メールアドレス: 所属:
URL	http://hdl.handle.net/20.500.12000/30814

Self-thinning process and its implications on aboveground mass dynamics and stands structure in overcrowded mangrove ***Kandelia obovata*** forest

by

© Mouctar Kamara

A thesis submitted to the Graduate School of Engineering and Science in partial
fulfillment of the requirements for the degree
of
Doctor of Science
in
Plant Ecophysiology
under

Chemistry, Biology and Marine Science
Graduate School of Engineering and Science
University of the Ryukyus
Okinawa, Japan

March 2015

Supervisor: Profs. Akio Hagihara / Yasuhiro Kubota

Doctoral Thesis of Science

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CERTIFICATION

We, the undersigned, hereby, declare that we have read this thesis and we have attended the thesis defense and evaluation meeting. Therefore, we certify that, to the best of our knowledge this thesis is satisfactory to the scope and quality as a thesis for the degree of Doctor of Science in Plant Ecophysiology under Marine and Environmental Science, Graduate School of Engineering and Science, University of the Ryukyus.

THESIS REVIEW & EVALUATION COMMITTEE MEMBERS

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Abstract

In this study, the effects of self-thinning process on aboveground mass dynamics and stand structure were investigated over eight years in a subtropical overcrowded (ground is always 100% covered) mangrove *Kandelia obovata* forest on Okinawa Island, Japan. Plants are concurrently engaged in variable competitive interactions that take place under continuously changing densities. Competition occurs also between organs that develop under different growth conditions which often results in the dominance of the more successful organs at the expense of their less fortunate counterparts. This somatic self-thinning might result in radically different self-thinning exponents for tree organs. Therefore, applying Weller's allometric model, the slope of the self-thinning exponent α_{x} of a partial organ "x" and total aboveground was calculated from the allometric constants θ_{x} and δ_{x} obtained from the allometric relationships of mean tree height $\overline{H}$ and mean organ mass density $\overline{d}$ (kg m^{-3}) with mean organ mass $\overline{w}_{\mathrm{x}}$. The self-thinning exponent, α_{x}, was estimated to be 1.509 for stem, 1.647 for branch, 1.090 for leaf, and 1.507 for aboveground. The ϕ_{x}-value was 0.6629 ± 0.0250 for stem, 0.6072 ± 0.0229 for branch, 0.9167 ± 0.0356 for leaf, and 0.6637 ± 0.0297 for aboveground. The value did not significantly differ from 2/3 but did significantly differ from 3/4 for stem, branch, and aboveground, indicating that the self-thinning exponents for woody parts did not significantly differ from 3/2. This result suggests that the self-thinning exponent is closer to 3/2 than to 4/3. In contrast, the ϕ_{L}-value for leaf significantly differed from both 2/3 and 3/4 but did not significantly differ from 1.0, indicating that stand leaf biomass was constant regardless of population density. The self-thinning exponent for leaf had a negligible effect on that for aboveground due to the small amount of leaf mass compared to the combined mass of all woody organs. The present results based on the allometric model of partial organs roughly support the 3/2 power law for aboveground self-thinning. For overcrowded *K. obovata* stands, self-thinning could be explained by a simple geometric model rather than a metabolic model. Self-thinning process was eventually accompanied by changes in the dynamics of aboveground mass and stand structure overtime. The rank of aboveground mass w was not completely constant as the stands grew, although the values of Spearman's rank correlation coefficient of w significantly differed from zero ($P < 0.01$). Therefore, the mass hierarchy of overcrowded *K. obovata* mangrove stands was dynamic as stands grew. The mode of the frequency distribution shifted to the right each year;

smaller trees suffered high mortality, and surviving trees that were suppressed gradually continued to grow. The variation of H becomes small as the stands grow, and finally all trees may have a similar height. On the other hand, SD of $D_{0.1\mathrm{H}}$ was stable as the stands grew. The frequency distribution of H was almost stable with the J-shape but at the same time, the frequency distributions of $D_{0.1\mathrm{H}}$ were L-shaped. These variations on tree hight, aboveground mass rank and frequency distribution, skewness of stem diameter and aboveground mass indicate that the mangrove have their own mechanisms to maintain the stand health in the face of density changing during the self-thinning process.

List of Publications

1. **Kamara. M**, Deshar. R, Sharma. S, Hagihara. A, "The self-thinning exponent in overcrowded stands of the mangrove, *Kandelia obovata*, on Okinawa Island, Japan," Journal of Oceanography, vol. 68, pp. 851-856, 2012.

2. **Kamara. M**, Deshar. R, Kamruzzaman. M, Analuddin. K, and Hagihara. A, "Dynamics of Aboveground Mass Hierarchy in Overcrowded Mangrove *Kandelia obovata* Stands on Okinawa Island, Japan," APCBEE Procedia, vol. 5, pp. 38-45, 2013.

3. **Kamara. M**, Deshar. R, Analuddin. K, Kamruzzaman. M, and Hagihara. A, "Self-thinning of stems, branches, and leaves in overcrowded mangrove *Kandelia obovata* stands on Okinawa Island, Japan," Aquatic Botany, vol. 119, pp. 20-27, 2014.

4. Deshar. R, Sharma. S, Rafiqul. A.T.M, Wu. M, **Kamara. M**, and Hagihara. A, "Self-thinning line in overcrowded stands of the mangrove, *Bruguierra gymnorrhiza*, Okinawa Island, Japan," Tropics, vol. 20 (3), pp. 71-77, 2012.

5. Deshar. R, Sharma. S, **Kamara. M**, and Hagihara. A, "Self-thinning exponents for partial organs in overcrowded mangrove, *Bruguiera gymnorrhiza* on Okinawa Island, Japan," Forest Ecology and Management, vol. 28, pp. 146-154, 2012.

6. Kamruzzaman. M, Sharma. S, **Kamara. M**, and Hagihara. A, "Phenological traits of the mangrove *Rhizophora stylosa* Griff. at the northern limit of its biogeographical distribution," Forest Ecology and Management, vol. 28, pp. 277-288, 2013.

7. Kamruzzaman. M, Sharma. S, **Kamara. M**, and Hagihara. A, "Vegetative and reproductive phenology of the mangrove *Bruguiera gymnorrhiza* (L.) Lam. On Okinawa Island, Japan," Trees Structure and Function, vol. 27, pp. 619-628, 2013.

8. Kamruzzaman. M, Sharma. S, **Kamara. M**, Deshar. R, and Hagihara. A, "Temporal variation in litterfall production of *Bruguiera gymnorrhiza* stands on Okinawa Island, Japan," APCBEE Procedia, vol. 5, pp. 16-21, 2013.

Conference Papers: Presented/Accepted

1. **Kamara. M**, Deshar. R, Sharma. S, and Hagihara. A, ”Geometry and Allometry models in Self-thinning: A case study of *Kandelia obovata* stands,” East China Sea Workshop International Workshop (ECS), Okinawa, Japan 2011.

2. **Kamara. M**, Analuddin. K, Deshar. R, Sharma. S, Hagihara. A, ”Self-thinning of overcrowded *Kandelia obovata* stands in Manko Wetland, Okinawa Island,” International Conference on Environmental Aspects of Bengladesh (ICEAB), Kitakyusyu, Japan, 2011.

3. **Kamara. M**, Deshar. R, Sharma. S, and Hagihara. A, ”The self-thinning exponent in overcrowded mangrove *Kandelia obovata* stands,” The 59th Annual Meeting of Ecological Society of Japan (ESJ), Otsu, Japan, 2012.

4. **Kamara. M**, Kamruzzaman. M, Deshar. R, Sharma. S, and Hagihara. A, ”Self-thinning exponents of partial organs and aboveground mass of mangrove *Kandelia obovata* stands,” The 60th Annual Meeting of Ecological Society of Japan (ESJ), Suzuka, Japan, 2013.

Acknowledgements

In the name of Allah (SWT) the most Gracious and the most Merciful, all praise and worship is due to him, the unique with wonderful attributes.

Foremost, I would like to express my sincere gratitude to my advisor Prof. Akio Hagihara whose encouragement, guidance and continuous support from the initial to the final level of this research. His patience, motivation, enthusiasm, and immense knowledge helped me in all the time during research and writing of this thesis. I could not have imagined having a better advisor and mentor for my study.

I am entirely grateful to Prof. Kubota who accepted to take me in his lab after the retirement of Prof. Akio Hagihara. I am also grateful to my referees for their helpful critics and suggestions that make this thesis satisfactory.

Many thanks to Drs. Md. Kamruzzaman, Rashila Deshar, A.T.M Rafiqul Hoque, and Sahadev Sharma for cordial help and valuable suggestions during my research. I thank also Dr. Kangkuso Analuddin for his help and support during my field work.

I deeply thank to the Ministry of Education, Culture, Sports, Science and Technology (MEXT) for funding my study in Japan and the Faculty of Science, University of the Ryukyus for the fulfillment of my study. I would like to thank the staffs of the Faculty of Science and Biology office for their valuable cooperation.

I appreciate the supports and helps from all of my friends and well-wishers in Okinawa specially Mr Mouhamed Dioum and his wife for their various support and encouragement which made my stay in Okinawa more comfortable. Many thanks to Dr. Said Mouhamed Said and his family for their kindness and valuable support. I really appreciated it brother thank you so much.

”Les Malheureux n’ont point de parents”

A ma mere qui n’a menage aucun effort pour m’assurer une bonne education.

A ma famille qui m’aura soutenu jusqu’au bout.

Les mots n’auront jamais assez de force pour exprimer ce que je leur dois. Qu’ils trouvent ici l’expression de ma plus profonde et affectueuse gratitude.

Et a tous ceux qui m’ont apporte leur soutien, je dedie ce travail.

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Chapter 1

General Introduction

1.1 Introduction

The study of interactions between plant populations and their implications for ecosystem function and dynamics has been an important ecological research theme. Among these interactions, the study of competition has occupied a prevalent place. The self-thinning (i.e. the natural process whereby numbers of trees per unit area decreases as average tree size increase over time) is an important component at plant competition at the population level. It is the result of infraspecific competition in densely planted populations. The response to density is the mortality of a fraction of the population and changes in the distribution of aboveground biomass among surviving members (Weller, 1987). The self-thinning and the changes in size structural of trees also have important implications for ecology and evolution of overcrowded plant populations (e.g. Weiner and Whigham, 1988), and for the structure and the dynamics of tree populations (e.g. Ogawa and Hagihara, 2003). It is considered as one of the most interesting themes in ecology. The acceptance of this rule by plant ecologists is based on many observations of this power relationship in plant populations ranging from mosses to trees. The theoretical importance of the self-thinning rule is evidenced by many published statements of plant ecologists. White (1981) called it one of the best generalization of plant demography. Westoby (1981) considers it the most general principle of plant demography and suggests that it be elevated beyond the status of an empirical generalization to take a ”central place in the concepts of population dynamics”. Hutchings and Budd (1981a) emphasized the uniqueness of its precise mathematical formulation to a science where most general statements can be stated in only vaguer, qualitative terms. The rule can be used also to compare the site qualities (fertility) or histories of plant populations growing at different site (Morris 2002). Ecologists have examined the effects of the availability of essential resources, such as light and mineral nutrients, on self-thinning. Harper, 1977 assumes that Plants grown at low levels of illumination thin faster and reach maximum biomass levels sooner (Hutchings and Budd l981b) than populations grown with higher illumination. It could be a useful management tool in forestry (Yoda et al. 1963), or in any other applications requiring predictions of the limits of biomass production for a given species at any density (Hutchings 1983).

The rule has empirically been discussed for more than 40 years (e.g. Yoda et al. 1963; Hozumi 1977; White 1981; Hutching and Budd 1981; Lonsdale and Watkinson 1983; Hutchings 1983; Long and Smith 1984; Hamilton et al. 1995; Enquiest et al. 1998; Hagihara 2000; Roderick and Barnes 2004; Coomes and Allen 2007; McCarthy and Weetman 2007; Zhang et al. 2007; Chen et al. 2008; Analuddin et al. 2009; Deshar et al. 2012). Some authors have developed some model which predicted that the thinning exponent α should vary from the idealized value of -3/2. Some extensions and applications of the self-thinning rule have been also proposed even though it was originally observed in monocultures. Recently some authors have applied the thinning rule to animal populations living in intertidal zone like bernacles, mussels (Keeley, 2003; Sibomana et al. 2013). There are two prevalent views of expected relationship between shifting (declining) density and average aboveground biomass of survivors trees. One is the classical view, based on a simple model of plant geometry, the other view, is based on a generalization of scaling laws broadly observed in both plant and animals.

Yoda et al. (1963) derived a simple, geometric explanation of the self-thinning from two assumptions: (1) plants of a given species are always geometrically similar regardless of habitat, size, or age; and (2) mortality occurs only when the total coverage of a plant stand exceeds the available area then acts to maintain 100% cover. The first assumption allows the ground area, s, covered by a plant to be expressed mathematically as a power function of plant weight, s $\propto w^{2/3}$, while the second assumption implies that the average area covered is inversely proportional to density, that $\overline{s} \propto 1/\rho$. Combining these two equations and adding a constant of proportionality, K, gives the thinning rule equation

$w = K \cdot \rho^{-3/2}$. This relationship is referred to as **the -3/2 power law**. Since eventually all area is covered by plants, there is a maximum biomass and density that can be achieved, called a constant final yield (Hagihara, 2014). The geometric model suggests that plants acquire their basic resource that means sunlight for photosynthesis producing carbon and energy-rich molecule based on the exposed surface area of the plant. However, the plant must distribute the resource throughout a three dimensional volume.

Meanwhile, According to some authors, the assumption that plant shape is invariant is not tenable, so, these derivations of the self-thinning rule are unsatisfactory (Weller, 1987a). Miyanishi et al. (1979) attempted to reconcile these simple geometric models with the fact of varying plant shapes in their generalized self-thinning law, which states that the power of the thinning equation depends on the proportionality between plant weight and ground area covered and the self-thinning exponent is equal to -3/2 only if the shape is truly invariant that is isometric growth. Weller, (1987b), reexamined the thinning rule and proposed an extension of the allometric model based on different biological parameters. He proposed an extension of the simple models to predict the relationships of the thinning exponent to allometric exponents derived from commonly measured stand dimensions, such as tree height, average aboveground mass and stem diameter at 10% of tree height ($D_{0.1\mathrm{H}}$).

A more recent view finds a different scaling law. It said that the power law should reflect the way both plants and animals distribute resources within their bodies. Both group use a branching network of tubes to supply resources throughout their bodies (Enquist et al. 1998). There are few suggested rules for these branching system: 1) the system must reach throughout organism , 2) the terminal branches have the same diameter, in independent of the body size of the organism, and 3) the summed diameter of each successive layer of branching should at least approximately equal the diameter of the percent branch (Enquiest et al. 1998). These authors who developed this idea assumed that the slope for an enormous range of plants will be closer to **-4/3**.

Plant ecologists are also interested in interpreting the constant K and its observed range of variation. K has been presented as a species constant invariant to changes in all environmental conditions except the level of illumination (Hickman 1979, Hozumi 1980, White 1981, Hutchings 1983). Many authors regard K as a parameter related to plant architecture (Harper 1977, Gorham 1979, Hutchings and Budd 198la, Lonsdale and

Watkinson 1983a), but some have proposed that K is insensitive to plant morphology (Westoby 1976, Furnas 1981). White (1981) suggested that K is a rough approximation of the density of biomass in the volume of space occupied by plants and can be considered as a weight to volume conversion, but Lonsdale and Watkinson (1983a) provided evidence against this hypothesis. Lonsdale and Watkinson (1983a) concluded that plant geometry, particularly leaf shape and disposition, do influence thinning intercepts. Westoby and Howell (1981), Lonsdale and Watkinson (1983a) have hypothesized that shade tolerant plants should have higher thinning intercepts than intolerant plants. Understanding of K is in a similar status as understanding of the -3/2 power.

Many theoretical and experimental studies realized that the -3/2 power law (e.g. Yoda et al. 1963; Hozumi 1977; Hutchings and Budd 1981; Hutchings 1983; Westoby 1984; Hagihara 2000, 2014) or the 4/3 power law of self-thinning (e.g. Enquist et al 1998; West et al. 1999a, 1999b; Gillooly et al. 2001;Niklas et al. 2003; Dai et al. 2009; Riveros, 2011) has been shown to be valid for the application of the self-thinning rule to forest communities. Many published scientific papers have applied the self-thinning theory for elucidating the physiology and the aspects of life history of plants and animals (e.g. West et al. 1997; Gillooly et al. 2001; West at al. 2002). Meanwhile few studies of the self-thinning process have been done on mangrove forests (Analuddin et al. 2009; Deshar et al. 2012). In fact, there is some needs to verify the theoretical importance, and applicability of the self-thinning rule, on mangrove forests especially on plant organs. Therefore, the objectives of this study was to examine how the process growth and mortality operate on total aboveground mass and partial organs on mangrove forests. Using Weller's allometric model to examine the effect of different parameters on the self-thinning exponent α and the constant K of the power rule equation and to examine if mangrove specie obey the same power rule.

The term "Mangrove" refers to an assemblage of tropical trees and shrubs that grows in the intertidal zone. Mangroves include approximately 20 families and 40 to 50 species. According to Tomilson (1986) the following criteria are required for a species to be designated a "true or strict mangrove":

-Complete fidelity to the mangrove environment.

-Plays a major role in the structure of the community and has the ability to form pure stands.

-Morphological specialization for adaptation to their habitat.

-Taxonomic isolation from terrestrial relatives.

Mangroves are among the world's most productive ecosystem and sustain a variety of marine and estuarine communities (Lugo and Snedaker, 1975; Boto and Bunt, 1982). However, mangroves are also one of the world's most threatened tropical and subtropical ecosystems and are being degraded in most countries mainly because of anthropogenic activities and unsustainable exploitation (Khan et al. 2007). Mangroves are the only tall tree forests situated between the land and the sea (Kathiresan and Bingham, 2001; Alongi, 2002) and they are tightly bound to the coastal environments in which they occur. Once they established, they offer recreational potential, a sustainable supply of seafood for aquatic animals and useful products for community subsistence (Alongi, 1996). As a primary produce, mangroves also serve as food for herbivores and detritivores and are important nursery and breeding sites for various animals, a renewable resource of wood, and sites for accumulations of sediment and nutrients (e.g. Twilley 1995; Kathiresan and Bingham 2001; Manson et al. 2005b).

Kandelia obovata (S., L.) Yong in regions of China and Japan has been classified as a new species that was previously recognized as *Kandelia candel* (L) Druce (Sheue et al. 2003b). According to these authors, *K. obovata* is distributed from the gulf of Tonkin northeastward to Kwantung, Fukien, Taiwan, and the Ryukyus. In Japan Amami Island (Northern part of the Ryukyu Archipelago) is the northernmost limit of its biogeographical distribution (Spalding et al. 2010). It thrives under a broad range of intertidal conditions, including salinity level from near freshwater to full strength seawater, and tolerates a range of flooding and other soil types (Allen and Duke, 2006).

In Manko Wetland Okinawa Island, *K. obovata* is the most dominant species and plays an important role as carbon source and sink for the adjacent costal area, but also by stabilizing sediments and protecting shorelines against erosion. Therefore a comprehensive understanding of the structural and functional maintenances of this mangrove forests through self-thinning process is crucial.

1.2 Study site

This study was conducted in overcrowded stands of *K. obovata* Sheue, in Manko Wetland (Fig.1), located in the southern part of Okinawa Island, Japan (26°11′N, 127°40′E). It is an estuary tidal flat formed at the confluence of the Kokuba River that flows through Naha City and the Noha River that flows through Tomigusuku City. Although located 3km inland from the coast, it is greatly affected by the tidal flow and a large tidal flat emerges at low tide. Based on data from 2000 to 2009 obtained from the Okinawa Meteorological Agency, the warmth index (Kira, 1991) was 219.8 ± 15.4 (SE) °C month, indicating that this area belongs to the subtropical region. During the study period of 2005 to 2011, the temperature fluctuated approximately 15°C from the coldest month to the hottest, and mean annual air temperature was 23.2 ± 1.2°C. Rainfall varied throughout the year but exceeded 100 mm month^{-1} in most months and the mean annual precipitation was 2284.4 ± 25.6 mm yr^{-1}. The study area is a brackish tidal flat covering an extensive area of 58 ha at low tide; the tidal range is 3 to 212 mm. Soil pore water salinity in the study area was 2.12 ± 0.04 (SE) % at low tide in September 2006 (Suwa and Hagihara 2008). Regular tidal inundation occurs at the study site. The mangroves grow in a mud flat area mainly composed of clay particles (RIS, 1999). The study site is rich in fish and benthos including crab and nereidae. The site is also an important area for migratory birds and has been registered on the Ramsar List of Wetlands of International Importance (a Ramsar site) since 1999. The wetland receives regular tidal inundation and some freshwater supply through run-off from adjacent areas. Along with *K. obovata*, a few patches of *Rhizophora stylosa* Griff., *Bruguiera gymnorrhiza* (L.) Lamk., and *Excoecaria agallocha* L. are also present.

1.3 Structure of Thesis

The thesis is divided into different chapters, each of which focuses on aspects of the investigation concerning the effects of the self-thinning process on aboveground mass dynamics and stand structure of overcrowded *K. obavata* forest.

Chapter-II (Self-thinning process and consideration of two models (Yoda et al.'s and Weller's model)

This chapter shows statistical and mathematical differences and similarity between different models to describe the self-thinning process such as Yoda et al.'model and Weller's allometric model. The objective was to find whether the self-thinning exponent and the multiplying factor sttastistically obtained from Weller's allometric model are mathematically or statistically same or different from those of the Self-thinning exponent and the multiplying factor statistically obtained from Yoda's equation.

Chapter-III (Self-thinning exponents of stems, branches, and leaves in overcrowded *Kandelia obovata* stands)

This chapter focused on the self-thinning exponents for tree organs (stem, branch, leaf) and aboveground. The objectives of this study were (1) to estimate mean masses for partial organs per plot, (2) to determine self-thinning exponents for partial organs using Weller's allometric model, (3) to compare differences in self-thinning exponents between woody organs (stem and branch) and the photosynthetic organs (leaf), and (4) to explain differences in the self-thinning exponents of partial organs in relation to their different growth patterns.

Chapter-IV (The self-thinning exponent of total aboveground mass)

This chapter provides more information about the self-thinning exponent of total aboveground mass. That means contrary to the to Chapter 3, the self-thinning exponent of total mass of trees will be determined at the same time. The method will be the same as previous chapter.

Chapter-V (Dynamics of aboveground mass hierarchy in overcrowded mangrove *kandelia obovata* stands)

This chapter provides information on dynamics of the aboveground mass of overcrowded stands undergoing self-thinning process. The objectives were (1) to examine the dynamics of the aboveground mass hierarchy over 8 years, (2) to observe and understand the changes in the stand structure.

Chapter-VI (General discussion and conclusion)

This chapter provides overall synthesis of the every chapter in which the self-thinning exponents of partial organs, the self-thinning exponent of aboveground mass and the dynamics of aboveground mass hierarchy in overcrowded mangrove *K obovata* stands are summarized. General conclusions from every chapter are also highlighted.

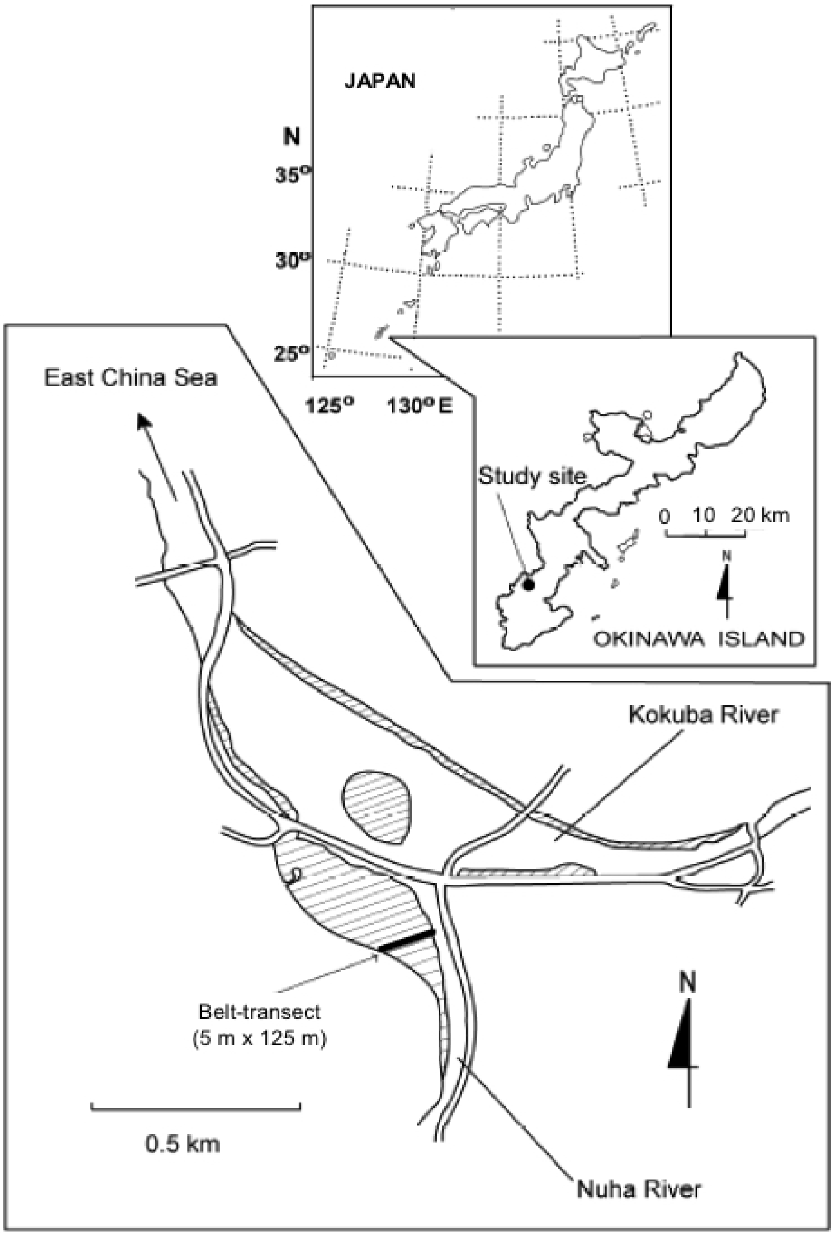

Figure 1.1: Location of the study site. The hatched area indicates the mangrove area. The black line indicates the plot area

Figure 1.2: A view of *K. obovata* stands at Manko Wetland, Okinawa Island, Japan. Light green indicates overcrowded mangrove *K. obovata* stands. Dark green indicates Tomigusuku Hill, whose altitude is 54,4m.

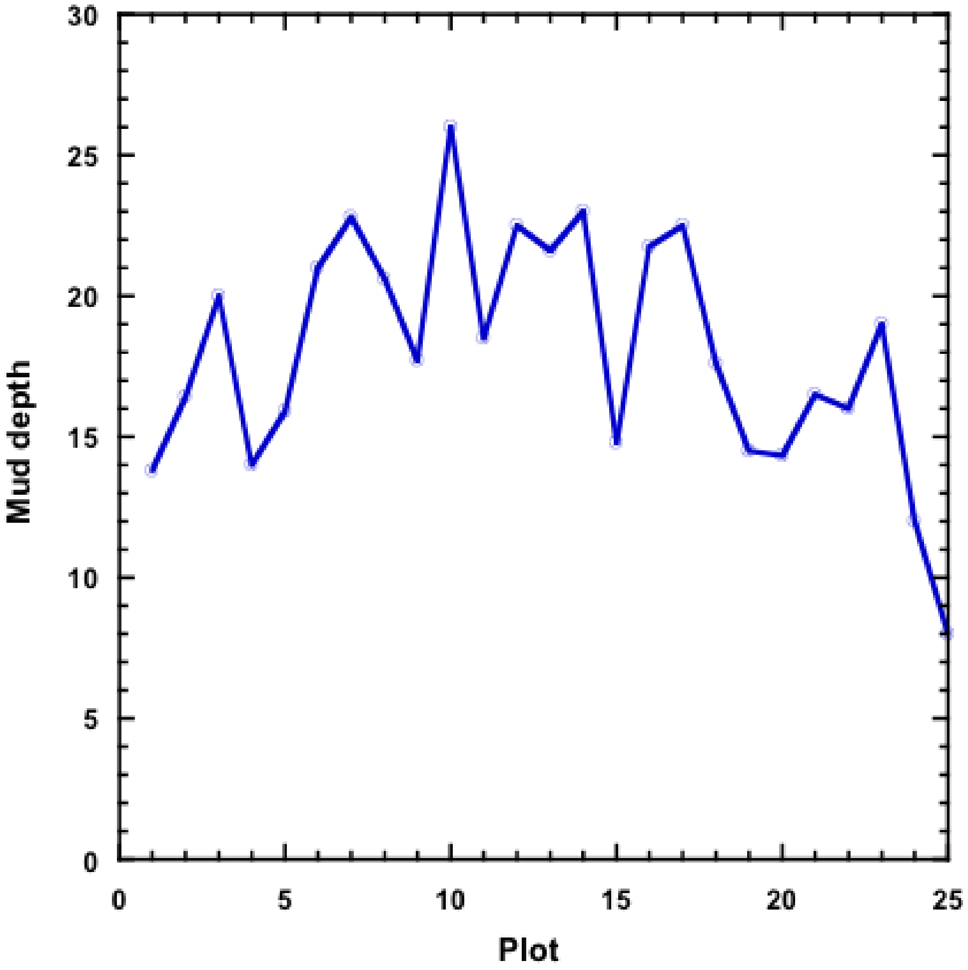

Figure 1.3: Mud deposition along the Transect (25 subplots) at Manko Wetland, Okinawa Island, Japan.

Chapter 2

Self-thinning process and consideration of two models: Simple geometric model (Yoda et al. 1963) and Weller's allometric model

2.1 Introduction

It is generally accepted that the mortality in a self-thinning stands occurs through competition for light; that it is the small, suppressed plants that die; and that death of a plant ensures when, even though maximally etiolated, it no longer holds its leaves high enough in the canopy to maintain a positive carbon balance, although this has not been formally demonstrated and there are contrary suggestions (Westoby, 1984). There is good physiological evidence on shade-induced mortality. The evidence that it is the smallest plants that die was originally indirect growth-rate and size are positively correlated and small plants have zero or negative growth rate (Koyama and Kira, 1956; White and Harper, 1970; Mohler, 1978; Westoby, 1984) but there is now also direct evidence of this (Thomas and Weiner, 1989b; Kikuzawa, 1993). The most direct evidence that competition for light, rather than nutrients, causes mortality in thinning stands, is that increasing light intensity shifts the limiting line upwards, reducing mortality (Yoda et al., 1963), whereas increasing nutrients increases the rate of progression up the line without changing the position of the line (Yoda et al., 1963; White and Harper, 1970). The implication is that increasing nutrient supply increases mortality rate by increasing growth rate, thus increasing competition for the factor (light) that causes mortality (Hamilton et al., 1995). Indirect evidence for the role of competition for light is that the fit 3/2 is better when based on shoot biomass than total biomass, and still better when based on canopy volume rather than shoot biomass (Lonsdale, 1990). The self-thinning rule has been hotly and empirically debated for more than 40 years. The history of the self-thinning rule has been detailed in English by White (1981) and in Japanese by Hozumi (1973). The rule was developed and proposed by Japanese foresters and plant biologists in a period of very fruitful work on density effects in plant populations beginning in the 1950s and continuing to the present. The rule have been described in a variety of ways among which, the self-thinning equation or the 3/2 power law of self-thinning (Yoda et al., 1963), has attracted much attention. It has been proposed that this single quantitative rule would describe completely the dynamics of any overcrowded plant stand (e.g. White, 1981).

Yoda et al. (1963) derived the self-thinning rule from geometric principles (see general Introduction).This derivation of the self-thinning rule rest on three assumptions (White, 1981): (**1**) Plant mass is a direct power function of the cube of some particular linear dimension. (**2**) plant retain their geometric similarity during growth, and (**3**) self-thinning occurs only when the total coverage of a stand is larger than or equal to 100 of the total ground area. This formulation became well known and in the past 20 years has evoked a large and still expanding literature, much of which has been reviewed (Westoby, 1984). It has become one of the best-founded generalizations of plant population dynamics. As a quantitative law, the thinning rule would have potential applications as a research and management tool for plant populations (Yoda et al., 1963; Westoby, 1981, 1984). Meanwhile, the assumption of invariant plant shape is not generally valid, so the explanation of Yoda et al. (1963) is unsatisfactory as a general explanation of the self-thinning rule (Westoby, 1976; White, 1981). Some other explanations of the self-thinning rule have been attempted. Westoby (1976), Mohler et al. (1978) and Miyanishi et al. (1979) recognizes that plants can change shape with increasing size (allometric growth) and the thinning exponents will deviate from 3/2. According to these authors, assume that Yoda et al.'s model is unacceptable as a general explanation of the thinning rule because many species do not grow isometrically. Weller (1987b) also proposed an extension of the allometric model predicting that the self-thinning exponent varies with plant shape and biomass density (mass per unit occupied space).

2.2 Simple geometric Model (Yoda et al. 1963)

Yoda et al. (1963) first proposed the following self-thinning equation:

$$\overline{w} = K \cdot \rho^{-\alpha} \tag{2.1}$$

where $\overline{w}$ is mean aboveground mass, α is the self-thinning exponent and K is the multiplying factor. The ordinary least squares (OLS) regression line of Eq. (2.1) is given in the form:

$$\mathrm{ln}\overline{w} = \mathrm{ln}K - \alpha \cdot \mathrm{ln}\rho \tag{2.2}$$

where $\mathrm{ln}\overline{w}$ is the response variable and $\mathrm{ln}\rho$ is the explanatory variable. As a result, the regression coefficient of $-\alpha$ and the constant term $\mathrm{ln}K$ can be respectively calculated from the following equations:

$$-\alpha = \frac{S_{\mathrm{ln}\rho\mathrm{ln}\overline{w}}}{S_{\mathrm{ln}\rho\mathrm{ln}\rho}} \quad SE_{\alpha} = \sqrt{\frac{S_{\mathrm{ln}\rho\mathrm{ln}\rho} \cdot S_{\mathrm{ln}\overline{w}\mathrm{ln}\overline{w}} - S^2_{\mathrm{ln}\rho\mathrm{ln}\overline{w}}}{(n-2) \cdot S_{\mathrm{ln}\rho\mathrm{ln}\rho}}} \tag{2.3}$$

and

$$\mathrm{ln}K = \overline{\mathrm{ln}\overline{w}} + \alpha{\cdot}\overline{\mathrm{ln}\rho} \quad \left(\text{or} \quad K = \exp\left(\overline{\mathrm{ln}\overline{w}} + \alpha{\cdot}\overline{\mathrm{ln}\rho}\right)\right) \tag{2.4}$$

where $S_{\mathrm{ln}\rho\mathrm{ln}\overline{w}}$ and $S_{\mathrm{ln}\rho\mathrm{ln}\rho}$ are the sum of cross products concerning $\mathrm{ln}\rho$ and $\mathrm{ln}\overline{w}$, and the sum of squares concerning $\mathrm{ln}\rho$, respectively n is the number of data, $\overline{\mathrm{ln}\overline{w}}$ and $\overline{\mathrm{ln}\rho}$ are the mean respectively after taking logarithms of mean mass $\overline{w}$ and of population density ρ, and SE_{α} is the standard error of the estimate α.

2.3 Weller's allometric model

Weller (1987b) re-examined the evidence of the self-thinning rule and proposed an allometric model for the self-thinning in overcrowded plant populations based on the following three assumptions. Assumption 1: the mean occupied area per tree $\overline{s}$ is related to mean mass $\overline{w}$ through the following allometric relationship:

$$\overline{s}\left(=\frac{1}{\rho}\right) = \mathrm{g}_{\phi} \cdot \overline{w}^{\phi} \tag{2.5}$$

where ρ, g_ϕ, and ϕ are the population density, a constant, and the allometric coefficient between $\overline{s}$ and $\overline{w}$, respectively. Equation (2.5) can be written in the form:

$$\overline{w}\left(=\frac{1}{\mathrm{g}_\phi}\right)^{1/\phi}\cdot\ \rho^{\frac{1}{\phi}} \tag{2.6}$$

This equation is mathematically the same as Eq. (2.1) thus, the following equalities hold mathematically,

$$\frac{1}{\phi}=\alpha \tag{2.7}$$

and

$$\left(\frac{1}{\mathrm{g}_\phi}\right)^{1/\phi}=K \tag{2.8}$$

Therefore, the self-thinning exponent $1/\phi$, i.e. the reciprocal of the allometric coefficient ϕ in Eq. (2.5), and the multiplying factor $(1/\mathrm{g}_\phi)^{1/\phi}$ in the allometric model of Eq. (2.6) are mathematically equivalent to the self-thinning exponent α and the multiplying factor K of Eq. (2.1), respectively.

On the other hand, the OLS regression line of Eq. (2.5) is given in the form:

$$\ln\rho=\ln\frac{1}{\mathrm{g}_\phi}-\phi\cdot\ln\overline{w} \tag{2.9}$$

where $\ln\rho$ is the response variable and $\ln\overline{w}$ is the explanatory variable. The resulting regression coefficient $-\phi$ and constant term $\ln\left(1/\mathrm{g}_\phi\right)$ are calculated from the equations, respectively.

$$-\phi=\frac{S_{\ln\overline{w}\ln\rho}}{S_{\ln\overline{w}\ln\overline{w}}}\quad SE_\phi=\sqrt{\frac{S_{\ln\overline{w}\ln\overline{w}}\cdot S_{\ln\rho\ln\rho}-S^2_{\ln\overline{w}\ln\rho}}{(n-2)\cdot S^2_{\ln\overline{w}\ln\overline{w}}}} \tag{2.10}$$

and

$$\ln\frac{1}{\phi}=\overline{\ln\rho}+\phi\cdot\overline{\ln\overline{w}}\quad\left(\text{or}\ \ \mathrm{g}_\phi=\exp\left(-\overline{\ln\rho}-\phi\cdot\overline{\ln\overline{w}}\right)\right) \tag{2.11}$$

where $S_{\ln\overline{w}\ln\overline{w}}$ is the sum of squares concerning $\ln\overline{w}$, and SE_ϕ is the standard error of the estimate ϕ.

Therefore, we can conclude that the values of the self-thinning exponent $1/\phi$ and the multiplying factor $\left(1/\mathrm{g}_\phi\right)^{1/\phi}$ statistically obtained respectively from Eqs. (2.10) and (2.11) in case of the allometric model of Eq. (2.6) are respectively different from those of the self-thinning exponent α and the multiplying factor K statistically obtained from

Eqs. (2.3) and (2.4) in the self-thinning equation of Eq. (2.1), though $1/\phi$ and $\left(1/\mathrm{g}_\phi\right)^{1/\phi}$ in the allometric model are mathematically the same as α (Eq. (2.7)) and K (Eq. (2.8)) in the self-thinning equation, respectively.

From the point of view of an allometric scaling, it is more reasonable to regard $\overline{s}$, i.e. ρ, as a function of $\overline{w}$ like Eq.(2.5), but not to regard $\overline{w}$ as a function ρ of like Eq.(2.1) (Schmidt-Nielsen 1984).

Assumption 2: the relationship between mean tree height $\overline{H}$ and mean mass can be expressed by the allometric relationship:

$$\overline{w} = \mathrm{g}_\theta \cdot \overline{w}^{\theta} \tag{2.12}$$

where, g_θ and θ are constant and the allometric coefficient between $\overline{H}$ and $\overline{w}$, respectively. Using the OLS regression analysis, the allometric coefficient θ and the constant g_θ in Eq.(2.12) are calculated as follows.

$$\theta = \frac{S_{\ln\overline{w}\ln\overline{H}}}{S_{\ln\overline{w}\ln\overline{w}}} \quad SE_\theta = \sqrt{\frac{S_{\ln\overline{w}\ln\overline{w}} \cdot S_{\ln\overline{H}\ln\overline{H}} - S^2_{\ln\overline{w}\ln\overline{H}}}{(n-2) \cdot S^2_{\ln\overline{w}\ln\overline{w}}}} \tag{2.13}$$

and

$$\ln\mathrm{g}_\theta = \overline{\ln\overline{H}} - \frac{S_{\ln\overline{w}\ln\overline{H}}}{S_{\ln\overline{w}\ln\overline{w}}} \cdot \overline{\ln\overline{w}} \quad \left(\text{or} \quad \mathrm{g}_\theta = \exp\left(\overline{\ln\overline{H}} - \theta\cdot\overline{\ln\overline{w}}\right)\right) \tag{2.14}$$

where $S_{\ln\overline{w}\ln\overline{H}}$ is the sum of cross products concerning and $\ln\overline{H}$, and $\overline{\ln\overline{H}}$ is the mean after taking logarithms of $\overline{H}$, and SE_θ is the standard error of estimate.

Assumption 3: the relationship between mean mass density $\overline{d}$ and mean mass $\overline{w}$ can also be expressed as:

$$\overline{d}\left(=\frac{\overline{w}}{\overline{s}\cdot\overline{H}}\right) = \mathrm{g}_\delta \cdot \overline{w}^{\delta} \tag{2.15}$$

where, g_δ and δ are a constant and the allometric coefficient between $\overline{d}$ and $\overline{w}$, respectively. The OLS regression analysis for Eq.(2.15) gives the allometric coefficient δ and the constant g_δ as follows:

$$\delta = \frac{S_{\ln\overline{w}\ln\overline{d}}}{S_{\ln\overline{w}\ln\overline{w}}} = \frac{S_{\ln\overline{w}\ln\left(\overline{w}\cdot\rho/\overline{H}\right)}}{S_{\ln\overline{w}\ln\overline{w}}} = \frac{S_{\ln\overline{w}\ln\overline{w}} + S_{\ln\overline{w}\ln\rho} - S_{\ln\overline{w}\ln\overline{H}}}{S_{\ln\overline{w}\ln\overline{w}}} \tag{2.16}$$

$$\left(SE_\delta = \sqrt{\frac{S_{\ln\overline{w}\ln\overline{w}}\left(S_{\ln\rho\ln\rho} - 2S_{\ln\rho\ln\overline{H}} + S_{\ln\overline{H}\ln\overline{H}}\right) - \left(S_{\ln\rho\ln\overline{w}} - S_{\ln\overline{w}\ln\overline{H}}\right)^2}{(n-2)\cdot S^2_{\ln\overline{w}\ln\overline{w}}}}\right)$$

and

$$\ln \mathrm{g}_\delta = \overline{\ln\overline{d}} - \tfrac{S_{\ln\overline{w}\ln\overline{d}}}{S_{\ln\overline{w}\ln\overline{w}}} \cdot \overline{\ln\overline{w}} = \overline{\ln\overline{w}} + \overline{\ln\rho} - \overline{\ln\overline{H}} - \tfrac{S_{\ln\overline{w}\ln\overline{w}} + S_{\ln\overline{w}\ln\rho} - S_{\ln\overline{w}\ln\overline{H}}}{S_{\ln\overline{w}\ln\overline{w}}} \cdot \overline{\ln\overline{w}}$$

$$\left(\text{or} \quad \mathrm{g}_\delta = \exp\left(\overline{\ln\overline{d}} - \delta \cdot \overline{\ln\overline{w}}\right)\right) \tag{2.17}$$

where $S_{\ln\overline{w}\ln\overline{d}}$ is the sum of cross products concerning $\ln\overline{w}$ and $\ln\overline{d}$, and $\overline{\ln\overline{d}}$ is the mean after taking logarithms of mean mass density $\overline{d}$, and SE_δ is the standard error of estimate of the estimate δ.

Substituting Eq. (2.5) for $\overline{s}$ and Eq. (2.12) for $\overline{H}$ in Eq. (2.15), the mean mass density $\overline{d}$ can be written as follows:

$$\overline{d} = \frac{\overline{w}}{\mathrm{g}_\phi \cdot \overline{w}^\phi \cdot \mathrm{g}_\delta \cdot \overline{w}^\theta} = \frac{1}{\mathrm{g}_\phi \cdot \mathrm{g}_\theta} \cdot \overline{w}^{1-(\phi+\theta)} \tag{2.18}$$

Comparing Eq. (2.18) with the right-hand side of the allometric model defined by Eq. (2.15), the following equations hold mathematically.

$$1 - (\phi + \theta) = \delta \tag{2.19}$$

and

$$\frac{1}{\mathrm{g}_\phi \cdot \mathrm{g}_\theta} = \mathrm{g}_\delta \tag{2.20}$$

These equations can be written in the forms, respectively.

$$\phi = 1 - (\theta + \delta) \tag{2.21}$$

and

$$\mathrm{g}_\phi = \frac{1}{\mathrm{g}_\theta \cdot \mathrm{g}_\delta} \tag{2.22}$$

Therefore, the self-thinning exponent $1/\phi$ and the multiplying factor $\left(1/\mathrm{g}_\phi\right)^{1/\phi}$ in the allometric model of Eq. (2.6) are mathematically written in the forms, respectively,

$$\frac{1}{\phi} = \frac{1}{1 - (\theta + \delta)} \tag{2.23}$$

and

$$\left(\frac{1}{\mathrm{g}_\phi}\right)^{1/\phi} = (\mathrm{g}_\theta \cdot \mathrm{g}_\delta)^{\frac{1}{1-(\theta+\phi)}} \tag{2.24}$$

Weller (1987) assumed that the self-thinning exponent $1/\phi$ in the allometric model of Eq. (2.6) is reasonably estimated from the allometric coefficient θ in Eq. (2.12) and δ in Eq. (2.15).

Considering the following derivations, first concerning the quantity $1/\left(1-(\theta+\delta)\right)$ in Eq. (2.24); if we substitute Eqs. (2.13) and (2.16) respectively for θ and δ in the quantity and consider Eq. (2.10), the following equality is provided.

$$\frac{1}{1-(\theta+\delta)}=\frac{1}{1-\left(\frac{S_{\ln\overline{w}\ln\overline{H}}}{S_{\ln\overline{w}\ln\overline{w}}}+\frac{S_{\ln\overline{w}\ln\overline{w}}+S_{\ln\overline{w}\ln\rho}-S_{\ln\overline{w}\ln\overline{H}}}{S_{\ln\overline{w}\ln\overline{w}}}\right)}=\frac{S_{\ln\overline{w}\ln\overline{w}}}{S_{\ln\overline{w}\ln\rho}}=\frac{1}{\phi} \tag{2.25}$$

Thus, it is provided that Eq. (2.23) holds not only mathematically, but also statistically. Concerning the quantity $1/\left(\mathrm{g}_\theta\cdot\mathrm{g}_\delta\right)^{1/(1-(\theta+\delta))}$ in Eq. (2.25); taking logarithms of the quantity and considering Eqs. (2.14) and (2.17) leads to the form:

$$\frac{1}{1-(\theta+\delta)}\left(\ln\mathrm{g}_\theta+\ln\mathrm{g}_\delta\right)=\frac{1}{\phi}\left(\overline{\ln\rho}-\frac{S_{\ln\overline{w}\ln\rho}}{S_{\ln\overline{w}\ln\overline{w}}}\cdot\overline{\ln w}\right)=\frac{1}{\phi}\ln\frac{1}{\mathrm{g}_\phi} \tag{2.26}$$

Thus, Eq. (2.26) is reduced to the form:

$$\left(\mathrm{g}_\theta\cdot\mathrm{g}_\delta\right)^{\frac{1}{1-(\theta+\delta)}}=\left(\frac{1}{\mathrm{g}_\phi}\right)^{1/\phi} \tag{2.27}$$

Therefore, Eq. (2.24) also holds not only mathematically, but also statistically. Here we call Eqs. (2.23) and (2.24) Weller's equalities.

As a result, we can conclude that the statistically estimated values of the self-thinning exponent $1/\left(1-(\theta+\delta)\right)$ and the multiplying factor $\left(1/(\mathrm{g}_\theta\cdot\mathrm{g}_\delta)\right)^{1/(1-(\theta+\delta))}$ respectively based on Weller's equalities, i.e. Eqs. (2.23) and (2.24), are just the same as the statistically estimated values of the self-thinning exponent $1/\phi$ and the multiplying factor $\left(1/\mathrm{g}_\phi\right)^{1/\phi}$ based on the allometric model of Eq. (2.6). However, we should keep in mind that the estimator δ is dependent on the estimators ϕ and θ which are independent of each other. Therefore, the significant test for the self-thinning exponent $1/\phi$ (Eq. (2.24)) based on θ and δ-values violates a statistical constraint, but $1/\phi$ based on Eq. (2.10) is available.

2.4 Relationship between the self-thinning equation and the allometric model

Coefficient of determination R^2 for Eq. (2.9) is defined as

$$R^2=\frac{S_{\ln\rho\ln\overline{w}}}{S_{\ln\rho\ln\rho}\cdot S_{\ln\overline{w}}\ln\overline{w}} \tag{2.28}$$

This definition is also coefficient of determination for Eq. (2.9) and then can be decomposed as follows.

$$R^2 = \frac{S_{\ln\overline{w}\ln\rho}}{S_{\ln\rho\ln\rho}} \cdot \frac{S_{\ln\overline{w}\ln\rho}}{S_{\ln\overline{w}\ln\overline{w}}} \tag{2.29}$$

Therefore, considering Eqs. (2-3) and (2.10), Eq. (2.29) is written in the form:

$$R^2 = \alpha \cdot \phi \tag{2.30}$$

Thus, multiplying the self-thinning exponent α in the self-thinning equation of Eq. (2.1) by the self-thinning exponent $1/\phi$ in the allometric model of Eq. (2.6) statistically leads to the coefficient of determination R^2 of Eq. (2.28). However, we should keep it in mind that the following equation holds on mathematically in Eq. (2.29)and never holds statistically,

$$\alpha \cdot \phi = 1 \tag{2.31}$$

Except for $R^2 = 1$, i.e. all data lie on the respective regression lines of Eq. (2.2) and Eq. (2.9).

2.5 Summary

We can conclude that the values of the self-thinning exponent $1/\phi$ and the multiplying factor $\left(1/\mathrm{g}_\phi\right)^{1/\phi}$ obtained from the allometric model are statistically different from those of the self-thinning exponent α and the multiplying factor K statistically obtained in the self-thinning exponent, though $1/\phi$ and $\left(1/\mathrm{g}_\phi\right)^{1/\phi}$ in the allometric model are mathematically the same as α and K in the self-thinning equation. We can also say that the statistically estimated values of the self-thinning exponent $1/\left(1-(\theta+\delta)\right)$ and the multiplying factor $\left(1/(\mathrm{g}_\theta \cdot \mathrm{g}_\theta)\right)^{1/(1-(\theta+\delta))}$ based on Weller's equalities are just the same as the statistically estimated values of the self-thinning exponent $1/\phi$ and the multiplying factor $\left(1/\mathrm{g}_\phi\right)^{1/\phi}$ based on the allometric model. However, we should keep in mind that the estimator δ is dependent on the estimators ϕ and θ, which are independent of each other. Therefore, the significant test for the self-thinning exponent $1/\phi$ based θ and δ-values violates a statistical constraint, but $1/\phi$ is available.

Chapter 3

Self-thinning of stems, branches, and leaves in overcrowded *Kandelia obovata* stdands

3.1 Introduction

Competition is a fundamental process affecting plant communities (Berger et al., 2008). This interference within stands creates or enhances size variation leading to density-dependent mortality or self-thinning (e.g., White and Harper, 1970; Begon et al., 2006). Self-thinning is a natural process reflected in decreases in density as average mass of trees increases over time (e.g., Morris, 2002). The relationship between population density ρ and mean individual mass $\overline{w}$ in monospecific even-aged overcrowded stands has been described as the "self-thinning rule" or the "3/2 power law of self-thinning", first formulated by Yoda et al. (1963). The relationship can be expressed as:

$$\overline{w} = K \cdot \rho^{-\alpha} \tag{3.1}$$

where K is a multiplying factor that varies across species, and α is the self-thinning exponent, which is close to 3/2 regardless of species, age, or site conditions. Weller assumed that, the history of an even-aged population can, then, be divided into up to four stages:

(1) a period of initial establishment, rapid growth, and low mortality;

(2) a period of adherence to the self-thinning rule;

(3) a period when constant biomass is maintained at the carrying capacity and;

(4) a period of population degeneration, when growth does not replace the biomass lost through mortality.

The ability of the -3/2 thinning rule was considered remarkable because it surfaced from comparisons made among successive growth stages in monotypic populations, different growth stages of plants in monotypic populations, and populations with heterogeneous species composition (populations composed with different species) (Niklas, 1994).

The earliest geometric model (Yoda et al., 1963) assumes that plants do not change their properties as they grow larger and compete; so that the self-thinning exponent will always be or close to 3/2. Many studies have confirmed the generality of the 3/2 power law of self-thinning for a range of plants, including grasses, commercial cultivars, weeds, grains, legumes, and trees (e.g., White and Harper, 1970; Harper, 1977; Westoby, 1984; Ogawa and Hagihara, 2003). However, the universality of the self-thinning exponent in Eq. (3.1) is continuously debated. Many studies have shown that the exponent is much more variable than stated by the 3/2 law (Zeide, 1985; Westoby and Howell, 1986; Weller, 1987a, 1987b; Enquist et al., 1998, 2000; Dai et al., 2009). The observed variability has led to doubts about the generality of the 3/2 power law of self-thinning (Weller, 1987a, 1987b; Zeide, 1987; Lonsdale, 1990). Enquist et al. (1998, 2000) assume that the origin of the self-thinning exponent is due to specific selection pressures that optimize resource uptake and distribution (Riveros and Enquist, 2011). These authors predicted that the self-thinning exponent was 4/3 based on the metabolic scaling theory (West et al., 1997; Brown and Sibly, 2012).

Several hypotheses have been proposed to interpret the self-thinning law (Mohler et al., 1978; White, 1981; Lonsdale and Watkinson, 1983; Pickard, 1983; Long and Smith, 1984; Westoby, 1984; Weller, 1987b; Norberg, 1988; Lonsdale, 1990; Osawa and Allen, 1993; Osawa, 1995; Pittman and Turnblom, 2003). Among them, the allometric model proposed by Weller (1987b) who assumed that no scaling exponent describes the relationship of plant mass and population density for every species. Rather, the self-thinning exponent depends on the ability of a particular species to tolerate shading, water deprivation, and other stress including factors (Niklas, 1994). In other words, the thinning exponent varies with plant shape and mass density (mass per unit occupied space), which can be derived from stand parameters, such as stem diameter and tree height. Practical applications of Weller's model in the analysis of stand density and plant mass have been demonstrated for some species (Weller, 1987b; Xue et al., 1999).

Most interest in self-thinning studies has focused on terrestrial plant populations (e.g., Harper, 1977; Silvertown and Charlesworth, 2001; Coomes and Allen, 2007; McCarthy and Weetman, 2007; Zhang et al., 2007), although some simulation models of self-thinning in mangroves have been carried out (Berger and Hildenbrandt, 2000, 2003, Berger et al., 2002, 2004, 2008). However, little is known about the self-thinning relationship in Eq. (3.1) of the different organs (Xue and Hagihara, 2008; Deshar et al., 2012) and no study about the self-thinning exponent of partial organs in *K obovata* stands. Plants are concurrently engaged in variable competitive interactions that take place under continuously changing densities. At very low densities, plants are expected to mainly avoid competition among their own organs and demonstrate little interactions with their neighbors (Novoplansky, 2009). In fact, At low density, individuals do not interfere with each other, so that population growth is density-independent. However, as density increases resources may become less available, each individual acquires less of the resource. Therefore, plants are expected to shift from avoidance to confrontation whereby plants allocate greater proportions of their resources to competitive functions and structure (O'Brien et al. 2005). Being genetically identical, organs that belong to the same plant are expected to overlapping between their depletion zones, which in turn results in greater probability for non-self encounters and confrontation (Falik et al. 2003; Holzapfel and Alpert 2003; semchenko et al. 2007b). Meanwhile competition between organs of the same may occur. In fact when plant undergoes growth spurts following dormancy or major damage. At the initial stage many similarly saturated buds, young branches or roots grow side by side and gradually develop size asymmetry, whereby a few become dominant, while others cease growing or even die (Marcelis et al. 2004). Depending on the plant's developmental history and external competitive challenges, such self-thinning might result in the coexistence of a few co-dominant organs e.g. multi-trunk trees; (Sach and Novoplansky, 1995), or the dominance of a single organ, e.g. a single shoot in a shaded understory climber (Novoplansky, 2009).

A second type of competition occurs between organ that develop under different growth conditions which often results in the domination of the more successful organs at the expense of their less fortunate counterparts (Sach and Novoplansky, 1997). Similarly to the population level interaction, intensified competition means that some of the plant's organs develop under at times self-imposed, poorer growth conditions (Novoplansky, 2009). This somatic self-thinning might result to radically different self-thinning exponents for tree organs. Therefore, it is necessary to explore the effects of thinning in individual tree organs on stand density.

Amami Island (Northern part of the Ryukyu Archipelago, Japan, 28°16′N, 129°21′E) is the northernmost distribution limit of *Kandelia obovata* Sheue, (Spalding et al., 2010). In Manko Wetland, Okinawa Island, *K. obovata* forest is overcrowded and grows under ambient condition since it is located in urban area. However, most of study on self-thinning has been done on terrestrial plant and little is known about competition of different tree organs on *K. obovata*. Since the whole plant growth and competitive ability depend not only on the photosynthetic organ (leaves), but also on the dynamics of non photosynthetic organs or woody organs (stem, branch). The interaction between organs may have an impact on the whole plant and may affect the entire stands. Such knowledge is of fundamental importance for understanding the ecology of this species and facilitating its management.

Therefore the objectives of this study were: (1) to estimate mean masses for each tree organs per plot, (2) to determine self-thinning exponents for tree organs using Weller's allometric model, (3) to compare differences in self-thinning exponents between woody organs (stem and branch) and the photosynthetic organ (leaf), and (4) to explain differences in the self-thinning exponents of partial organs in relation to their different growth patterns.

3.2 Materials and methods

3.2.1 Tree census

A 125-m-long, 5-m-wide belt-transect was established in *K. obovata* stands perpendicular to river flow. The transect was divided into 25 subplots (5 m x 5 m each), each of which consisted of a growing and crowded cohort (Analuddin et al., 2009). All individuals in the subplots were numbered. In each subplot, tree height H (m) and stem diameter $D_{0.1\mathrm{H}}$ (cm) at $H/10$ were measured every summer from 2005 to 2011. As of 2010, the mean and mean $D_{0.1\mathrm{H}}$ (± SE) of every subplot ranged from 3.80 ± 0.10 to 4.70 ± 0.02 m and from 4.30 ± 0.13 to 5.90 ± 0.30 cm, respectively.

3.2.2 Weller's allometric model

Plants are not usually isometric, even when organized in similar patterns. Instead, certain proportions change in a regular fashion. Such non-isometric scaling is referred to as allometry (Schmidt-Nielsen, 1984), where mass is always plotted on the abscissa. When an animal, plant, organ or tissue changes shape in response to size changes, we say that it scales allometrically (allo = different, metric = measure). Allometric scaling is common in nature, both when comparing two animals or plants of different sizes and when comparing the same animal or plant at two different sizes (i.e., growth)

Weller (1987b) proposed an allometric model for self-thinning in overcrowded plant populations based on the following three assumptions. Assumption 1: the mean occupied area per tree $\overline{s}$ is related to the mean mass $\overline{w}_\mathrm{x}$ of partial organ "x" through the following allometric relationship:

$$\overline{\mathrm{s}}\left(=\frac{1}{\rho}\right)=\mathrm{g}_{\phi_\mathrm{x}}\cdot\overline{w}_\mathrm{x}^{\phi_\mathrm{x}}\ , \tag{3.2}$$

where ρ , $\mathrm{g}_{\phi_\mathrm{x}}$, and ϕ_x are the population density, a constant, and the allometric coefficient between $\overline{s}$ and $\overline{w}$, respectively. Assumption 2: the relationship between mean tree height $\overline{H}$ and mean partial organ mass $\overline{w}_\mathrm{x}$ can be expressed by the allometric relationship:

$$\overline{H}=\mathrm{g}_{\theta_\mathrm{x}}\cdot\overline{w}_\mathrm{x}^{\theta_\mathrm{x}} \tag{3.3}$$

where $\mathrm{g}_{\theta_\mathrm{x}}$ and θ are a constant and the allometric coefficient between $\overline{H}$ and $\overline{w}_\mathrm{x}$, respectively. Assumption 3: the relationship between mean partial organ mass density $\overline{d}_\mathrm{x}$ and mean partial organ mass $\overline{w}_\mathrm{x}$ can be expressed as:

$$\overline{d}_\mathrm{x}=\left(=\frac{\overline{w}_\mathrm{x}}{\overline{s}\cdot\overline{H}}\right)=\mathrm{g}_{\delta_\mathrm{x}}\cdot\overline{w}_\mathrm{x}^{\delta_\mathrm{x}} \tag{3.4}$$

where $\mathrm{g}_{\delta_\mathrm{x}}$ and δ_x are a constant and the allometric coefficient between $\overline{d}_\mathrm{x}$ and $\overline{w}_\mathrm{x}$, respectively.

Consideration of Eqs (3.2), (3.3), and (3.4) yields the following relationship:

$$\overline{d}_\mathrm{x}=\frac{\overline{w}_\mathrm{x}}{\overline{s}\cdot\overline{H}}=\frac{1}{\mathrm{g}_{\phi_\mathrm{x}}\cdot\mathrm{g}_{\theta_\mathrm{x}}}\overline{w}_\mathrm{x}{}^{1-(\phi_\mathrm{x}+\theta_\mathrm{x})}=\mathrm{g}_{\delta_\mathrm{x}}\cdot\overline{w}_\mathrm{x}^{\delta_\mathrm{x}}. \tag{3.5}$$

This relationship represents the validity of the following equalities:

$$\delta_{\mathrm{x}} = 1 - (\phi_{\mathrm{x}} + \theta_{\mathrm{x}}) \tag{3.6}$$

and

$$\mathrm{g}_{\delta_{\mathrm{x}}} = \frac{1}{\mathrm{g}_{\phi_{\mathrm{x}}} \cdot \mathrm{g}_{\theta_{\mathrm{x}}}}. \tag{3.7}$$

Equation (3.2) can be transformed as follows:

$$\overline{w}_{\mathrm{x}} = \left(\frac{1}{\mathrm{g}_{\phi_{\mathrm{x}}}}\right)^{\frac{1}{\phi_{\mathrm{x}}}} \cdot \rho^{-\frac{1}{\phi_{\mathrm{x}}}}. \tag{3.8}$$

Comparing Eqs. (3.1) and (3.8), and considering Eq. (3.6), the self-thinning exponent of the partial organ α_{x} in Eq. (3.1) can be expressed as:

$$\alpha_{\mathrm{x}} = \frac{1}{\phi_{\mathrm{x}}} = \frac{1}{1 - (\delta_{\mathrm{x}} + \theta_{\mathrm{x}})}. \tag{3.9}$$

By further considering Eqs. (3.7) and (3.9), the multiplying factor K_{x} of the organ x in Eq. (3.1) is given by:

$$K_{\mathrm{x}} = \left(\frac{1}{\mathrm{g}_{\phi_{\mathrm{x}}}}\right)^{\frac{1}{\phi_{\mathrm{x}}}} = \left(\mathrm{g}_{\delta_{\mathrm{x}}} \cdot \mathrm{g}_{\phi_{\mathrm{x}}}\right)^{\alpha_{\mathrm{x}}} \tag{3.10}$$

Therefore, values of the self-thinning exponent α_{x} and the multiplying factor K_{x} of the self-thinning line for partial organs can be calculated using the allometric model as follows. The self-thinning exponent α_{x} can be estimated from Eq. (3.9) using the θ_{x}-value from Eq. (3.3) and the θ_{x}-value from Eq. (3.4). The multiplying factor K_{x} in Eq. (3.1) can also be estimated from Eq. (3.10) using the α_{x}-value from Eq. (3.9), the $\mathrm{g}_{\theta_{\mathrm{x}}}$-value from Eq. (3.3) and the $\mathrm{g}_{\delta_{\mathrm{x}}}$-value from Eq. (3.4).

3.2.3 Statistical analysis

The simple regression for all allometric equations was conducted after linearization by taking the logarithms of both sides of the equations using Microsoft Excel 2003. The *t* test was performed for the allometric exponents ϕ_{x} in Eq. (3.2), θ_{x} in Eq. (3.3), and δ_{x} in Eq. (3.4).

3.3 Results

3.3.1 Establishment of the allometric relationship between organ masses and $D_{0.1\mathrm{H}}^2 H$

Khan et al. (2005) confirmed that the conventional allometric relationship using diameter at breast height (DBH) had a much better goodness-of-fit than the allometric relationship using $D_{0.1\mathrm{H}}^2 H$ in the mangrove *K. obovata*. Deshar et al. (2012) found similar results for the mangrove *Bruguiera gymnorrhiza* on Okinawa Island. Therefore, we used $D_{0.1\mathrm{H}}^2 H$ as an explanatory variable for establishing the allometric relationships.

Figure 3.1 shows allometric relationships, whose data are taken from Khan et al. (2005), between stem w_{S} (kg), branch w_{B} (kg), and leaf w_{L} (kg) with $D_{0.1H}^2 H$ (cm^{2}m). The allometric equations were established as follows:

$$w_{\mathrm{S}} = 0.02363 \left(D_{0.1\mathrm{H}}^2 H\right)^{1.032}, \tag{3.11}$$

$$w_{\mathrm{B}} = 0.006882 \left(D_{0.1\mathrm{H}}^2 H\right)^{1.142}, \tag{3.12}$$

and

$$w_{\mathrm{L}} = 0.009675 \left(D_{0.1\mathrm{H}}^2 H\right)^{0.7054}. \tag{3.13}$$

The census results for $D_{0.1\mathrm{H}}$ and H were inserted into Eqs. (3.11), (3.12), and (3.13), respectively, to estimate values of w_{S}, w_{B}, and w_{L} for individual trees in each plot. Then, mean masses for stem $\overline{w}_{\mathrm{S}}$, branch $\overline{w}_{\mathrm{B}}$, leaf $\overline{w}_{\mathrm{L}}$, and aboveground $\overline{w}_{\mathrm{T}}$ $(= \overline{w}_{\mathrm{S}} + \overline{w}_{\mathrm{B}} + \overline{w}_{\mathrm{L}})$ were calculated for each plot.

3.3.2 Allometric relationships between mean tree height and mean organ masses

Allometric relationships were calculated between mean tree height H and mean stem mass $\overline{w}_{\mathrm{S}}$ (Fig. 3.2a), mean branch mass $\overline{w}_{\mathrm{B}}$ (Fig. 3.2b), mean leaf mass $\overline{w}_{\mathrm{L}}$ (Fig. 3.2c), and mean aboveground mass $\overline{w}_{\mathrm{T}}$ (Fig. 3.2d). The logarithms of mean tree height $\overline{H}$ increased significantly with logarithms of mean organ mass $\overline{w}_{\mathrm{x}}$ ($p < 0.01$). The allometric coefficient θ_{x} in Eq. (3.3) was 0.3801 ± 0.0187 for stem, 0.3464 ± 0.0174 for branch, 0.5386 ± 0.0249 for leaf, and 0.3812 ± 0.0187 for aboveground (Table 1). The values of $g_{\theta_{\mathrm{x}}}$ in Eq. (3.3) were estimated to be 2.581m kg$^{-\theta_\mathrm{S}}$ for stem, 3.415 m kg$^{-\theta_\mathrm{B}}$ for branch, 8.181 m kg$^{-\theta_\mathrm{L}}$ for leaf, and 2.154 m kg$^{-\theta_\mathrm{T}}$ for aboveground.

3.3.3 Allometric relationships between mean organ mass densities and corresponding mean masses

Mean partial organ mass density $\overline{d}_\mathrm{x}$ was calculated by dividing mean partial organ mass $\overline{w}_\mathrm{x}$ by the product of mean tree height $\overline{H}$ and the mean space occupied by a tree $\overline{s}$, which is equal to the reciprocal of population density ρ. The resulting values for mean stem mass density $\overline{d}_\mathrm{S}$, mean branch mass density $\overline{d}_\mathrm{B}$, mean leaf mass density $\overline{d}_\mathrm{L}$, and mean aboveground mass density $\overline{d}_\mathrm{T}$ ranged from 1.358 to 2.469, 0.6715 to 1.157, 0.1008 to 0.2528, and 1.117 to 3.965 kg m^{-3}, respectively.

Figure 3.3 presents allometric relationships between mean organ mass density and mean mass. The allometric coefficient δ_x in Eq. (3.4) was -0.0436 ± 0.0203 (SE) for stem, 0.0464 ± 0.0190 for branch, -0.4553 ± 0.0268 for leaf, and -0.0449 ± 0.0203 for aboveground (Table 1).

Values of the multiplying factor $\mathrm{g}_{\delta_\mathrm{x}}$ in Eq. (3.4) were estimated to be 1.745 m^{-3} kg$^{1-\delta_\mathrm{S}}$ for stem, 0.8111 m^{-3} kg$^{1-\delta_\mathrm{B}}$ for branch, 0.07620 m^{-3} kg$^{1-\delta_\mathrm{L}}$ for leaf, and 2.864 m^{-3} kg$^{1-\delta_\mathrm{T}}$ for aboveground.

3.3.4 Self-thinning exponents of partial organs

The self-thinning exponent α_S and the multiplying factor K_S for mean stem mass per tree $\overline{w}_\mathrm{S}$ were estimated to be 1.508 (Table 1) from Eq. (3.9) and 9.689 kgm$^{-2\alpha_\mathrm{S}}$ from Eq. (3.10), respectively. As shown in Fig. 3.4a, the self-thinning line for stem can be described in the form:

$$\overline{w}_\mathrm{S} = 9.689 \cdot \rho^{-1.508} \tag{3.14}$$

For mean branch mass per tree $\overline{w}_\mathrm{B}$, the self-thinning exponent α_B and the multiplying factor K_B were 1.646 (Table 1) and 5.355 kgm$^{-2\alpha_\mathrm{B}}$, respectively. As shown in Figure 3.4b, the self-thinning line can be written by the following equation:

$$\overline{w}_\mathrm{B} = 5.355 \cdot \rho^{-1.646} \tag{3.15}$$

Similarly, the self-thinning exponent α_{L} and the multiplying factor K_{L} for mean leaf mass per tree $\overline{w}_{\mathrm{L}}$ were estimated to be 1.090 (Table 1) and 0.5972 $\mathrm{kgm}^{-2\alpha_{\mathrm{L}}}$, respectively. As shown in Fig. 3.4c, the self-thinning line can be expressed in the form:

$$\overline{w}_{\mathrm{L}} = 0.5972 \cdot \rho^{-1.090} \tag{3.16}$$

Considering Eqs. (3.14), (3.15), and (3.16), the mean aboveground mass per tree $\overline{w}_{\mathrm{T}}$ is defined by the following sum of power equations:

$$\overline{w}_{\mathrm{T}} = \overline{w}_{\mathrm{S}} + \overline{w}_{\mathrm{B}} + \overline{w}_{\mathrm{L}} = 9.689 \cdot \rho^{-1.509} + 5.355 \cdot \rho^{-1.647} + 0.5972 \cdot \rho^{-1.090} \tag{3.17}$$

As shown by the black dotted line in Fig. 3.5, Eq. (3.17) provided a good description of the observed data. The self-thinning exponent α_{T} and the multiplying factor K_{T} for mean aboveground mass per tree $\overline{w}_{\mathrm{T}}$ were 1.507 (Table 1) and 15.52, respectively. As illustrated by the red solid line in Fig. 3.5d, the self-thinning line of aboveground takes the form:

$$\overline{w}_{\mathrm{T}} = 15.52 \cdot \rho^{-1.507} \tag{3.18}$$

The black dotted and red solid lines overlapped.

3.4 Discussion

As compiled in Table 1, the δ_{x}-value was not significantly different from zero ($t = 2.153$, df = 166, $P = 0.032$) in stem (Fig. 3.3a), ($t = 2.441$, df = 166, $P = 0.015$) and in branch Fig. 3.3b) at a 1% significance level. On the other hand, the δ_{x}-value was significantly negatively correlated ($t = 17.01$, df = 166, $P = 3.221 \times 10^{-38}$) in leaf (Fig. 3.3c), likely because the amount of space without leaves increased with increasing tree height. This decreasing trend of $\overline{d}_{\mathrm{L}}$ with increasing $\overline{w}_{\mathrm{L}}$ did not affect the trend of mean aboveground mass density $\overline{d}_{\mathrm{T}}$ with increasing mean aboveground mass $\overline{w}_{\mathrm{T}}$ (Fig. 3.4d), because leaf mass contributed only 4-8% of the total aboveground mass and the rest was contributed by woody organs. Therefore, the δ_{x}-value for aboveground did not significantly differ from zero ($t = 2.212$, df = 166, $P = 0.02827$). This constancy may be designated as constant mean mass density.

Our results generally agree with the assumption of Weller (1987b) that the biomass density $\overline{d}$ was constant regardless of $\overline{w}$, i.e., that δ was zero. Our study also confirmed this assumption for woody organs (stem, branch) and aboveground. If we assume that $\delta = 0$ for woody organs and aboveground, the self-thinning exponent was 1.613 for stem, 1.530 for branch and 1.616 for aboveground (Table 1). Similar results were also found in *B. gymnorrhiza* in the northern part of Okinawa Island (Deshar et al., 2012) and in *Pinus densiflora* Sieb. et Zucc. (Xue and Hagihara, 2012).

The average $\overline{d}_{\mathrm{T}} \left(= \overline{d}_{\mathrm{T}} \cdot \rho/\overline{H}\right)$ of aboveground mass was 2.66 ± 0.02 kg m^{-3}. The $\overline{d}_{\mathrm{T}}$-value was similar to the findings of Khan et al. (2009) who reported that the biomass density of *K. obovata* stands on Okinawa Island was 2.23 kg m^{-3}. Our result is also identical with that of Deshar et al. (2012), who reported that the biomass density for aboveground mass of *B. gymnorrhiza* stands on Okinawa Island was 2.40 ± 0.09 kg m^{-3}. However, the present $\overline{d}_{\mathrm{T}}$ was considerably higher than the 1.3-1.5 kg m^{-3} of most terrestrial forests, except for dwarf pine (*Pinus pumila* Regel) forests, which had quite high biomass densities of approximately around 9.0 kg m^{-3} (Kira and Shidei, 1967). The observed higher average $\overline{d}_{\mathrm{T}}$ is likely due to the fact that *K. obovata* trees growing near the northernmost limit of the species distribution are comparatively short (Suwa et al., 2009), with a mean tree height ranging from 2.17 to 4.81 m (Fig. 3.2); nevertheless, leaf mass can be large.

From Eq. (3.3) and the definition of $\overline{d}_{\mathrm{x}}$ in Eq. (3.4), the estimators θ_{x} and δ_{x} are apparently dependent (Deshar et al., 2012; Kamara et al., 2012), so that the δ_{x}-value obtained from the estimates θ_{x} and δ_{x} cannot be used to test the hypothesis that the expectation of the estimator $\theta_{\mathrm{x}} + \delta_{\mathrm{x}}$ equals 1/3, i.e., $\alpha = 3/2$ (Yoda et al., 1963) or 1/4, i.e., $\alpha = 4/3$ (Enquiest et al., 1998). On the other hand, the ϕ_{x}-value obtained from Eq. (2) can be used in the significance test. Equation (2) yielded a ϕ_{x}-value of 0.6629 ± 0.0250 for stem, 0.6072 ± 0.0229 for branch, 0.9167 ± 0.0356 for leaf, and 0.6637 ± 0.0297 for aboveground (Table 1). These values are the same as the reciprocal of the self-thinning exponent α_{x} of 1.509 for stem, 1.647 for branch, 1.090 for leaf, and 1.507 for aboveground obtained from Eq. (3.9) based on Weller's allometric model. The ϕ_{x}-value did not significantly differ from 2/3 in stem (t = 0.1506, df = 166, p = 0.8804), branch (t = 2.600, df = 166, p = 0.01015) at a 1% significance level, and aboveground (t = 0.1194, df = 166, p= 0.9050), i.e., $\alpha_{\mathrm{x}} = 3/2$; however, the ϕ_{x}-value did significantly differ from 3/4 in stem (t = 3.474, df = 166, p = 6.582 x 10^{-4}), branch (t = 1.245, df = 166, p = 3.438 x 10^{-9}), and aboveground (t = 3.438, df = 166, p = 7.391 x 10^{-4}), suggesting that the self-thinning exponent was closer to the value of 3/2 proposed by Yoda et al. (1963) than to the value of 4/3 proposed by Enquist et al. (1998, 2000).

The ϕ_{L} value for leaf was significantly different from 2/3 ($t = 7.015$, $\mathrm{df} = 166$, $p = 5.543 \ \ 10^{-11}$) and from 3/4 ($t = 4.676$, $\mathrm{df} = 166$, $p = 6.013 \ \ 10^{-6}$) but did not significantly differ from 1.0 ($t = 2.338$, $\mathrm{df} = 166$, $p = 2.063 \ \ 10^{-2}$); i.e., the self-thinning exponent for mean leaf mass was 1.0, confirming the constancy of leaf biomass for overcrowded *K. obovata* stands (i.e., $\overline{w}_{\mathrm{L}} \cdot \rho = \text{constant}$). Our result is consistent with the finding of Deshar et al. (2012) who reported that leaf biomass was constant regardless of population density in *B. gymnorrhiza* stands. Sprugel (1984) and Osawa & Kurachi (2004) also found a constant amount of leaf biomass per ground area in wave-regenerated *Abies balsamea* (L.) Mill. forests and in self-thinning stands of *Pinus banksiana* Lamb. and *Populus tremuloides* Michx, respectively. The allometric explanation of the self-thinning rule (Osawa and Allen, 1993; Osawa, 1995) was based on the assumption of constant leaf biomass. Hozumi et al. (1962) found that leaf biomass tends to reach constant values more rapidly than the biomass of woody organs at an early stage in *Hibiscus moscheutos* Linn. populations. Xue and Hagihara (2008) reconfirmed that constant final leaf biomass values occurred in overcrowded *Pinus densiflora* stands. Therefore, it can be postulated that predictable relationships between mean leaf mass and population density in overcrowded populations can be explained by the regulation and redistribution of a fixed amount of leaf biomass among a declining number of individuals.

The self-thinning exponent for leaf $\alpha_{\mathrm{L}}\,(= 1/\phi_{\mathrm{L}})$ was 1.090, which was much lower than 3/2 and 4/3. This value was counterbalanced by self-thinning exponents of 1.508 for stem and 1.646 for branch. Together, these values resulted in a self-thinning exponent of 1.507 for aboveground. The overall variation in self-thinning exponents among *K. obovata* organs could be interpreted as a consequence of the ratio of the distribution of photosynthates to the organs. Deshar et al. (2012) also found the variation in the self-thinning exponents among *B. gymnorrhiza* organs.

The results from our study indicate that the self-thinning exponent for stem was not significantly different from 3/2, which can be explained by the isometric growth of stems. The self-thinning exponent for branch was also not significantly different from 3/2. Branches near the bottom and inside the crown are shaded as new branches grow at the top, so that secondary, tertiary, and smaller branches are shaded. In overcrowded population, such self-shading may function to regulate the mass of branches so as to keep roughly the similarity of the mean branch volume per tree (Norberg, 1988). Mean stem, branch, and mean aboveground mass follow the 3/2 power law of self-thinning in overcrowded *K. obovata* stands because the effect of leaves on the self-thinning exponent for mean aboveground mass was negligible. The self-thinning exponent was 1.506 for aboveground, which was closer to 3/2 than to 4/3. Therefore, in terms of the present overcrowded *K. obovata* stands, self-thinning can be explained using the simple geometric model (Yoda et al., 1963), although whether the self-thinning exponent is 3/2 or 4/3 remains debatable.

3.5 Summary

In conclusion of our study, the mean mass of woody organs (mean stem mass, mean branch mass and mean aboveground mass follow the 3/2 power law of self-thinning in overcrowded mangrove *K. obovata* stands. This was because the effect of leaves on the self-thinning exponent for aboveground mass was negligible. The self-thinning exponent was 1.507 for aboveground, which was close to 3/2 rather than 4/3. Therefore, regarding the present overcrowded *K. obovata* stands, self-thinning can be explained using the simple geometric, although whether the self-thinning exponent is 3/2 or 4/3 as proposed by Enquist et al. (1998, 2000) on the basis of a metabolic model (West et al. 1997) remains debatable.

Table 3.1: Allometric coefficients for mean tree height $\overline{H}$ to mean organ mass $\overline{w}_\mathrm{x}$ [θ_x; Eq. (3.3)], mean organ mass density $\overline{d}_\mathrm{x}$ to $\overline{w}_\mathrm{x}$, [δ_x; Eq. (3.4)], and population density ρ to $\overline{w}_\mathrm{x}$, [ϕ_x; Eq. (3.8)]; values of the self-thinning exponent α_x [Eq. (3.9)] are also shown. The values in parenthesis show α-values under the assumption of $\delta = 0$.

Organ (x)	$\theta \pm$ SE	$\delta \pm$ SE	$\phi \pm$ SE	α
Stem	0.3801 ± 0.0187	-0.0436 ± 0.0203	0.6629 ± 0.0250	1.509 (1.613)
Branch	0.3464 ± 0.-174	0.0464 ± 0.0190	0.6072 ± 0.0229	1.647 (1.530)
Leaf	0.5386 ± 0.0249	-0.4553 ± 0.0268	0.9167 ± 0.0356	1.090
Aboveground	0.3812 ± 0.0187	-0.0449 ± 0.0203	0.6637 ± 0.0297	1.507 (1.616)

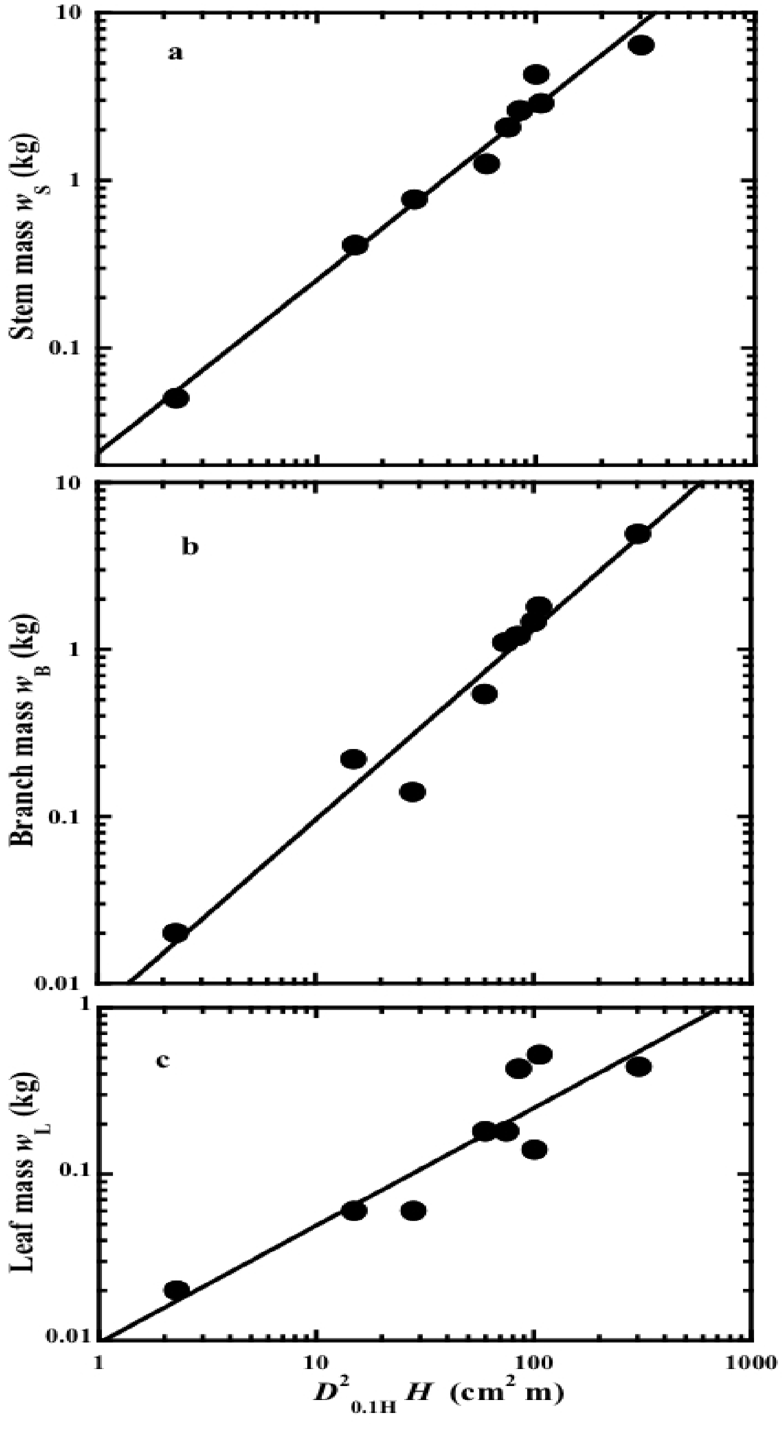

Figure 3.1: Allometric relationships between organ mass $\overline{w}_{\mathrm{x}}$ and $D^2_{0.1H}H$ on log-log scales. The straight lines show Eq. (3.11) ($R^2 = 0.8169$) for stem (a), Eq. (3.12) ($R^2 = 0.9887$) for branch (b), and Eq. (3.13) ($R^2 = 0.5391$) for leaf (c).

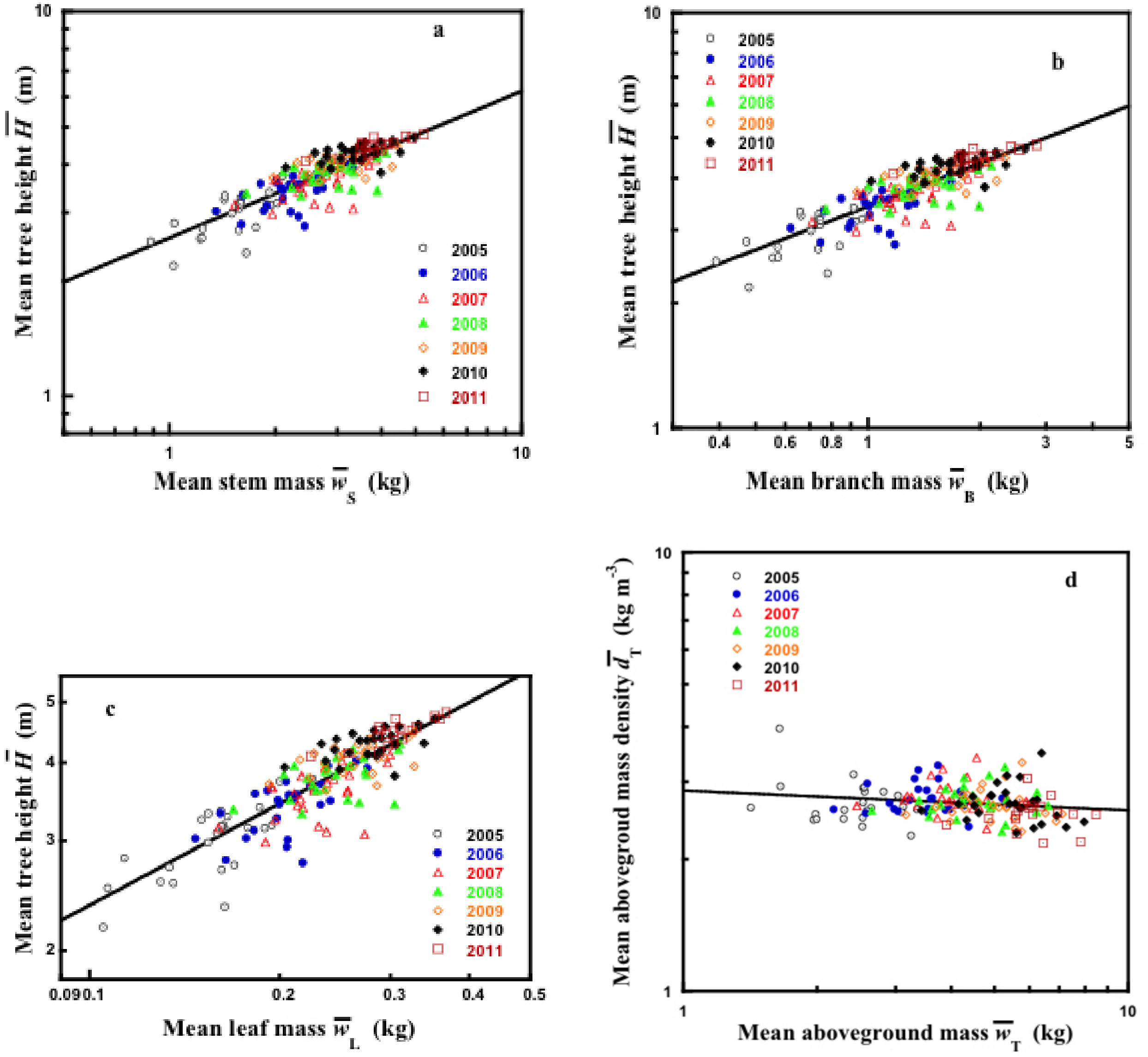

Figure 3.2: Allometric relationship between mean tree height $\overline{H}$ and mean organ mass $\overline{w}_{\mathrm{x}}$ on log-log coordinates. The straight lines are fitted using Eq. (3); where R^2 =0.7148 for stem (a), R^2 = 0.70522 for branch (b), R^2 = 0.7389 for leaf (c), and R^2 = 0.7149 for aboveground (d).

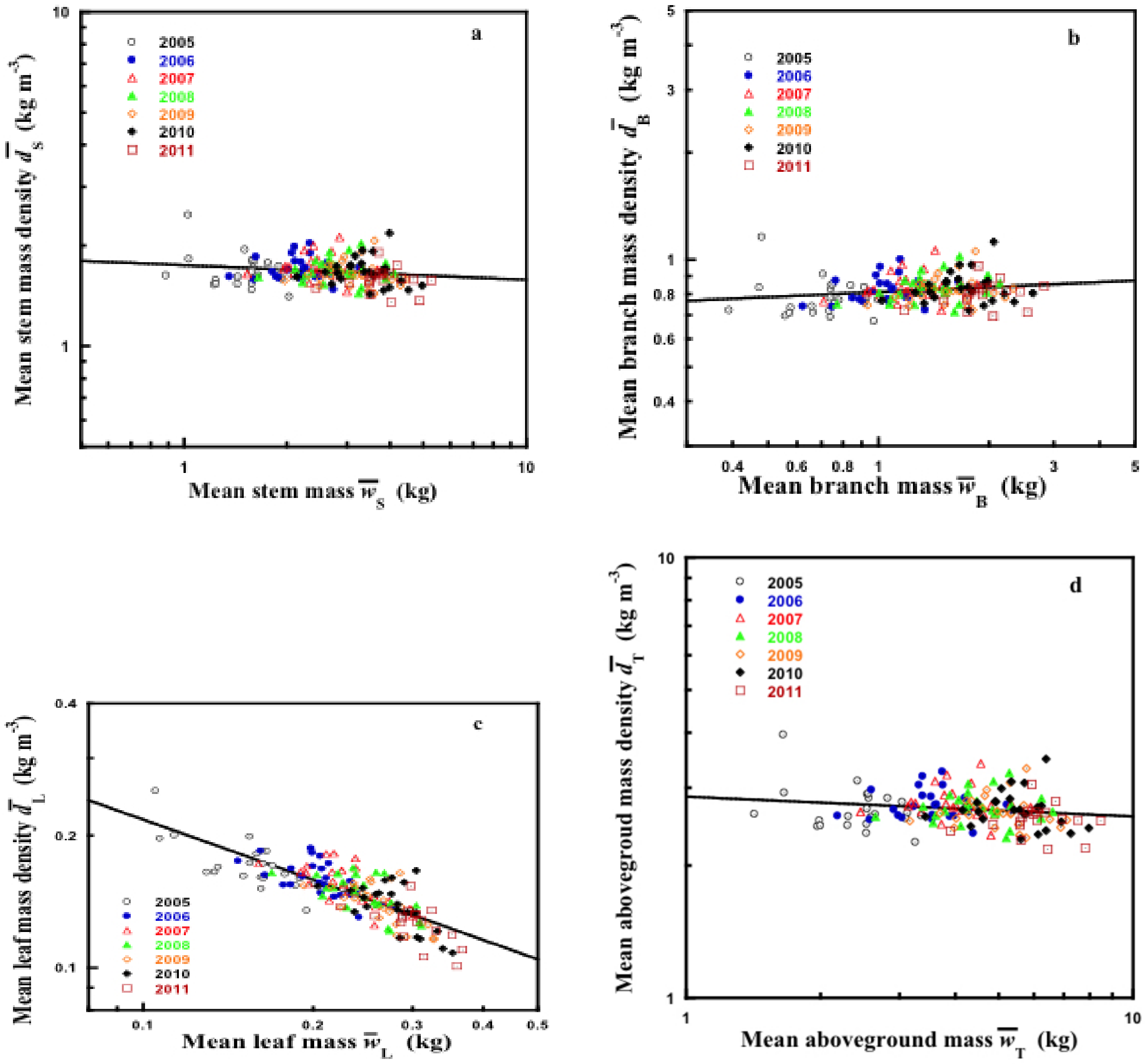

Figure 3.3: Allometric relationship between mean organ mass density $\overline{d}_x$ and mean organ mass $\overline{w}_x$ on log-log coordinates. The straight lines are fitted using Eq. (4); where $R^2 = 0.02641$ for stem (a), $R^2 = 0.02824$ for branch (b), $R^2 = 0.6314$ for leaf (c), and $R^2 = 0.02780$ for aboveground (d).

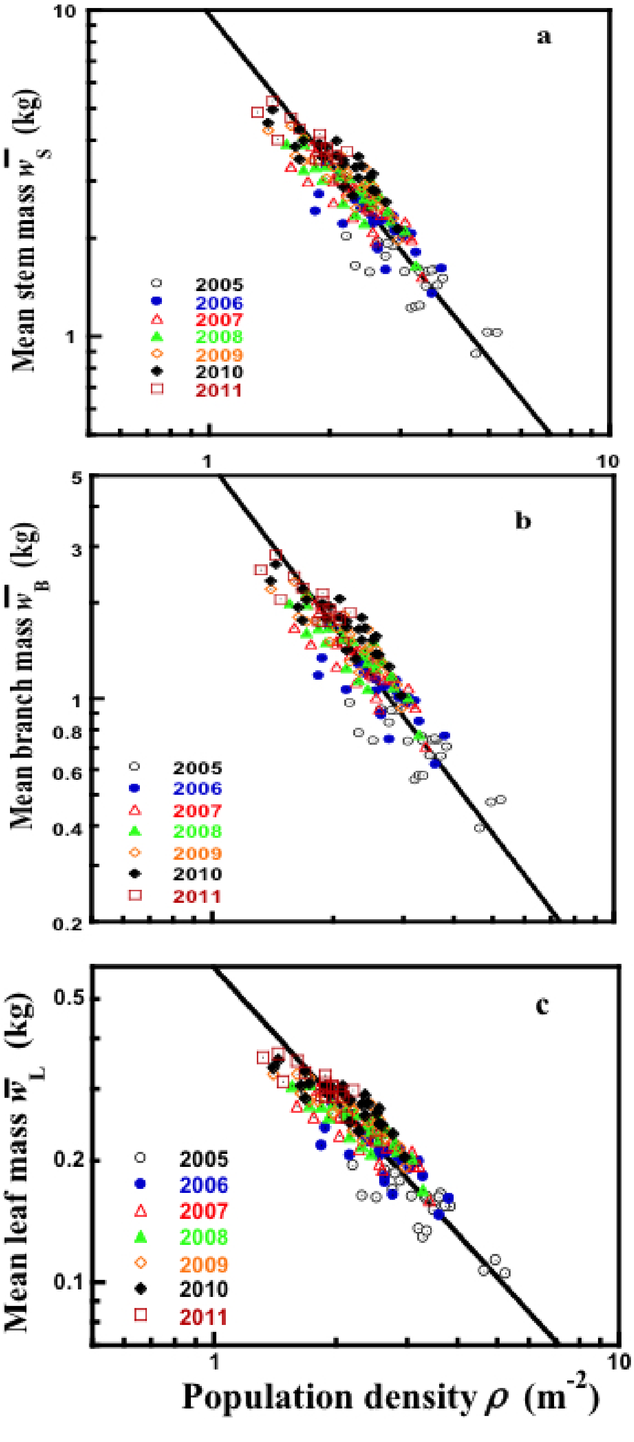

Figure 3.4: Scatter plots of mean organ mass $\overline{w}_x$ against population density ρ on log-log coordinates. The straight lines are given by Eqs. (3.14) ($R^2 = 0.6793$) for stem (a), (3.15) ($R^2 = 0.6768$) for branch (b), and (3.16) ($R^2 = 0.6791$) for leaf (c).

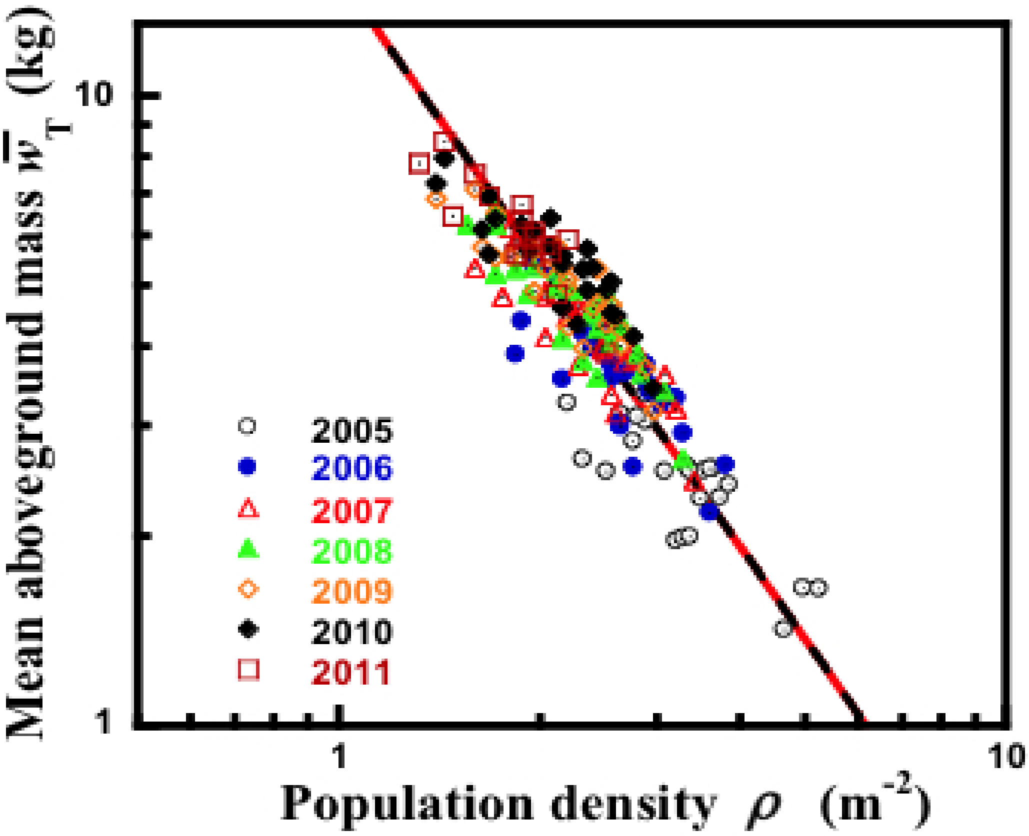

Figure 3.5: Scatter plot of mean aboveground mass $\overline{w}_{\mathrm{T}}$ and population density ρ on log-log coordinates. The straight line is given by Eq. (3.17) (black dotted line, $R^2 = 0.6794$) or Eq. (3.18) (red solid line, $R^2 = 0.6794$).

Chapter 4

The self-thinning exponent of total aboveground mass

4.1 Introduction

Small trees grow without competition in the initial stage of stand development, but sooner or later the gaps between them are filled with growing trees. They begin to compete with each other for access to resources such as light, water, and nutrients (Silvertown and Charlesworth 2001). This process is called self-thinning and it is observed in natural and artificial plant populations (Han & Fang 2008). As a centerpiece in stand level forest management, self-thinning has received considerable attention in forest research.The self-thinning rule is one of the few long-lived quantitative propositions in ecology, despite recurrent episodes of criticism of its empirical and conceptual foundations. A number of empirical studies and thinning trials were initiated to quantify the effect of different thinning intensities, intervals and structures (i.e., thinning from aboveground mass)mainly on stem wood growth (e.g. Pretzsch, 2005) (Franklin et al. 2009).

The -3/2 power law of self-thinning proposed by Yoda et al.1963, has attracted much attention and has been considered by some as general rules in plant ecology .This law expresses the relationship between mean plant mass w and population density ρ in overcrowded stands during the development of an even-aged population with complete canopy closure. The relationship can be expressed as:

$$\log(\overline{w}) = \log(K) + \alpha \cdot \log(\rho) \tag{4.1}$$

where K is a species-specific multiplying factor, and α is the self-thinning exponent, which is close to 3/2. This implies, for example, a 17% increase in mean plant mass is always associated with a 10% decrease in population density, regardless of species, stand spatial structure or initial density (Reynolds & Fords 2005). This empirical relationship has produced two lines of research: empirical studies exploring the relationship's generality and theoretical models exploring possible underlying mechanisms that might produce this constancy. Gorham 1979; White 1981; Westoby1984 using field data suggest that the self-thinning relationship in Eq. (6.1) with constant slope for all stands, is too simple as a summary of the self-thinning process. Some have considered whether variation is associated with particular plant characteristics (e.g. Zeide 1985,1987; Weller 1987b; Ellison 1989), differences between species, soil nutrient conditions (Morris 2003). Theoretical models have attempted to explain Eq. (6.1) from assumptions about how plants increase in size in relation to the volume they occupy, or more generally how their ability to acquire resources develops, and what controls the outcome of competition between individuals (Reynolds & Fords 2005).

However, Weller (1987a) argued that the self-thinning exponent can differ from 3/2. The allometric model proposed by Weller (1987b) predicts that the thinning exponent varies with plant shape and mass density (mass per unit occupied space), which can be derived from stand parameters, such as mass, tree height, and crown projection area. This model merits further investigation to test its applicability to diverse species because of its biological implications. Although plant shape and biomass density have been reported to have an important influence on the self-thinning exponent (Lonsdale and Watkinson 1983; Norberg 1988; Weller 1989b), very few reports on plant shape and biomass density have been based on experimental data.

Although there is debate (there is disagreement amongst researchers about the most accurate value for use in the power function, and whether the factor is indeed universal.The main disagreement is whether metabolic rate scales to the power of 4/3 or 3/2). The self-thinning rule is widely accepted and has become the most applied principle in plant population dynamics. Therefore the self-thinning exponent of total aboveground mass has been elucidated in this chapter for a better understanding of the thinning process in *K. obovata* stands on Okinawa Island which play an important role as a vital ecosystem for many animals.

The importance of mangrove forests in the marine food web, their role in stabilizing sediments and protecting shorelines against erosion, and their utility to local human communities are now well recognized (e.g., Alongi 2009). However, not many studies on self-thinning have been undertaken for mangroves. Such knowledge would be of fundamental importance for understanding mangrove ecology and management.

In the Manko Wetland, Okinawa Island, Japan, *Kandelia obovata* Sheue, Liu Yong is the most dominant mangrove species. A better understanding of the forest structure through the study of the self-thinning of the total aboveground mass of the forest is necessary for its management. Therefore, the purposes of this chapter is to determine the self-thinning exponent of total aboveground mass overcrowded *K. obovata* stands using Weller's allometric model, but also to examine whether the self-thinning exponent differs from 3/2 based on the simple geometric model (Yoda et al. 1963) or 4/3 based on the metabolic model (Enquist et al. 1998).

4.2 Materials and methods

4.2.1 Tree census and estimation of aboveground mass

A 125-m-long belt-transect (5m × 5m) was established in the *K. obovata* forest perpendicular to river flow and was divided into 25 subplots (5 m × 5 m). Stem analysis revealed that tree age increased continuously from 6 years near the riverside to 10 years near the land as of 2005, so that trees within a subplot could be assumed to be of uniform age. All individuals in the subplots were numbered. In each subplot, tree height H (m) and stem diameter $D_{0.1H}$ (cm) at H/10 were measured every summer from 2004 to 2011. Mean H and mean $D_{0.1H}$ of every subplot ranged from 2.17 to 3.76 m and 2.80 to 4.84 cm, respectively, as of 2010. Aboveground mass w (kg) was estimated by inserting the census result into the following allometric relationship:

$$w = 0.03923 \left(D_{0.1\mathrm{H}}^2 H\right)^{1.022}, \tag{4.2}$$

which was obtained by Khan et al. (2005) at Manko Wetland for overcrowded *K. obovata* stands. The data of mass were arranged by subplot every year.

4.2.2 Weller's allometric model

See Chapter 3

4.2.3 Statistical Analysis

See Chapter 3

4.3 Results

4.3.1 Allometric relationship of mean tree height to mean aboveground mass

Figure 1 shows the allometric relationship of mean tree height $\overline{H}$ to mean aboveground mass $\overline{w}$. The H increased significantly with increasing $\overline{w}$ ($t = 26.55$, $df = 191$, $p = 5.174$ 9×10^{-66}). The allometric relationship was formulated as Eq. (3.4), where the allometric coefficient θ was 0.3857 ± 0.0145 (Table 1) and the constant g_θ was 2.157 m $kg^{-\theta}$.

4.3.2 Allometric relationship of mean aboveground mass density to mean aboveground mass

Mean aboveground mass density $\overline{d}$ was calculated by dividing mean total aboveground mass $\overline{w}$ by the product of mean tree height $\overline{H}$ and mean space occupied by a tree $\overline{s}$, which is equal to the reciprocal of population density ρ. As shown in Fig. 4.2, mean aboveground mass density $\overline{d}$ tended to be constant regardless of $\overline{w}$. This allometric relationship was defined in Eq. (3.5), where δ and g_θ are -0.01673 ± 0.01707 (Table 1) and 2.685 m^{-3} $kg^{1-\delta}$, respectively. The δ-value was not significantly different from zero ($t = 0.9800$, $df = 191$, $P = 0.3280$). The average of $\overline{d}$ was estimated to be 2.641 ± 0.022 kg m^{-3}.

4.3.3 Self-thinning exponent of total abovegound mass

Figure 4.3 shows the self-thinning line based on Weller's allometric model. The self-thinning exponent α in Eq. (4.1) was obtained to be 1.585 from Eq. (3.10), where the ϕ-value was 0.6310 based on the θ-value in Eq. (3.4) and the δ-value in Eq. (3.5). On the other hand, the multiplying factor K in Eq. (4.1) was 16.18 kg $m^{-2\alpha}$ from Eq. (3.11), using the α-value of Eq. (3.10), the g_θ-value of Eq. (3.4) and the g_δ-value of Eq. (3.5). Therefore, the self-thinning line was as follows:

$$\overline{w} = 16.18 \cdot \rho^{-1.585} \tag{4.3}$$

4.4 Discussion

The average of $\overline{d}$, i.e., biomass density ($\overline{w} \cdot \rho / \overline{H}$), was 2.641 ± 0.022 kg m^{-3}. Khan et al. (2009) reported that the biomass density of *K. obovata* stands on Okinawa Island was 2.23 kg m^{-3}, i.e., similar to the present value. Our results are also very close to those of Deshar et al. (2012), who reported that the biomass density of *Bruguiera* obtained from Eq. (3.10). The ϕ-value was not significantly different from 2/3 (t = 1.860, *df* = 191, P = 0.06429), i.e., α=3/2, but it was significantly different from 3/4 (t = 6.213, *df* = 191, P = 3.182 9 10-9), i.e., α=4/3. This suggests that the self-thinning exponent is close to the value of 3/2 proposed by Yoda et al. (1963), rather than the value of 4/3 proposed by Enquist et al. (1998, 2000) on the basis of the metabolic model (West et al. 1997). Using Weller's allometric model, Deshar et al. (2012) also found a similar result in *B. gymnorrhiza* at the Okukubi River, Okinawa Island.

Equation (4.1) shows that the ratio of the relative growth rate (RGR) of mean aboveground mass to the relative mortality rate (RMR) is α Therefore, the self-thinning rule holds on the balance of RGR and RMR, i.e., an increase of RGR is adjusted by a corresponding increase of RMR, and vice versa. Thus the present self-thinning exponent α could be applicable for *K. obovata* stands growing in heterogeneous environmental conditions.

This present results based on Weller's allometric model strengthen the justification for the simple geometric model proposed by Yoda et al. (1963). They originally derived a simple geometric explanation for the self-thinning rule based on two assumptions: plants of a given species maintain the same shape regardless of habitat, size, or age; and mortality occurs only when the total coverage of a plant population exceeds the available area, and then acts to maintain 100 % cover. As far as the present overcrowded *K. obovata* stands are concerned, our results show that self-thinning can be explained using the simple geometric model. The existence of the -3/2 power relationship among the *K. obovata* population could be interpreted as an evidence that natural self-thinning is occurring in the forest, canopies are closed, growth and mortality are ongoing, and competition is the cause of mortality.

Allometric coefficient	Mean	SE
θ	0.3857	0.01452
δ	-0.01673	0.01707
ϕ	0.6310	0.01914

Table 4.1: Allometric coefficients for mean tree height $\overline{H}$ to mean total aboveground mass $\overline{w}$ [θ; Eq. (3.3)], mean organ mass density $\overline{d}$ to $\overline{w}$, [δ; Eq. (3.4)], and population density ρ to $\overline{w}$, [ϕ; Eq. (3.8)].

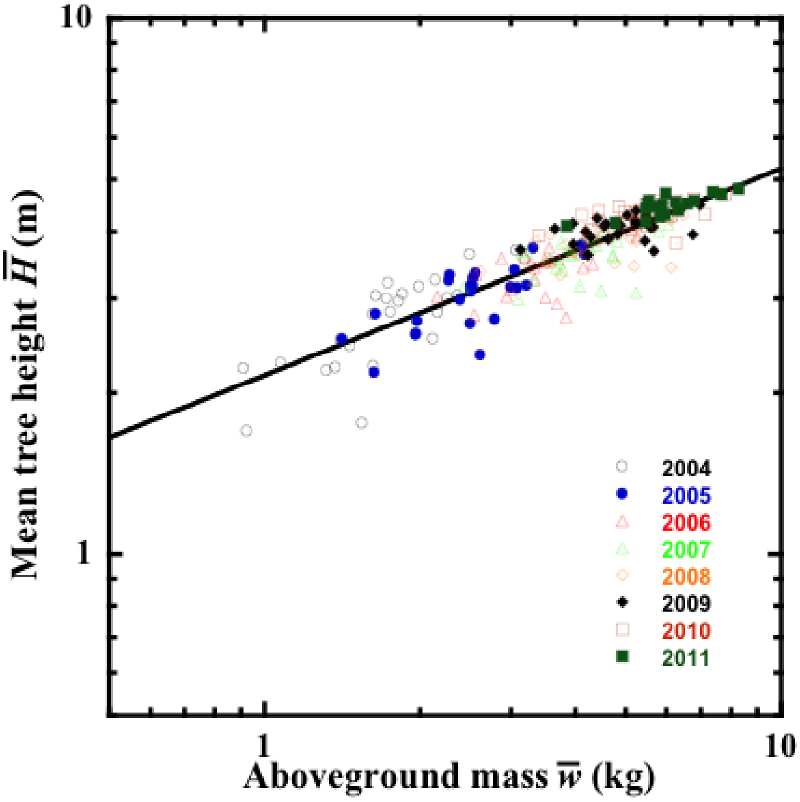

Figure 4.1: Allometric relationship between mean tree height $\overline{H}$ and mean total aboveground mass $\overline{w}$, on log-log coordinates. The straight line is fitted using Eq. (3.4) where θ and g_θ were 0.3857 and 2157 m $kg^{-\theta}$, respectively ($R^2 = 0.78$)

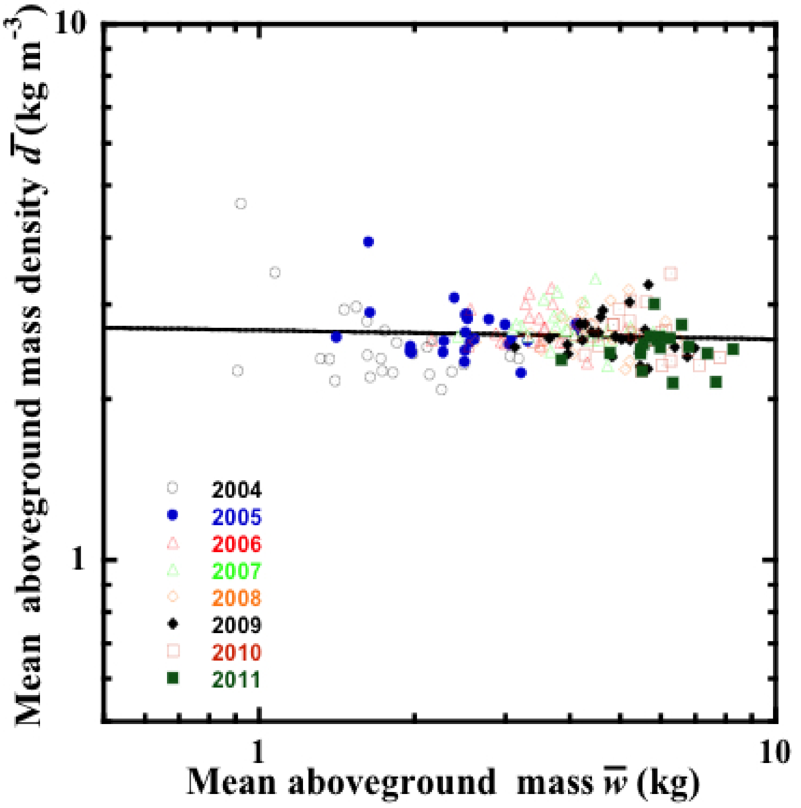

Figure 4.2: Allometric relationship between mean total aboveground mass density $\overline{d}$ and mean total aboveground mass $\overline{w}$, on log-log coordinates. The straight line is fitted using Eq. (3.5) where δ and g_δ were -0.01673 and 2157 m^{-3} kg$^{1-\delta}$, respectively ($R^2 = 0.0050$)

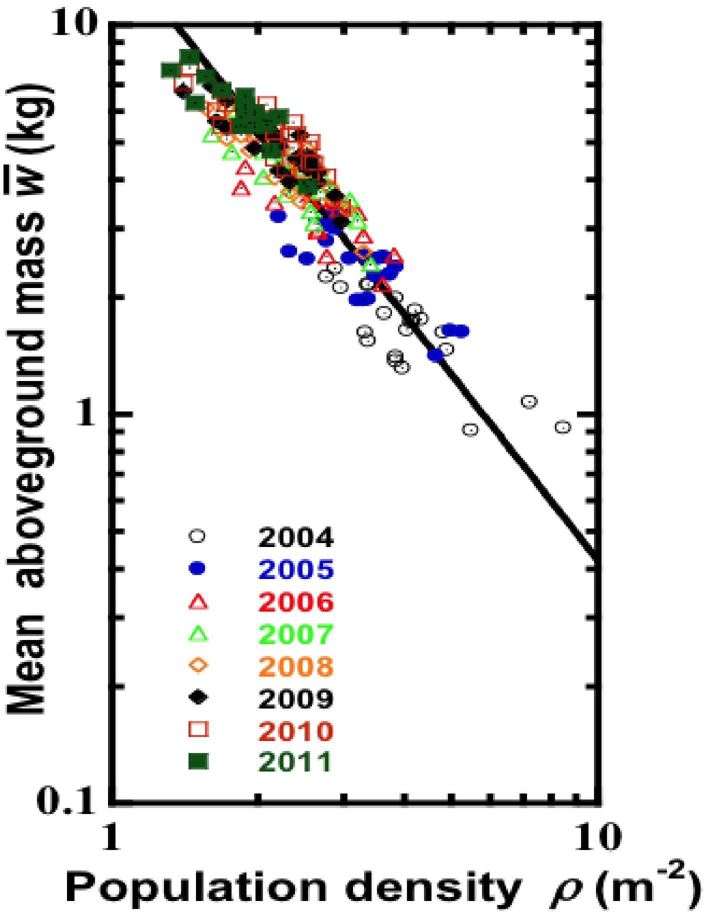

Figure 4.3: Scatter plot of mean total aboveground mass $\overline{w}$ against population density ρ on log-log coordinates. The straight line is given by Eq. (4.3) ($R^2 = 0.82$)

Chapter 5

Dynamics of aboveground mass hierarchy and stand structure in overcrowded mangrove *Kandelia obovata* stands

5.1 Introduction

When a population of plants first begins to grow, each individual may have access to all of the resources it needs to grow as fast as genetically possible in the environment (Hutchings and Budd, 1981). However, as time passes, plants continue to grow and begin to compete with each other for resources such as light and nutrients, smaller, weaker plants become dominated by larger, stronger plants, and eventually die (Lane and Prusinkiewicz, 2002). Such intense competition (simultaneous demand by two species or two individuals for an essential common resource that is actually or potentially in limited supply) within stands leads to self-thinning (Harper, 1977; Weiner and Thomas, 1992). The rule describes a relationship between size and density in even-aged plant populations that are crowded but actively growing. Self-thinning is the result of intraspecific competition in densely planted population. The response to density is the mortality of a fraction of the population and changes in the distribution of biomass among surviving members. It is considered as one of the most important plant demographic processes and has important implications for the ecology of overcrowded plant populations. Self-thinning is eventually accompanied by concomitant changes in the dynamics of stand structure over time. Stand structure describes the manner in which stand growth is distributed within the stand and is typically described by a number of parameters such as the size distribution of stems, the size variability of stems, the spatial distribution of stems, and the phenology of and variability in tree morphology. Self-thinning means that some individuals die, it's not random which plant die. As density and growth lead to self-thinning, the size and mass distribution of individuals within the population changes. The larger individuals (due to earlier germination, larger seed size, or other factors) capture more than equal resources and tend to grow more rapidly. A "Hierarchy" develops. The term hierarchy has different meanings in different disciplines, and this has contributed to confusion about its use by plant population biologists with reference to size frequency distributions (Weiner and Solbrig, 1984). Hierarchy is defined by the Shorter Oxford English Dictionary (Third Edition) as "a body of persons or things ranked in grades, orders or classes ... "(Weiner and Solbrig, 1984). This is consistent with the concept of aboveground mass hierarchy, size distribution, in which one ranks individuals and assigns them to successively larger size classes. In fact interaction among neighboring individualism populations lead to some inequalities specially size and aboveground mass (Yoda et al., 1963; Mohler at al., 1978; Kikuzawa, 1999). During the development of overcrowded monospecific stands, aboveground mass inequality generally increases over time until the onset of self-thinning (density decreases, whereas aboveground masses increases) due to the difference in growth rate between larger and smaller suppressed plants. Larger individuals are more likely to continue to live and have more offspring than smaller individuals. The inequality decreases as self-thinning progresses because of the higher mortality rates of smaller plants. The variation in individual aboveground mass strongly affects the structure of the stands. The relationship between mean aboveground mass and population density in self-thinning stands represents the process of quantitative relationships between mean mass and population density overtime, and it is essential for analyze the stand dynamics of overcrowded stands. Much interest about the changes in tree structure that accompanied the self-thinning has been focus on terrestrial forests (Mohler et al., 1978; Westoby and Howell, 1986; Weller, 1987; Weiner and Whigham, 1988; Ogawa and Hagihara, 2003; Benjamin and Hardwick, 1986; Kubota and Hara, 1996; Nagashima et al., 1995).

In Manko Wetland, Okinawa Island, *Kandelia obovata* (S., L.) is the most dominant mangrove species and the forest is closed in canopy. The importance of mangrove forests in the marine food web, role in stabilizing sediment and protecting shorelines against erosion and their utility to local human communities are now well recognized (e.g., Saenger, 2002). The Wetland constitutes an important transit point for shorebird whose migration route brings them along the Nansei Islands and has particular significance since it is located in an urban area. Therefore, study on the changes of stand aboveground mass hierarchy is an important step in planning the management and sustainable use of mangrove resources.

5.2 Materials and methods

5.2.1 Tree census and estimation of aboveground mass

See Chapter 4

5.2.2 Statistical analysis

After trees in a subplot were ranked in order of aboveground mass w for every year, Spearman's rank correlation coefficient r_s was calculated for the rank of w to evaluate the degree of concordance in rank among years in each subplot.

$$r_s = \frac{\sum_{i=1}^{N} (x_i - \overline{x})(y_i - \overline{y})}{\sqrt{\sum_{i=1}^{N} (x_i - \overline{x})^2 \sum_{i=1}^{N} (y_i - \overline{y})^2}} \tag{5.1}$$

where x_i and y_i are ranking of the i^{th} tree in the first and second years, first and third year year and so on respectively, $\overline{x}$ and $\overline{y}$ are respectively means of x and y, and N is the number of living trees among years. When r_s= +1, the ranks of trees are the same among years; when r_s = 0.0, the ranks of trees are completely different among years; and when r_s = -1, the ranks of trees are completely opposite among years. The value of r_s was obtained for each subplot for the first year to the second year, the first year to the third year, the first year to the fourth year, the first year to the fith year, the first year to the six year, the first year to the seventh year, the first year to the eighth year. In the calculation of r_s , dead trees were excluded.

The skewness b_1 of the frequency distribution of w in each subplot was also calculated over the study period.

$$b_1 = \frac{n}{(n-1)(n-2)} \sum_{i=1}^{N} \left(\frac{x_i - \overline{x}}{SD} \right) \tag{5.2}$$

where SD is the standard deviation of x_i , $\overline{x}$ is the mean, and n is the number of individuals.

Some researchers believe that skewness is the result of competition and reflect biologically important attribute. Weiner and Solbrig (1984) argued that skewness is misleading in that it only measures the asymmetry of the distribution without reflecting its spread. Thus, a population could have a highly skewed distribution while having very low relative variation. Knox et al. (1989) looked at the behavior of several of the summary statistics that have been used to describe size distributions, and found that measures of inequality provided robust indicators of density effects on growth and size-selective mortality.

If the b_1 value is positive, the frequency distribution is L-shaped; if the b_1 value is negative, the frequency distribution is J-shaped; and if the b_1 value is zero, the frequency distribution is bell-shaped.

5.3 Results

5.3.1 Aboveground mass hierarchy

As shown in Fig.5.1, Sperman's rank correlation coefficient r_s of aboveground mass w was calculated for the first year to the second year (open circles), third year (filled circles), fourth year (open triangles), fifth year (closed triangles), sixth year (open diamonds), seventh year (closed diamonds), and eighth year (open squares). The positive values of r_s did not significantly differ from zero ($P < 0.01$), but decreased significantly with increasing mean aboveground mass $\overline{w}$ ($r = 0.63$, $P < 0.01$). As shown in Fig.5.2, the rank of a tree was not completely constant and could change throughout its lifetime.

5.3.2 Frequency distribution of aboveground mass

Figure 5.3, depicts an example of the transition of the frequency distribution of w in a subplot. The trees that died during the ensuing year belonged to the lower classes of the frequency distribution (filled columns), which indicated that the smaller trees died as the stand continue to grow.

5.3.3 Skewness b_1 of w to its mean $\overline{w}$

Figures 5 .1 to 5.4 illustrate the relationship between the skewness b_1 of the frequency distribution of w to its mean $\overline{w}$. All the b_1 values of the frequency distribution of w were positive, indicating that the frequency distribution of w was L-shaped. The values of b_1 did not change significantly as the stand grew ($r = 0.13$, $P > 0.05$), which mean that the frequency of w is stable in the L-shape even if the stands grow.

5.3.4 Skewness b_1 of H and $D_{0.1\mathrm{H}}$ to their respective mean

Skewnesses b_1 frequency distribution of H and $D_{0.1\mathrm{H}}$ are shown in Fig. 5.5 and 5.6. Most of the b_1-values of H were negative (positive b_1-values were not significantly different from 0.0 at the significance level of 0.05), meaning that most of the frequency distributions of H is J-shaped though stands grow. Although the b_1-values of H tended to decrease, but the decrease trend was not significant ($r = -0.0036$, $P = 0.97$), and it indicates that the frequency distribution of H is almost stable with the J-shape even if stands grow. On the other hand, most of the b_1-values of $D_{0.1\mathrm{H}}$ were positive (all negative b_1-values were not significant different from 0.0 at the significance level of 0.05), indicating that most of the frequency distributions of $D_{0.1\mathrm{H}}$ were L-shaped. The b_1-value of $D_{0.1\mathrm{H}}$ did not significantly change with stand growth ($r = 0.103$, $P = 0.25$), which indicates that the frequency distribution of $D_{0.1\mathrm{H}}$ is stable with the L-shape even if stands grow.

5.4 Standard Deviation SD of H and $D_{0.1\mathrm{H}}$ to their respective mean

The standard deviation SD of H and $D_{0.1\mathrm{H}}$ were studied over the experimental periods. The SD of H decreased significantly by the vicinity of zero with stand growth ($r = -0.722$, $P = 2.28 \times 10^{-21}$), indicating that the variation of H becomes small as the stands grow, and finally all trees may have a similar height. On the other hand, SD of $D_{0.1H}$ was stable ($r = 0.093$, $P = 0.31$) as the stands grew. These results suggest that the size inequalities of H and $D_{0.1\mathrm{H}}$ become small as the stands grew.

5.5 Discussion

Kikuzawa (1988,1999) assumed that the rank of mass remains constant over time; however, our results suggested that the rank of mass can change as the stands grow, although values of sperman's rank correlation coefficient r_s of w significantly differed from zero as mentioned above. In fact, as illustrated in fig. 5.1, most of ranks of trees in w changed over the 8 years of study. These results suggest that the aboveground mass hierarchy of the overcrowded *K. obovata* stands was dynamic as the stand grew, although the changes were not dramatic.

The frequency distribution of w was retained as an L-shape throughout the study period. The mode of the frequency distribution shifted to the right each year, because the mortality of suppressed trees was high and the dominant trees continue to grow. Analuddin et al. (2009) also observed an L-shaped frequency distribution of w in overcrowded *K. obovata* stands. Similar results have also been reported for terrestrial plant populations for various species.(Begon et al., 2006).

All positive values of skewness of w show the frequency distribution of w is L-shaped, i.e. few large and many small individuals at the beginning (Fig. 5.3). It is said that the L-shaped frequency distribution of w is common among plant populations of various species. Therefore, the mortality or self-thinning in the overcrowded *K. obovata* stands occurs probably without changing the frequency distribution of w . Similar results were also reported for terrestrial plant populations (e.g., Koyama and Kira, 1956; Ogawa and Hagihara, 2003; cf. Harper, 1977; Silverstown and Charlesworth, 2001; Begon et al.,, 2006). Therefore, the L-shaped frequency distribution of w may be common among plant populations of various species.

Skewnesses b_1 of H and $D_{0.1\mathrm{H}}$ were almost stable with developing stands, i.e. the frequency distributions of H were keeping in J-shape as the stands grew, while the frequency distribution of D_0.1H was keeping in L-shape. These trends suggest that the mortality or self-thinning occurs in the crowded *K. obovata* stands without changing the frequency distributions of tree height and stem diameter. It was reported that skewness was reduced by the intensive self-thinning (e.g. Hara 1984).

5.6 Summary

The rank of tree was not completely constant and could change throughout its lifetime. That mean the aboveground mass hierarchy of the overcrowded mangrove *K. obovata* stands is dynamic as the stands grow, although the changes were not dramatic. All the positives value of skewness w show that the frequency distribution of is L-shaped, i.e. few large and many small small individuals. The mode of the frequency distribution shifted to the right each year, because the mortality of suppressed trees was high and the dominant trees continued to grow. Therefore, overcrowded stands were able to change stand structure, which might be a necessary mechanism for sustaining the overcrowded stands.

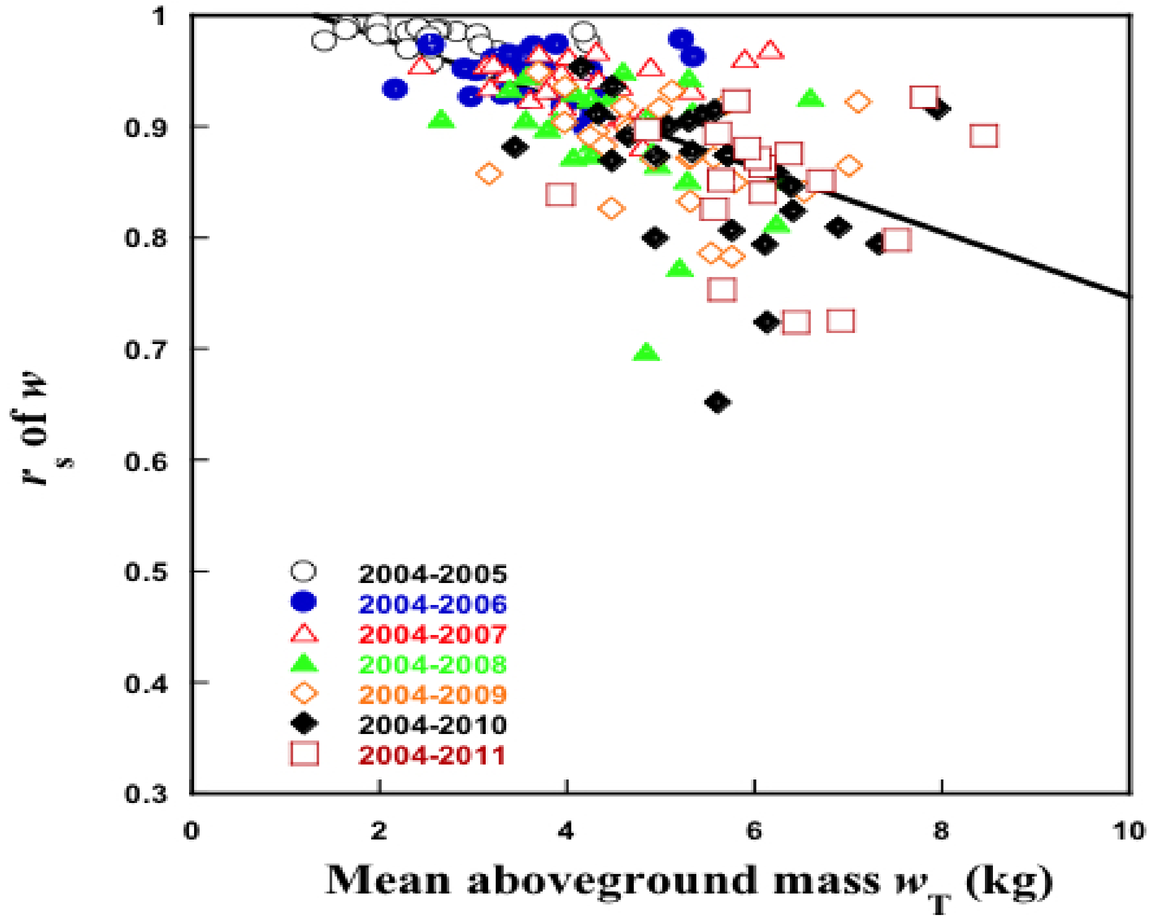

Figure 5.1: Relationship of Sperman's rank correlation coefficient r_s of aboveground mass w to mean aboveground mass $\overline{w}$. The straight line indicates the regression line ($r_s = 0.63$, $P<0.01$)

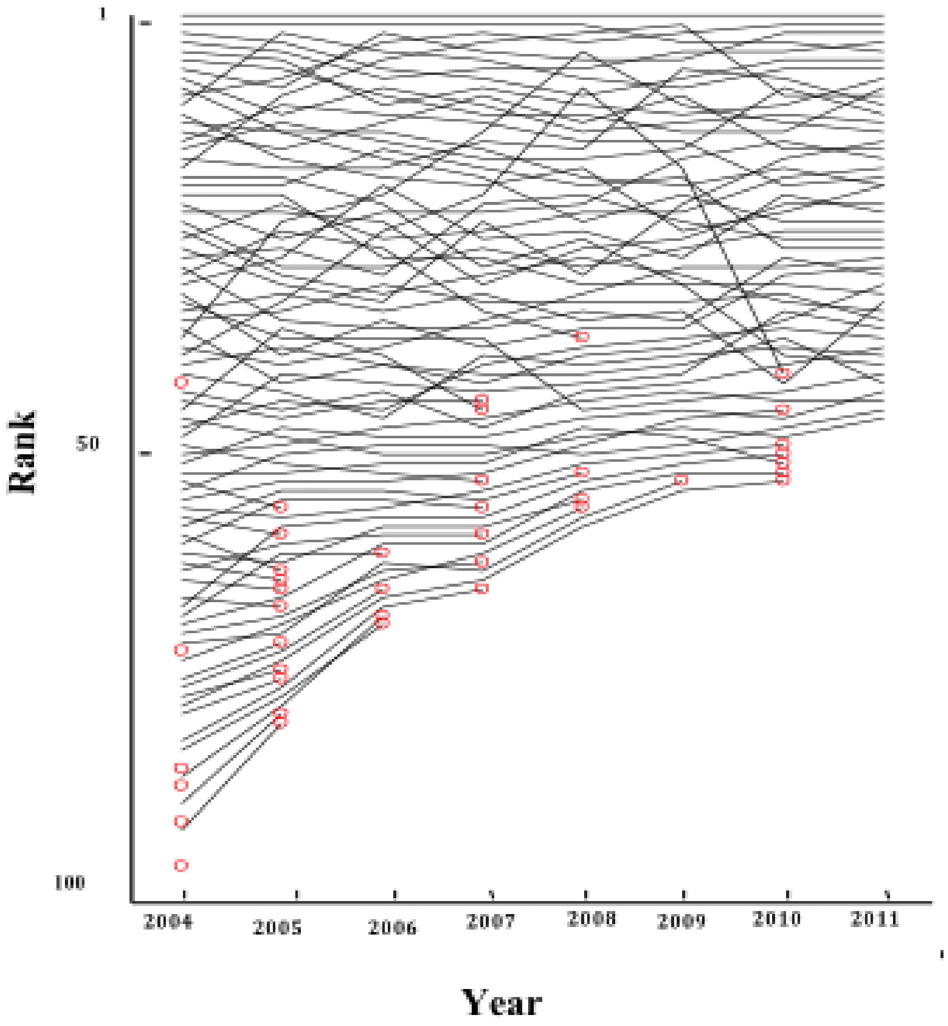

Figure 5.2: An example of the time trends of the rank in aboveground mass of trees in a subplot over 8 years. The open red circles are trees that died during the ensuing year.

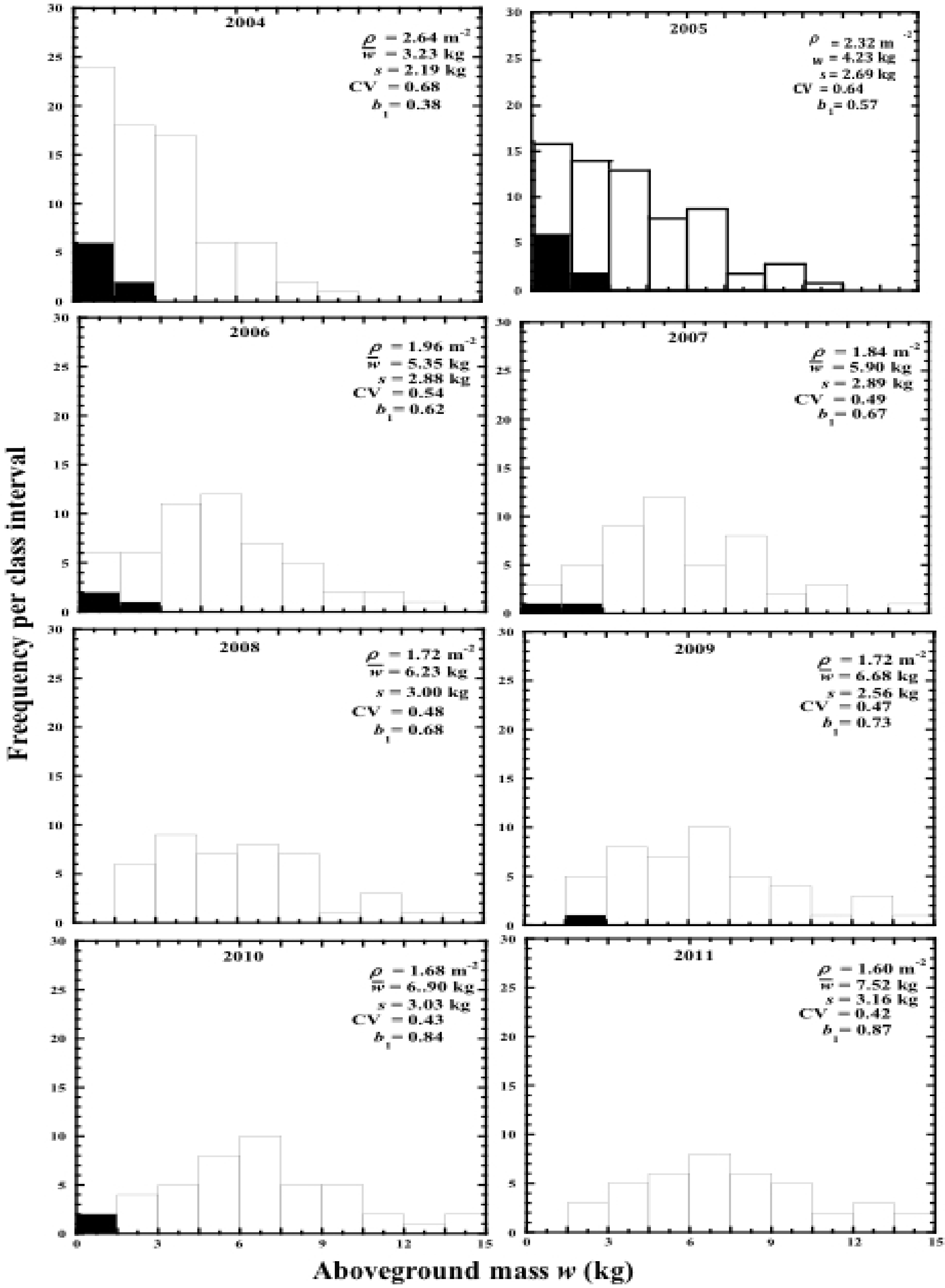

Figure 5.3: An example of the frequency distributions of aboveground mass $\overline{w}$ in a subplot over 8 years (2004-2011). Open columns, living trees; filled columns, trees that died during the ensuing year. ρ, population density; w, mean; s, standard deviation; CV, coefficient of variation ($= s/w$); b_1, skewness.

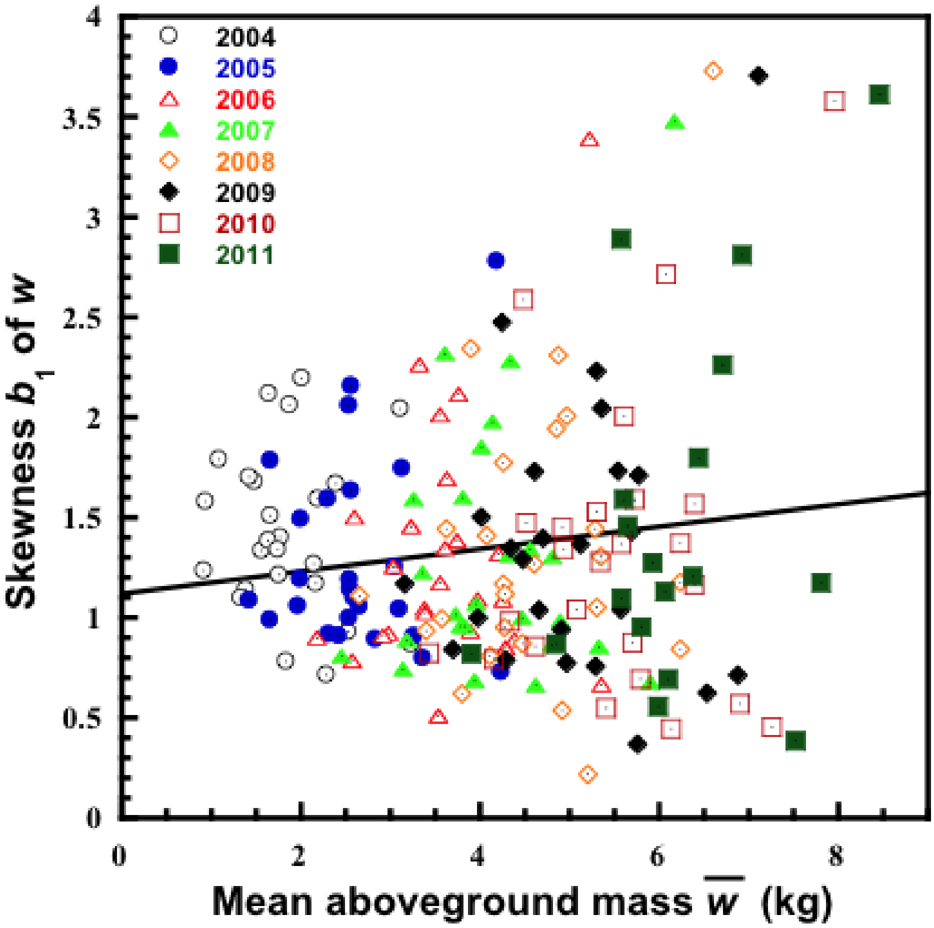

Figure 5.4: Relationship of skewness b_1 of the frequency distribution of aboveground mass w to its mean $\overline{w}$. Symbols are the same as in Fig. 5.1 The straight line shows the regression line ($r = 0.13$, P>0.05).

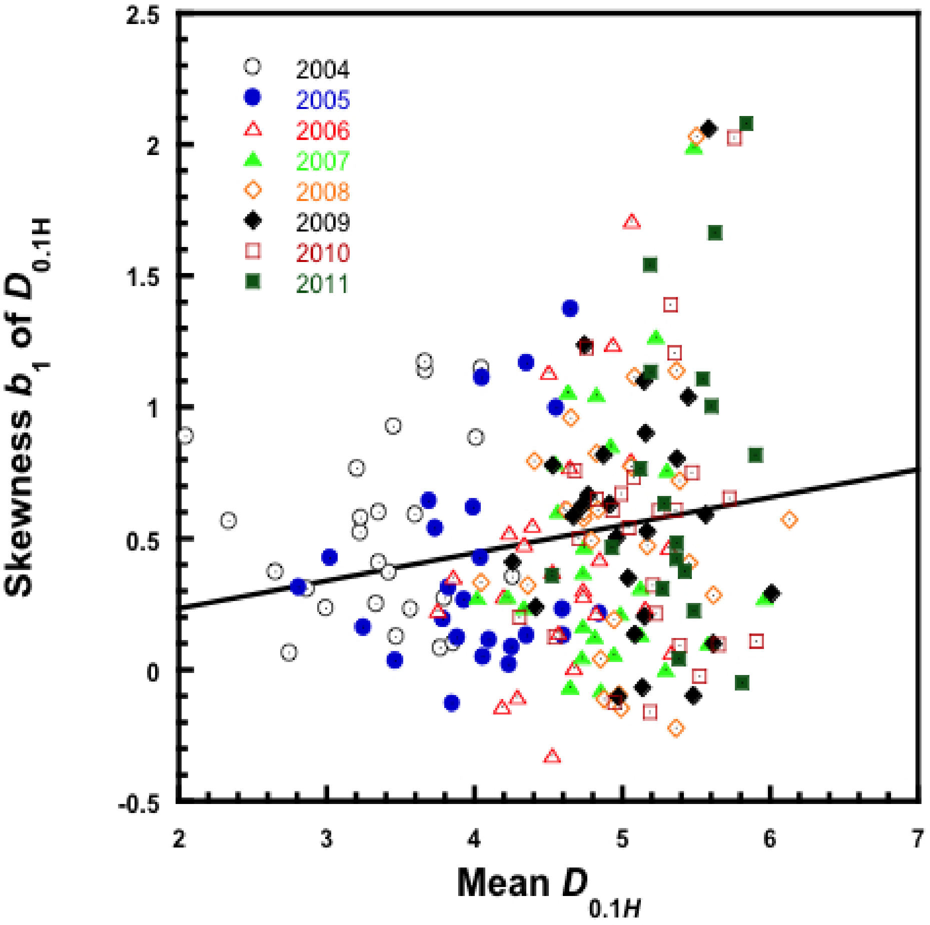

Figure 5.5: Relationship of skewness b_1 of stem diameter $D_{0.1\mathrm{H}}$ to its mean $\overline{D}_{0.1\mathrm{H}}$. Symbols are the same as in Fig. 5.1 The straight line shows the regression line ($r = 0.103$, $P = 0.25$).

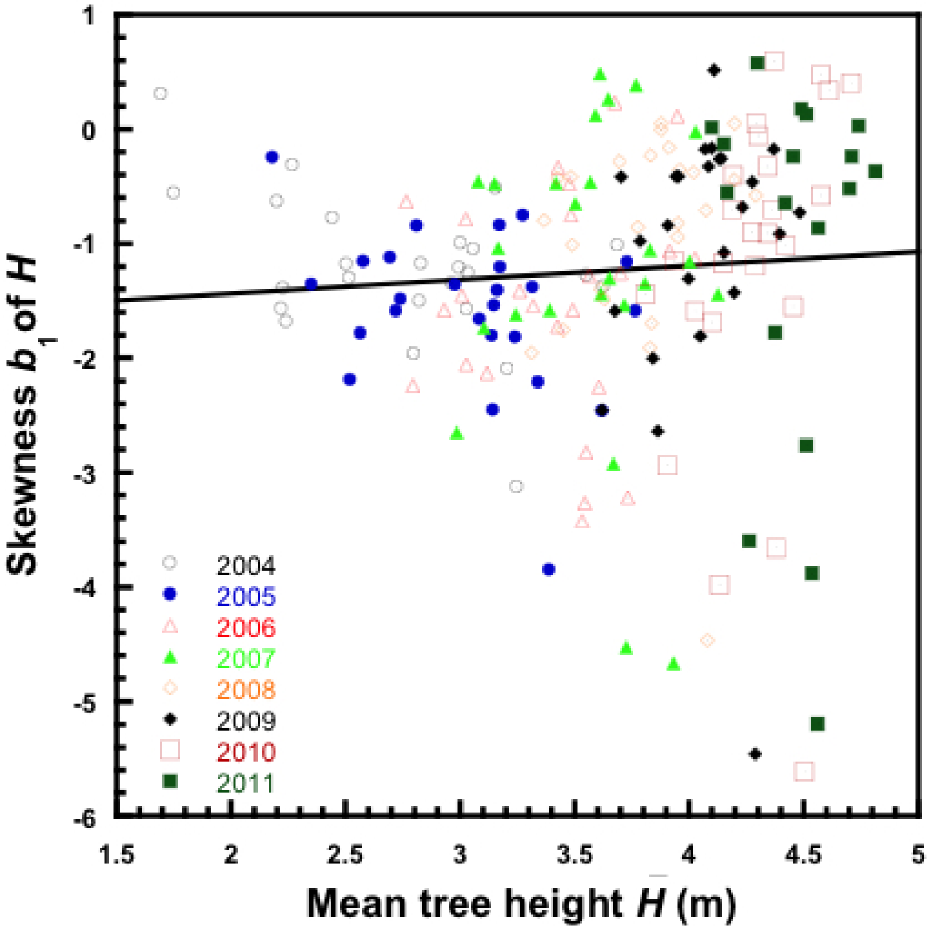

Figure 5.6: Relationship of skewness b_1 of tree height H to its mean $\overline{H}$. Symbols are the same as in Fig. 5.1 The straight line shows the regression line ($r = -0.0036, P = 0.97$).

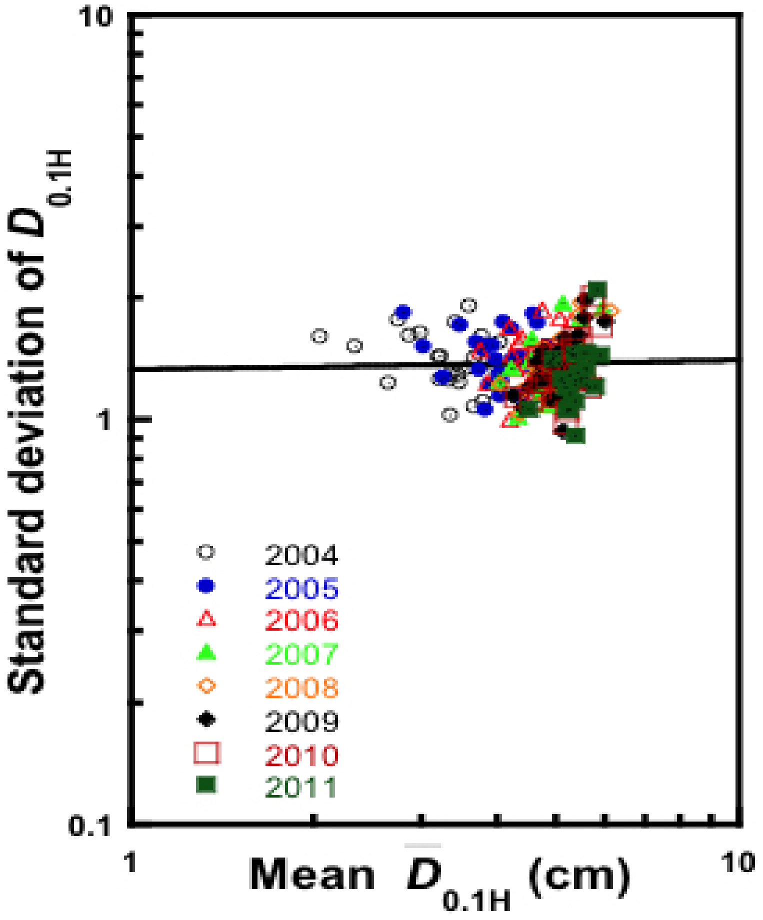

Figure 5.7: Relationship of standard deviation of stem diameter $D_{0.1\mathrm{H}}$ to its mean $\overline{D}_{0.1\mathrm{H}}$.

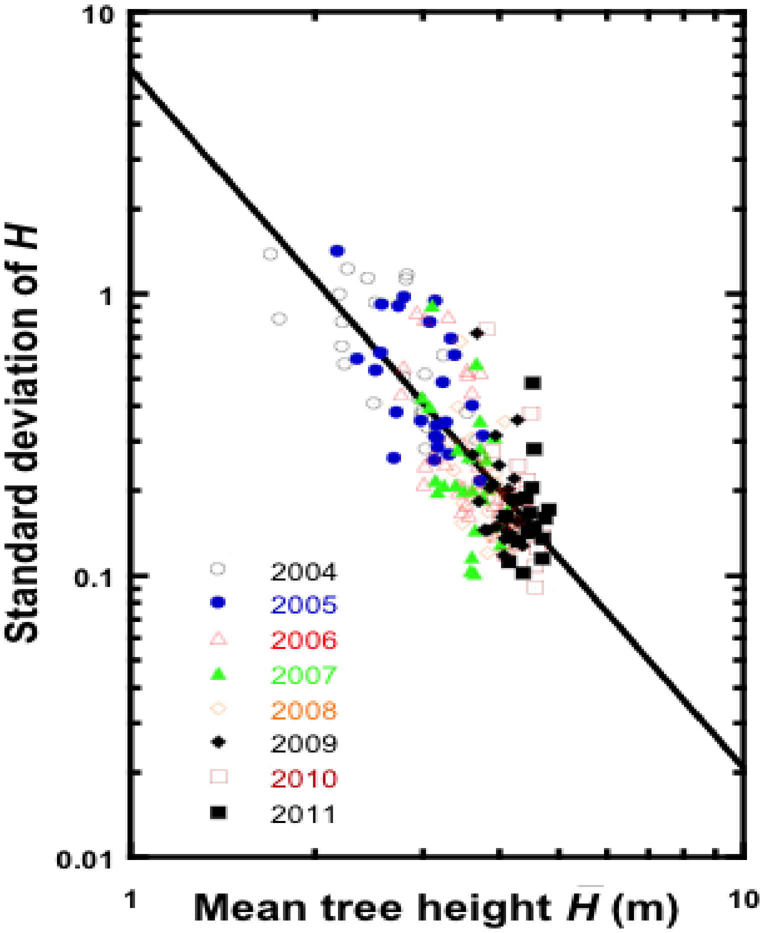

Figure 5.8: Relationship of standard deviation of tree height H to its mean $\overline{H}$.

Chapter 6

General Discussion and Conclusion

6.1 Discussion

Mortality or "thinning" is caused by the stresses of competition within the population, hence the term "Self-thinning". Yoda et al. (1963) proposed a $\overline{w} - \rho$ relationship, where mean mass $\overline{w}$ is a response variable and population density ρ is an explanatory variable, gives the self-thinning exponent α and multiplying factor K. The $\rho - \overline{w}$ relationship based on first assumption of Weller (1987), where ρ is a response variable and $\overline{w}$ is an explanatory variable, gives the self-thinning exponent α, calculated as $1/\phi$ and the multiplying factor $\left(\frac{1}{\mathrm{g}_\phi}\right)^{1/\phi}$, which are mathematically equivalent to the self-thinning exponent α and the multiplying factor K. The statistically estimated values of the self-thinning exponent and the multiplying factor based on Weller's second and third assumptions are just the same as the statistically estimated values of the self-thinning exponent $1/\alpha$ and the multiplying factor $\left(\frac{1}{\mathrm{g}_\phi}\right)^{1/\phi}$ based on the allometric model of $\rho - \overline{w}$ relationship. However, the estimator δ is dependent on the estimators ϕ and θ, which are independent of each other. Therefore, the significant test for the self-thinning exponent $1/\phi$ based on θ-values violates a statistical constraint. Nevertheless, the self-thinning exponent $1/\phi$ obtained from $\rho - \overline{w}$ can be used for a statistical test.

Applying Weller's allometric model for partial organs, self-thinning exponents, α_{x}, for organs in overcrowded *K. obovata* stands were examined. The model describes the allometric relationships of mean tree height $\overline{H}$ to mean mass $\overline{w}_{\mathrm{x}}$ of an organ "x" and of mean organ mass density $\overline{d}_{\mathrm{x}}$, i.e. how much $\overline{w}_{\mathrm{x}}$ is packed into the mean space occupied by a tree $\overline{s}$, to $\overline{w}_{\mathrm{x}}$. The value of $\overline{H}$ increased with $\overline{w}_{\mathrm{x}}$, showing that the allometric constants

θ_x between $\overline{H}$ and $\overline{w}_\mathrm{x}$ was 0.3801 ± 0.0187 (SE) for stem, 0.3464 ± 0.0174 for branch, 0.5386 ± 0.0249 for leaf, and 0.3812 ± 0.0187 for aboveground. The allometric constants δ_x between $\overline{d}_\mathrm{x}$ and $\overline{w}_\mathrm{x}$ was -0.0436 ± 0.0203 (SE) for stem, 0.0464 ± 0.0190 for branch, -0.4553 ± 0.0268 for leaf, and -0.0449 ± 0.0203 for aboveground. The δ_x-value was not significantly different from zero ($t = 2.153$, df = 166, $p = 0.032$) in stem, ($t = 2.441$, df = 166, $p = 0.015$) and in branch at a 1% significance level. On the other hand, the δ_x-value was significantly negatively correlated ($t = 17.01$, df = 166, $p = 3.221$ 10-38) in leaf, likely because the amount of space without leaves increased with increasing tree height. This decreasing trend of $\overline{d}_\mathrm{L}$ with increasing $\overline{w}_\mathrm{L}$ did not affect the trend of mean aboveground mass density $\overline{d}_\mathrm{T}$ with increasing mean aboveground mass $\overline{w}_\mathrm{T}$ (Fig. 4d), because leaf mass contributed only 4?8% of the total aboveground mass and the rest was contributed by woody organs. Therefore, the δ_x-value for aboveground did not significantly differ from zero ($t = 2.212$, df = 166, $p = 0.02827$). This constancy may be designated as constant mean mass density. Weller (1987b) assumed that biomass density $\overline{d}$ was constant regardless of $\overline{w}$, i.e., that δ was zero. Our study confirmed this assumption for aboveground mass only. Similar results were also found in *Pinus densiflora* Sieb. et Zucc. (Xue and Hagihara, 2012); however, in *Pinus tabulaeformis* Carr. And *Larix principis-rupprechtii* Mayr stands, Xue et al. (1999) reported that δ values for mean stem volume were significantly greater than zero. The average of $\overline{d}_\mathrm{T}$, aboveground biomass density (aboveground biomass/$\overline{H}$), 2.66 ± 0.02 kg m^{-3}, which is considerably higher than 1.3-1.5 kg m^{-3} that is observed in most terrestrial forests, except dwarf pine (*Pinus pumila* Rgel) forests that have considerably higher biomass densities of approximately 9.0 kg m^{-3} (Kira and shidei, 1967). This is because *K. obovata* trees growing near the northernmost limit of the species distribution are short, with a mean height ranging from 2.17 to 4.81 m; nevertheless, leaf mass can be large. Deshar et al. (2012) reported on Okinawa Island that the biomass density of *Bruguiera gymnorrhiza* stands was 2.40 ± 0.02 kg m^{-3}, which is similar to the value obtained for *K. obovata* stands. Mean mass $\overline{w}$ is a function of the population density ρ or the mean ground area occupied by a tree $\overline{s}$. Traditionally, plant ecologists have implicitly treated individual size as if it is determined by population density, plotting mass as a responses variable when depicting thinning relationships (Enquist et al., 1998, 2000). However, we should regard $\overline{s}$, or ρ, as a function of $\overline{w}$ instead of plotting $\overline{w}$ as a function of ρ, from the point of view of allometric scaling (Scmidt-Nielsen, 1984). In fact, Reineke

(1933), who first pointed out the quantitative relationship between population density ρ and tree size (DBH), regarded ρ as a function of DBH. Furthermore, Zeide (2010) emphasized that if mortality is driven by increasing volume, it would be more reasonable to consider volume as an independent variable and the number of trees as dependent. The $\rho - \overline{w}$ relationship where ρ is a response variable and mean mass $\overline{w}_{\mathrm{x}}$ as an explanatory variable, gives the self-thinning exponent α_{x}, i.e. $1/\phi$, which is mathematically and statistically (in terms of OLS) equivalent to $1/\left(1-(\delta+\theta)\right)$. The self-thinning exponent, $\alpha_{\mathrm{x}}\,(=1/(1-(\delta_{\mathrm{x}}+\theta_{\mathrm{x}})))$, was estimated to be 1.508 for stem, 1.646 for branch, 1.090 for leaf, and 1.507 for aboveground. The ϕ_L value for leaf was significantly different from 2/3 ($t = 7.015$, df = 166, $p = 5.543 \quad 10^{-11}$) and from 3/4 ($t = 4.676$, df = 166, $p = 6.013 \quad 10^{-6}$) but did not significantly differ from 1.0 ($t = 2.338$, df = 166, $p = 2.063 \quad 10^{-2}$); i.e., the self-thinning exponent for mean leaf mass was 1.0, confirming the constancy of leaf biomass for overcrowded *K. obovata* stands (i.e., $\overline{w}_L \cdot \rho \cong constant$). Our result is consistent with the finding of Deshar et al. (2012) who reported that leaf biomass was constant regardless of population density in *B. gymnorrhiza* stands. Sprugel (1984) and Osawa Kurachi (2004) also found a constant amount of leaf biomass per ground area in wave-regenerated *Abies balsamea* (L.) Mill. forests and in self-thinning stands of *Pinus banksiana* Lamb. and *Populus tremuloides* Michx, respectively. The allometric explanation of the self-thinning rule (Osawa and Allen, 1993; Osawa, 1995) was based on the assumption of constant leaf biomass. Hozumi et al. (1962) found that leaf biomass tends to reach constant values more rapidly than the biomass of woody organs at an early stage in *Hibiscus moscheutos* Linn. populations. Xue and Hagihara (2008) reconfirmed that constant final leaf biomass values occurred in overcrowded *Pinus densiflora* stands. Therefore, it can be postulated that predictable relationships between mean leaf mass and population density in overcrowded populations can be explained by the regulation and redistribution of a fixed amount of leaf biomass among a declining number of individuals. Leave don't thicken and the self-thinning process doesn't affect them.

The self-thinning exponent for leaf $\alpha_{\mathrm{L}}\,(=1/\phi_{\mathrm{L}})$ was 1.090, which was much lower than 3/2 and 4/3. This value was counterbalanced by self-thinning exponents of 1.508 for stem and 1.646 for branch. Together, these values resulted in a self-thinning exponent of 1.507 for aboveground. The overall variation in self-thinning exponents among *K. obovata* organs could be interpreted as a consequence of the ratio of the distribution of photosynthates to the organs. Deshar et al. (2012) also found the variation in the self-thinning exponents among *B. gymnorrhiza* organs. The results from our study indicate that the self-thinning exponent for stem was not significantly different from 3/2, which can be explained by the isometric growth of stems. The self-thinning exponent for branch was also not significantly different from 3/2. Branches near the bottom and inside the crown are shaded as new branches grow at the top, so that secondary, tertiary, and smaller branches are shaded. In overcrowded population, such self-shading may function to regulate the mass of branches so as to keep roughly the similarity of the mean branch volume per tree (Norberg, 1988). Mean stem, branch, and mean aboveground mass follow the 3/2 power law of self-thinning in overcrowded *K. obovata* stands because the effect of leaves on the self-thinning exponent for mean aboveground mass was negligible. The self-thinning exponent was 1.506 for aboveground, which was closer to 3/2 than to 4/3. Therefore, in terms of the present overcrowded *K. obovata* stands, self-thinning can be explained using the simple geometric model (Yoda et al., 1963), although whether the self-thinning exponent is 3/2 or 4/3 remains debatable.

The thinning process was accompanied by changes in in the stand structure during the study period. Kikuzawa (1988, 1989) assumed the rank of mass remain constant over time, but our results suggested that the rank of aboveground mass is changeable as the stand grow even though the changes were not dramatic. The frequency distribution of w was L-shaped and shifted to the right year by year due to the mortality of suppressed trees which was high and the dominant trees continued to grow. Similar result was also found in terrestrial plant population for various species (Begon et al., 2006).The frequency distributions of H kept a J-shape as the stands grew, while the frequency distribution of stem diameter was keeping an Lshape.

6.2 Conclusion

This study has examined the self-thinning rule in explaining the observed aboveground mass-density relationships in overcrowded mangrove forests and its effect on the stand structure. It shows that the slope of the thinning line is determined by the allometry between the area occupied by an individual and its mass following Weller's model. The intercept of the thinning line is complexly related to plant allometry, the mass density in occupied space, and the partitioning of contested areas among competing individuals.

The values of the self-thinning exponent $1/\phi$ and the multiplying factor $\left(1/\mathrm{g}_\phi\right)^{1/\phi}$ obtained from the allometric model are statistically different from those of the self-thinning exponent α and the multiplying factor K statistically obtained in the self-thinning equation, through $1/\phi$ and $\left(1/\mathrm{g}_\phi\right)^{1/\phi}$ in the allometric model are mathematically the same as α and K in the self-thinning equation.

Mean stem mass, branch mass, and mean aboveground mass follow the 3/2 power law of self-thinning in overcrowded *K. obovata* stands. The self-thinning exponent was 1.507 for aboveground, which was close to 3/2 rather than 4/3. Therefore, regarding the present overcrowded *K. obovata* stands, self-thinning can be explained using the simple geometric model, although whether the self-thinning exponent is 3/2 or 4/3 as proposed by Enquist et al. (1998, 2000) on the basis of the metabolic model (West et al., 1997) remains debatable.

All the positive values of skewness of $\overline{w}_\mathrm{T}$ showed that the frequency distribution of $\overline{w}_\mathrm{T}$ is L-shaped, i.e. few large and many small individual. But the mode of the frequency distribution shifted to the right year by year because the mortality of suppressed trees was high and the dominant continued to grow. It is said that the L-shaped frequency distribution of is common among plant populations of various species.

The results of this study have important implications for the importance of the self-thinning rule. it also support the Yoda et al' hypothesis and verify that the slopes and intercepts of thinning lines can be explained by the simple geometric model.

Bibliography

[1] Allen, J. A., Duke, N.C, "Bruguiera gymnorrhiza (large-leafed mangrove), Species profiles forPacific Island Agroforestry,"Available source: www.traditionaltree.org, 2006.

[2] Alongi, D. M, "The dynamics of benthic nutrients pools and fluxes in tropical mangrove forests," J Mar Res, vol. 54, pp. 123-148, 1996.

[3] Alongi, D. M, "Present status and future of the world?s mangrove forests," Environ Conserv, vol. 9, pp. 331-349, 2002.

[4] Analuddin, K., Suwa, R., Hagihara, A, "The self-thinning process in mangrove *Kandelia obovata*," J Plant Res, vol. 122, pp. 53-59, 2009.

[5] Barkhman, J.P, "Pedunculate oak woodland in a severe environment: Black Tor Copse, Dartmoor," J Ecol Res, vol. 66, pp. 707-740, 1978.

[6] Begon, M., Townsend, C.R., Harper, J.H, "Ecology: From individuals to Ecosystems," Fourth ed., Blackwell, Oxford, 2006.

[7] Benjamen, L.R., Hardwick, R.C, "Sources of variation and measures of variability in even-aged stands of plants," Ann Bot, vol. 78, pp. 757-778, 1986.

[8] Berger, U., Hildenbrandt, H., Grimm, V, "A new approach to spatiality explicit modeling of forest dynamics: spacing, aging and neighborhood competition of mangrove trees," Ecol Model, vol. 132, pp. 287-302, 2000.

[9] Berger, U., Hildenbrandt, H, "The strength of competition among individual trees and the biomass-density trajectories of the cohort," Plant Ecol, vol. 167, pp. 89-96, 2003.

[10] Berger, U., Hildenbrandt, H., Grimm, V, "Age-related decline in forest production: modeling the effects of growth limitation, neighborhood competition and self-thinning," J Ecol, vol. 92, pp. 846-853, 2004.

[11] Berger, U., Piou, C., Schiffers, K., Grimm, V, "Competition among plants: concepts, individual-based modeling approaches, and a proposal for a future research strategy," Perspect Plant Ecol Evol Syst, vol. 9, pp. 121-135, 2008.

[12] Boto, K.G., Bunt, J.S, "Carbon export from mangroves. In: Clough, B.F (ed.). Mangrove Ecosystems in Australia," ANU Pres, Canberra, pp. 239-257, 1982.

[13] Brown, J.H., Sibly, R.M, "The metabolic theory of ecology and its central equation, In: R.M. Sibly, J.H. Brown,(eds) Metabolic Ecology: A scaling approach" Wiley-Blackwell, Oxford, pp. 21-33, 2012.

[14] Coomes, D.A., Allen, R.B, "Mortality and tree-size distributions in natural mixed-age forests," J Ecol, vol. 95, pp. 27-40, 2007.

[15] Chen, K., Kang, H.M., Bai, J., Fang, X.W., Wang, G, "Relationship between the virtual dynamic thinning line and the self-thinning boundary line in simulated plant populations," J Integra Plant Biol, vol. 50, pp. 280-290, 2008.

[16] Dai, X., Jia, X., Zhang, W., Bai, Y., Zhang, J., Wang, Y., Wang, G,"Plant height-crown radius and canopy coverage-density relationships determine above-ground biomass-density relationship in stressful environments," Biol Lett, vol. 5, pp. 571-573, 2009.

[17] Deshar, R., Sharma, S., Mouctar, K., Wu, Min., Hoque, A.T.M., Hagihara, A," Self-thinning exponents for partial organs in overcrowded mangrove *Bruguiera gymnorrhiza* stands on Okinawa Island, Japan," For Ecol Manage, vol. 278, pp. 146-154, 2012.

[18] Drew, R., Flewlling, J.W,"Some recent theories in in yield-density relationship and their application to *Monterey pine* plantations," For Sci, vol. 25, pp. 517-534, 1977.

[19] Drew, R., Flewlling, J.W,"Stand density management: an alternative approach and its application to *Douglas-fir* plantations," For Sci, vol. 25, pp. 518-532, 1979.

[20] Ellison, A. M., "Morphological determinants of self-thinning in plant monocultures and a proposal concerning the role of self-thinning in plant evolution," Oikos, vol. 279, pp. 148-150, 1989.

[21] Enquist, B. J., West, G.B., Brown, J. H, "Quarter-power allometric scaling in vascular plants: functional basis and ecological consequences. In: Brown, J.H., West, G.B, (eds) Scaling Biology ," Oxford University Press, Oxford, pp. 167-198, 2000.

[22] Enquist, B.J., Brown, J.H., West, G.B,"Allometric scaling of plant energetics and population density," Nature, vol. 395, pp. 163-165, 1998.

[23] Falik, O., Reides, P., Gersani, M., Novoplansky, A., "Self/non-self discrimination in roots,"J Ecol, vol. 91, pp. 525-531, 2003.

[24] Franklin, O., Kentaro, A., Rupert, S., "A generic model of thinning and stand density effects on forest growth, mortality and net increment," Ann. For. Sci, vol. 66, pp. 815, 2009.

[25] Gillooly, J.F, "Effects of size and temperature on metabolic rate," Science, vol. 293, pp. 2248-2251, 2001.

[26] Gorham, E., "Shoot height, weight and standing crop in relation to density of monospecific plant stands," Nature, vol. 54, pp. 287-293, 1979.

[27] Hara, T., "A stochastic model and the moment dynamics of the growth and size distribution in plant populations," J Theor Biol, vol. 109, pp. 173-193, 1984.

[28] Hagihara, A, "Time-trajectory of mean phytomass and density in self-thinning plant populations," Bull Fac Sci, University of the Ryukyus vol. 70, pp. 99-112, 2000.

[29] Hagihara, A, "Deriving the mean mass?density trajectory by reconciling the competition?density effect law with the self-thinning law in even-aged pure stands," J For Res, vol. 19, pp. 125-133, 2014.

[30] Hamilton, N.R.S., Matthew, C., Lemaire, G.,"In defense of the -3/2 boundary rule: A re-evaluation of the self-thinning concepts and status," Ann Bot, vol. 76, pp. 569-577, 1995.

[31] Hamilton, N.R.S., Mattew, C., Lemaire, G., "A Re-evaluation of the Self-thinning Concepts and Status," Ann Bot, vol. 76, pp. 569-577, 1995.

[32] Han, W.X., Fang, J.Y., "Self-thinning law in plant populations: -3/2 vs -4/3," Acta Scientiarum Naturalium Universitatics Pekinensi, vol. 44, pp. 661-668, 2008.

[33] Harper, J. L, "Population biology of plants, "Academic Press,London, 1977.

[34] Holzapfel, C., Alpert, P., "Root cooperation in a clona plant: connected strawberries segregate roots," Ecological vol. 134, pp. 72-77, 2003.

[35] Hozumi, K., " Interactions among higher plants," Kyoritsu Shuppan, Tokyo (In Japanese)

[36] Hozumi, k, "Ecological and mathematical considerations on self-thinning in even aged pure stands. I mean plant weight-density trajectory during the course of self-thinning," Bot Mag Tokyo, vol. 90, pp. 65-179, 1977.

[37] Hozumi, k., Shinozaki, K., Kira, T, "Effects of light intensity and planting density on the growth of *Hibiscus moscheutos* Linn III. Analysis of leaf growth based on the logistic theory," Physiol Ecol vol. 11, pp. 62-77, 1962.

[38] Hutchings, M.J., Budd, C.S, "Plant competition and its course through time," Bioscience, vol. 31, pp. 640-645, 1981.

[39] Hutchings, M.J, "Ecology's law in search of a theory," New Sci, vol. 98, pp. 765-767, 1983.

[40] Kamara, M., Deshar, R., Sharma, S., Kamruzzaman, M.D., Hagihara, A, "Self-thinning exponents in overcrowded stands of the mangrove *Kandeli obovata*, on Okinawa Island, Japan," J Oceanogr, vol. 68, pp. 851-856, 2012.

[41] Kathiresan, K., Bingham, B.L, "Biology of mangroves and mangrove ecosystems," Adv Mar Biol, vol. 40, pp. 81-251, 2001.

[42] Keeley, E.R, "An experimental analysis of self-thinning in juvenile steelhead trout," Oikos, vol. 102, pp. 543-550, 2003.

[43] Khan, M.N.I., Suwa, R., Hagihara, A, "Carbon and nitrogen pools in mangrove stand of *Kandelia obovata* (S., L.) Yong: vertical distribution in the soil-vegetation system," Wtl Ecol Manag, vol. 15, pp. 141-153, 2007.

[44] Khan, M.N.I., Suwa, R., Hagihara, A, "Biomass and aboveground net primary production in a subtropical mangrove stand of *Kandelia obovata* (S., L.) Yong at Manko Wetlands," Wtl Ecol Manag, vol. 17, pp. 585-599, 2009.

[45] Khan, M.N.I., Suwa, R., Hagihara, A., "Allometric relationships for estimating the aboveground phytomass and leaf area mangrove *Kandelia candel* (L.) Druce trees in Manko Wetland, Okinawa Island, Japan," Trees, vol. 19, pp. 266-272, 2005.

[46] Kikuzawa, K., "Theoretical relationships between mean plant size, size distribution and self-thinning under one-side competition," Ann Bot, vol. 83, pp. 11-18, 1999.

[47] Kikuzawa, K., "Self-thinning and B-pint line yield-density disgram in a young birch stand," For Ecol Manage, vol. 58, pp. 287-298, 1993.

[48] Kikuzawa, K., "Intraspecific competition in a natural stand of *Betula ermanii*," Ann. Bot, vol. 61, pp. 727-734, 1988.

[49] Kira, T., "A climatological interpretation of Japanese vegetation zones. In: Tuxen R, editors. Vegetation Science and environmental protection," Tokyo: Maruzen, pp. 21-30, 1977.

[50] Kira, T, "Forest ecosystems of east and southeast Asia in a global perspective, "Ecol Res, vol. 6, pp. 185-200, 1991.

[51] Kira, T., Shidei, T, "Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific" Jpn J Ecol, vol. 17, pp. 70-87, 1967.

[52] Knox, R.G., Peet, R.K., Christiensen, N.L., "Population dynamics in loblolly pine stands: changes in skewness and size inequality," Ecology, vol. 70, pp. 1153-1166, 1989.

[53] Koyama, H., Kira, T., "Intraspecific competition among higher plants. Frequency distribution of individual plant weight as affected by the interaction between plants," J Inst Polytech, Osaka University, vol. 58, pp. 73-94, 1956.

[54] Kubota, Y., Hara, T., "Allometry and competition between saplings of *Picea jezoensis* and *Abies sachalinensis* in a sub-boreal coniferous forest, northern Japan," Ann bot, vol. 77, pp. 529-537, 1996.

[55] Lane, B., Prusinkiewicz, P., "Generating spatial distributions for multilevel models of plant communities," In Proceedings of graphics interface 2002: Calgary, Alberta, Canada,pp. 69-80, 2002.

[56] Lonsdale, W.M., Watkinson, A.R, "Plant geometry and self-thinning," J Ecol, vol. 71, pp. 285-297, 1983.

[57] Lonsdale, W. M., "The self-thinning rule: dead or alive," Ecology, vol. 71 pp. 1373-1388, 1990.

[58] Long, J.N., Smith, F.W, "Relation between size and density in developing stands: a description and possible mechanisms," For Ecol Manage, vol. 7, pp. 191-206, 1984.

[59] Lugo, A.C., Snedaker, S.C, "The ecology of mangroves," Ann Rev Ecol Sys, vol. 5, pp. 39-64, 1975.

[60] Manson, F.J., Loneragan, N.R., Skilleter, G.A., Phinn, S.R.,, "An evaluation of the evidence for linkages between mangroves and fisheries: A synthesis of the literature and identification of research directions," Oceanogr Mar Biol Ann Rev, vol. 43, pp. 483-513, 2005b.

[61] Marcelis, L.F.M., Heuvelink, E., Baan Hofman-Eijer, L.R., Bakker, J.D., Xue, L.B., "Flower and fruit abortion in sweet pepper in relation to source and sink strength ," J Expr Bot, vol. 55, pp. 2261-2268, 2004.

[62] McCarthy, J.W., Weetman, G, "Self-thinning dynamics in a balsam fir (*Abies balsamea* (L.) Mill.) insect-mediated boreal forest chronosequence," For. Ecol. Manage, vol. 241, pp. 295-309, 2007.

[63] Miyanishi, K., Hoy, A., Cavers, P.B., "A Generalized law of self-thinning in plant populations ", J Theor Biol, vol. 78, pp. 439-442, 1979.

[64] Mohler, C.L., Marks, P.L., Sprugel, D.G., "Stand structure and allometry of trees during self-thinning of pure stands," J Ecol. Manage, vol. 66, pp. 599-614, 1978.

[65] Morris, E.C, "Self-thinning line differ with fertility level," Ecol Res, vol. 17, pp. 17-28, 2002.

[66] Moris, E.C., "How does fertility of the substrate affect intraspecific competition? Evidence and synthesis from self-thinning," Ecol Res, vol. 18, pp. 287-305, 2003.

[67] Nagashima, H., Terashima, I., Katoh, S., "Effects of plant density on frequency distributions of plant height in *Chenopodium album* stands: analysis based on continuous monitoring of height growth of individual plants," Ann Bot, vol. 75, pp. 173-180, 1995.

[68] Niklas, K.J., Midgley, J.J., Enquist, B.J, "A general model for mass growth density relations across tree-dominated communities," Evol Eco Res , vol. 5, pp. 459-468, 2003.

[69] Niklas, k.J., "Plant allometry: The scaling process," Univ Chicago Press, 1994.

[70] Norberg, R.A, "Theory of growth geometry of plants and self-thinning of plant population: geometric similarity, elastic similarity, and different growth modes of plants parts," Am Nat, vol. 131, pp. 220-256, 1988.

[71] Novoplansky, A., "Picking battles wisely: plant behavior under competition," Plant Cell Envion, vol. 32, pp. 726-741, 2009.

[72] O'Brien, E.E., Gersani, M., Brown, J.S.,"Root proliferation and seed yield in response to spatial heterogeneity of below-ground competition ," New Physiol, vol. 168, pp. 401-412, 2005.

[73] Ogawa, K., Hagihara, A, "Self-thinning and size variation in a sugi (*Cryptomeria japonica* D. Don) plantation," For Ecol Manage, vol. 174, pp. 413-421, 2003.

[74] Osawa, A, "Inverse relationship of crown fractal dimension to self-thinning exponent of tree populations: a hypothesis," Can J For Res, vol. 25, pp. 1608-1617, 1995.

[75] Osawa, A., Allen, R.B, "Allometric theory explains self-thinning relationships of mountain beech and red pine" Ecology, vol. 74, pp. 1020-1032, 1993.

[76] Osawa, A., Kurachi, N, "Spatial leaf distribution and self-thinning exponent of *Pinus banksiana* and *Populus tremuloides*," Trees, vol. 18, pp. 327-228, 2004.

[77] Pickard, W.F, "Three interpretations of self-thinning rule," Ann Bot, vol. 51, pp. 749-757, 1983.

[78] Pittman, S.D., Turnblom, E.C, "A study of Self-thinning using coupled allometric equations: implication for coastal *Douglas-fir* and stand dynamics," Can J For Res vol. 33, pp. 1661-1669, 2003.

[79] Pretzsch, H., "Species-specific allometric scaling under self-thinning: evidence from long-term plots in forest stands," Ecologica, vol. 146, pp. 572-583, 1988.

[80] Reineke, L.H., "Perfecting a stand-density index for even-aged forests," J Agric Res, vol. 46, pp. 749-757, 1933.

[81] Reynolds, J.H., Fords, E.D., "Improving competition representation in theoretical models of self- thinning: a critical review," J Ecol, vol. 93, pp. 362-372, 2005.

[82] RIS, "Information sheet on Ramsar Wetlands (RIS). In: A Directory Of Wetlands of International importance," Ramsar site data base $http://www.wetlands.org/reports/ris/2J011.en.pdf$, Accessed 23 apr 2013.

[83] Riveros, A.J., Enquist, B.J, "Metabolic scaling in insects support the predictions of the WBE model. J. Insect," J Insect Physiol, vol. 57, pp. 688-693, 2011.

[84] Roderick, M.L., Barnes, B, "Self-thinning plant populations from a dynamic viewpoint," Funct Ecol, vol. 18, pp. 197-203, 2004.

[85] Saenger, P., "Mangrove ecology, silviculture and conservation," Academic Publishers, Dordrecht, 360 pp. 2002.

[86] Sachs, T., Novoplansky, A., "What does aclonal organization suggest concern-ing clonal plants In: de Kroom, H., van Groenendael, J. (Eds.), The Ecology andEvolution of Clonal Growth in Plants," SPB Academic Publishing, Leinden, the Netherlands, pp. 55?78, 1997.

[87] Sachs, T., Novoplansky, A., "Tree form: architectural models do not suffice," Israel J Plant Sci, vol. 43, pp. 203-212, 1995.

[88] Schmidt-Nielsen, K, "Scaling: Why is Animal Size Importance," Cambridge University Press, Cambridge, 1984.

[89] Semchenko, M., John, E.A., Hutchings, M.J.,"Effect of physical connection and genetic identity of neighboring ramets on root placement patterns in two clonal species ," New Physiol, vol. 176, pp. 644-654, 2007b.

[90] Sheue, C.R., Lui, H.Y.,Yong, J.W.H.,"*Kandelia obovata* (Rhizophoraceae), a new mangrove species from Eastern Asia," Taxon, vol. 57, pp. 287-294, 2003b.

[91] Sibomana, C., Jia, X., Qui, Y.P., Wang, X., "Self-thinning in a space-limited rocky intertidal barnacle system," Ann Zool Fennici, vol. 50, pp. 64-70, 2013.

[92] Silverstown, J.W., Charlesworth, D, "Introduction to Plant Population Biology," Blackwell, Oxford, 2001.

[93] Spalding, M., Kainuma, M., Collins, "World Atlas of Mangroves," Earthscan Publications, London, pp. 1-261, 2010.

[94] Sprugel, D.G, "Density, biomass, productivity, and nutrient-cycling changes during stand development in wave-regenerated *Balsam fir* forests," Ecol Monogr, vol. 54, pp. 165-186, 1984.

[95] Suwa, R., Hagihara, A, "Seasonal changes in canopy photosynthesis and foliage respiration in a *Rhizophora stylosa* stand at the northern limit of its natural distribution," Wetlands Ecol Manage, vol. 16, pp. 313-321, 2008.

[96] Suwa, R., Deshar, R., Hagihara, A, "Forest structure of a subtropical mangrove along a river inferred from potential tree height and biomass," Aquat Bot, vol. 91, pp. 99-104, 2009.

[97] Thomas, S.C., Weiner, J., "Growth, death and size distribution change in an *Impatiens pallida* population," J Ecol, vol. 77, pp. 524-536, 1989b.

[98] Tomilson, P.B., "The botany of mangroves," Cambridge Univ Press, pp. 413, 1986.

[99] Twilley, R.R., "Properties of mangroves ecosystems and their relation to the energy signature of coastal environments.," In: Hall C. A. S. (Ed.). Maximum Power: The ideas and applications of H. T. Odum. Colorado Press, Colorado, pp. 43-62.

[100] Weller, D.E, "A reevaluation of the -3/2 power rule of plant self-thinning," Ecol Monogr, vol. 57, pp. 23-43, 1987a.

[101] Weller, D.E, "Self-thinning exponent correlated with allometric measures of plant geometry," Ecology, vol. 68, pp. 813-821, 1987b.

[102] Weiner, J., Solbrig, O.T., "The meaning and definition of size hierarchies in plant population," Oecologica, vol. 61, pp. 334-336, 1984.

[103] Weiner, J., Thomas, S.C., "Competition and allometry in three species of annual plants," Ecology, vol. 73, pp. 648-656, 1992.

[104] Weiner, J., Whigham, D.F, "Size variability and competition in plant monocultures," Oikos, vol. 47, pp. 211-222, 1988.

[105] Westoby, M, "The self-thinning rule," Adv Ecol Res, vol. 14, pp. 167-225, 1984.

[106] Westoby, M., Howell, J, "Influence of population structure on self-thinning of plant populations," J Ecol, vol. 74, pp. 343-359, 1986.

[107] Westoby, M., "The place of the self-thinning rule in population dynamic," Amer Nat, vol. 118, pp. 581-587, 1981.

[108] Westoby, M., "Self-thinning in *Trifolium subterraneum* not affected by cultivar shape," Aust J Ecol, vol. 1, pp. 245-247, 1976.

[109] West, G.B., Brown, J.H., Enquist, B.J., "A general model for the origin of allometric scaling laws in biology," Science, vol. 276, pp. 122-126, 1997.

[110] West, G.B., Brown, J.H., Enquist, B.J., "A general model for the structure and allometry of plant vascular systems," Nature, vol. 400, pp. 664-667, 1999a.

[111] West, G.B., Brown, J.H., Enquist, B.J., "The fourth dimension of life:fractal geometry and allometric scaling of organism," Science, vol. 284, pp. 1677-1679, 1999b.

[112] White, J, "The allometric interpretation of self-thinning rule," J Theor Biol, vol. 89 pp. 475-500, 1981.

[113] White, J., Harper, J.L., "Correlated changes in plant size and number in plant populations," J Ecol, vol. 58, pp. 467-485, 1970.

[114] White, J., "Demographic factors in populations of plants," In: Solbrig, O.T., (EDS), Demography and Evolution in Plant Populations, University of California Press Berkeley, California, US, 1981.

[115] Xue, L., Hagihara, A, "Density effect on organs in self-thinning *Pinus densiflora* Sieb & Zucc. stands," Ecol Res, vol. 23 pp. 689-695, 2008.

[116] Xue, L., Hagihara, A, "Self-thinning lines of organs and aboveground parts based on the allometric relationships in overcrowded *Pinus densiflora* stands," Ecol Res, vol. 27 pp. 15-21, 2012.

[117] Xue, L., Ogawa, K., Hagihara, A., Liang, S., Bai, J, "Self-thinning exponents based on the allometric model in Chinese Pine (*Pinus tabulaeformis* Carr.) and Prince Rupprecht's larch (*Larix principis-rupprechtii* Mayr) stands," For Ecol Manage, vol. 117 pp. 87-93, 1999.

[118] Yoda, K., Kira, T., Ogawa, H., Hozumi, K, "Self-thinning in overcrowded pure stands under cultivated and natural condition. (Intraspecific competition among higher plants)," J Biol Osaka City Univ, vol. 14 pp. 107-129, 1963.

[119] Zeide, B, "Tolerance and self-tolerance of trees," For Ecol Manage, vol. 13 pp. 149-166, 1985.

[120] Zeide, B, "Analysis of the 3/2 power law of self-thinning," For Sci, vol. 33 pp. 517-537, 1987.

[121] Zhang, J., Oliver, W.W., Ritchie, M.W, "Effect of stand densities on stand dynamics in white fir (*Abies con color*) forests in northeast California, USA," For Ecol Manage, vol. 244 pp. 50-59, 1985.

Appendix

Example of last two years censuses data (2010 and 2011). H, tree height; H_L, height of the lowest living leaf; $D_{0.1H}$, stem diameter at $H/10$; R_1, maximum crown length; R_2 crown length perpendicular to R_1.

2010

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
1	51	385	117	9.2	210	195
1	52	363	199	6.9	112	163
1	53	421	212	3.5	123	92
1	54	416	327	6.6	118	142
1	55	384	105	9.4	132	176
1	56	158	65	3.35	180	115
1	57	212	80	3.15	185	112
1	58	397	196	6.4	109	142
1	59	392	323	5.45	105	86
1	62	416	340	4.95	85	147
1	63	426	337	6.5	90	158
1	68	437	376	6.25	128	113
1	70	425	379	11.0	187	176
1	72	447	391	5.0	78	64
1	73	462	425	5.25	77	90
1	74	447	400	6.4	96	100
1	76	442	314	5.5	124	117
1	77	426	378	4.2	125	95
1	78	215	147	3.5	70	82
1	79	390	210	10.6	168	152
1	81	401	334	7.0	129	130
1	82	402	347	7.35	125	150
1	84	224	80	5.35	135	139
1	85	382	326	4.05	72	86
1	86	340	135	7.35	124	134
1	87	260	80	8.35	177	133

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
1	88	226	161	4.1	68	50
1	91	336	222	5.2	125	126
1	93	364	271	5.45	96	146
1	94	404	229	3.85	84	100
1	97	374	326	6.0	87	118
1	98	400	333	6.7	108	102
1	99	385	335	7.4	120	95
1	100	278	188	2.7	58	46
1	101	412	352	5.25	72	106
1	102	409	362	7.6	122	107
1	104	369	306	6.6	136	102
1	105	253	180	2.8	58	74
1	107	290	270	3.0	40	45
1	109	402	312	3.85	30	30
1	110	412	362	5.25	95	182
1	111	418	357	6.2	96	100
1	113	433	400	3.7	53	87
1	114	430	378	7.8	100	150
1	115	452	394	5.7	100	112
1	116	434	409	3.8	54	61
1	119	419	355	3.6	28	33
1	122	430	402	6.5	135	130
1	125	454	411	7.3	129	94
1	126	443	372	4.0	83	85
1	127	449	385	5.4	115	107
1	128	455	392	5.2	90	80
2	135	450	392	6.8	127	130
2	136	468	390	6.65	110	114
2	143	407	329	5.8	140	100
2	144	396	344	3.7	70	75
2	146	393	312	4.5	56	96
2	147	407	335	8.1	180	110
2	148	407	341	8.1	165	112

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
2	171	435	365	7.6	135	110
2	172	414	329	4.4	57	85
2	172A	402	364	3.9	80	88
2	175	418	368	6.3	67	70
2	178	392	351	2.4	33	35
2	181	396	320	9.2	149	157
2	182	400	291	8.3	156	145
2	183	410	369	9.2	114	120
2	185	430	373	4.7	75	83
2	187	445	376	6.5	156	140
2	188	444	386	6.9	110	128
2	189	419	370	4.9	85	76
2	191	456	372	4.65	87	86
2	192	454	397	4.5	70	65
2	193	455	388	8.0	156	128
2	195	449	377	5.7	130	90
2	196	452	387	5.9	120	80
2	197	463	394	5.85	98	108
2	198	461	349	7.4	154	130
2	201	453	399	5.3	108	90
2	205	457	388	7.0	116	124
2	206	465	413	4.7	80	60
2	207	438	326	3.05	70	60
2	210	452	394	5.9	100	85
2	213	432	381	5.1	106	70
2	217	410	355	3.8	56	62
2	218	417	362	6.8	92	140
3	223	351	228	4.3	103	70
3	225	399	338	6.0	88	100
3	228	352	311	2.7	40	47
3	231	404	308	6.3	84	152
3	233	402	333	6.8	150	160
3	234	378	340	5.2	70	87

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
3	235	397	335	4.6	60	80
3	236	390	339	5.3	90	85
3	237	247	241	1.3	10	10
3	238	411	368	8.4	120	110
3	243	406	368	5.68	70	100
3	244	407	348	5.4	75	90
3	246	400	364	6.41	120	130
3	247	401	359	6.5	115	97
3	249	418	358	6.6	120	130
3	250	416	354	5.3	13	96
3	251	419	376	4.4	60	70
3	253	400	361	4.0	70	70
3	254	409	363	5.2	110	73
3	255	397	356	6.5	110	90
3	256	404	363	4.2	77	80
3	257	392	347	4.2	90	80
3	258	405	347	5.0	118	100
3	260	410	345	5.1	82	37
3	262	424	364	6.6	142	95
3	263	390	344	6.4	100	105
3	264	350	330	2.7	25	25
3	265	395	346	7.6	200	160
3	266	385	328	4.0	77	68
3	267	387	354	4.2	80	51
3	268	386	338	3.7	68	56
3	271	380	294	5.0	100	92
3	272	381	328	4.6	50	89
3	273	375	217	5.6	95	108
3	275	378	331	5.1	65	80
3	278	361	302	3.15	50	60
3	279	390	353	4.6	105	90
3	280	393	327	5.3	78	110
3	281	382	325	5.6	130	92

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
3	282	391	330	3.8	90	80
3	284	426	382	6.2	110	55
3	288	393	327	3.7	55	72
3	293	342	313	2.3	25	30
3	294	410	363	4.5	68	88
3	296	394	344	6.25	125	150
3	297	398	357	3.2	52	50
3	299	395	350	4.8	115	70
3	301	402	359	4.5	90	102
3	304	392	327	4.0	70	75
3	305	407	345	5.91	150	98
3	309	394	357	4.3	89	100
3	310	406	354	5.6	90	80
3	312	348	315	3.3	85	70
3	315	413	371	5.05	120	115
4	317	421	363	5.3	120	90
4	320	423	366	4.9	80	70
4	325	413	360	4.0	106	90
4	326	415	368	5.5	90	65
4	329	428	347	6.2	58	69
4	332	418	356	5.9	115	135
4	333	401	314	4	55	55
4	335	402	356	4.4	68	70
4	336	401	351	5.0	65	93
4	340	403	356	4.1	75	74
4	341	414	350	4.8	98	70
4	343	408	351	5.6	60	80
4	344	390	339	5.0	35	50
4	345	412	360	3.7	75	70
4	347	416	370	4.7	82	95
4	348	398	359	4.2	65	45
4	349	399	355	3.9	50	30
4	350	422	354	9.5	180	165

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
4	351	416	360	6.4	120	120
4	352	410	357	4.7	90	120
4	355	416	366	4.6	68	76
4	356	420	371	5.0	60	130
4	357	420	376	3.7	80	75
4	358	418	369	5.1	90	85
4	359	413	360	9.0	110	135
4	360	411	353	5.5	105	120
4	363	416	354	6.5	105	105
4	366	420	350	4.9	105	110
4	367	416	332	9.0	142	120
4	374	426	366	5.1	96	90
4	378	418	360	6.1	115	140
4	381	412	352	6.2	115	100
4	382	415	363	4.2	70	75
4	383	408	354	6.2	116	122
4	385	412	363	6.9	140	107
4	386	413	361	4.3	110	80
4	390	409	350	4	90	117
4	391	365	296	5.6	60	50
4	395	404	358	7	95	105
4	396	404	351	6.3	150	70
4	397	398	354	4.9	95	110
4	398	382	320	2.8	50	60
5	400	411	356	4.9	65	76
5	401	366	346	3.4	20	20
5	403	384	346	4.1	30	37
5	404	412	359	6.4	100	120
5	406	414	374	4.9	94	90
5	407	413	341	6.5	67	90
5	408	383	341	3.5	45	38
5	409	403	359	4.0	68	61
5	410	410	358	5.6	158	100

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
5	412	409	350	4.2	83	90
5	414	422	367	5.1	93	70
5	417	415	354	6.9	160	130
5	418	382	347	5.5	115	93
5	420	413	344	5.7	123	145
5	421	401	357	3.1	31	31
5	422	408	364	10	182	152
5	423	392	366	2.4	18	30
5	424	429	398	5.5	90	72
5	427	435	372	3.8	88	92
5	428	388	359	4.3	41	57
5	429	418	386	6.2	100	95
5	430	429	380	5.3	130	100
5	431	406	362	5.9	126	130
5	434	422	375	4.3	55	55
5	436	408	362	4.15	50	62
5	437	413	380	4.25	55	42
5	440	403	369	4.9	70	80
5	441	431	316	4.4	110	60
5	444	440	396	4.0	54	80
5	445	428	367	4.3	55	60
5	446	407	382	3.6	65	78
5	447	412	360	3.8	66	70
5	449	393	352	4.8	85	91
5	450	403	262	3.2	33	33
5	452	419	368	6.0	110	120
5	453	398	378	3.2	36	36
5	455	418	385	4.1	62	50
5	456	417	368	4.5	90	66
5	458	424	381	4.2	90	75
5	459	390	318	4.0	54	36
5	461	434	370	5.4	120	117
5	464	431	387	5.4	110	120

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
5	465	429	380	4.3	58	60
5	466	424	383	4.2	60	50
5	467	449	390	4.6	80	77
5	468	438	392	5.2	105	50
5	469	455	381	4.9	75	70
5	470	445	414	3.5	47	61
5	472	434	387	5.2	110	95
5	476	438	363	6.3	96	120
5	477	433	402	3.4	40	44
5	478	431	373	3.1	54	87
5	479	449	398	6.4	133	124
5	480	450	407	5.3	84	75
5	483	448	382	7.0	140	143
5	486	434	325	5.6	90	97
5	487	439	381	5.1	97	95
5	488	417	372	5.5	130	97
5	489	392	377	3.4	28	28
5	490	434	384	5.2	76	89
5	491	444	391	4.3	90	88
5	492	440	397	5.7	60	45
5	493	427	395	3.2	40	43
5	494	440	394	4.3	82	70
5	495	424	393	3.6	40	55
6	1	445	383	6.1	142	147
6	2	451	402	4.8	112	80
6	3	448	408	4.6	73	62
6	6	454	399	6.0	119	120
6	7	461	403	4.7	80	85
6	8	327	228	3.2	25	25
6	10	441	397	5.8	98	98
6	12	448	396	4.55	92	96
6	13	457	391	9.3	93	105
6	15	451	367	8.4	133	107

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
6	16	452	345	4	67	82
6	17	454	395	6.4	103	116
6	18	450	381	5.1	64	108
6	19	453	394	4.25	71	93
6	21	438	411	3.8	40	55
6	22	442	385	5.0	100	120
6	24	432	371	3.7	35	45
6	25	427	396	4.0	35	30
6	26	434	372	3.2	25	30
6	27	455	385	4.6	106	69
6	30	445	397	4.5	61	66
6	32	436	382	5.2	92	110
6	34	441	395	5.8	125	118
6	35	437	389	6.8	122	128
6	37	454	406	4.8	93	75
6	38	440	383	7.4	153	167
6	40	439	389	6.1	96	84
6	41	463	400	6.2	103	140
6	42	436	383	5.8	78	89
6	45	440	386	7.2	116	120
6	47	438	390	4.8	86	93
6	52	433	391	4.6	45	65
6	53	440	386	5.7	105	100
6	58	432	376	4.7	60	68
6	68	448	391	4.8	126	82
6	69	436	190	6.2	139	120
6	70	449	398	5.9	147	59
6	73	454	402	5.5	105	155
6	74	433	320	3.6	72	75
6	75	437	380	5.4	90	64
6	76	426	380	5.3	88	94
6	82	432	394	4.2	58	62
6	83	418	374	4.0	44	55

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
6	84	431	389	4.4	70	40
6	90	440	389	5.9	77	91
6	91	423	390	2.8	30	45
6	94	442	393	6.3	84	73
6	95	418	370	3.5	60	55
6	98	423	368	4.3	56	60
6	107	433	358	6.3	95	90
6	108	429	387	5.6	73	60
6	109	435	371	5.6	120	120
6	112	429	378	5.7	125	100
6	114	422	352	6.1	144	135
6	120	443	383	7.5	162	130
6	121	459	434	4.2	75	70
6	122	435	378	6.0	79	116
6	123	436	395	6.1	110	130
6	124	408	353	3.3	48	40
7	126	447	388	3.9	90	98
7	127	428	379	5.0	102	95
7	129	425	379	6.3	130	118
7	131	429	375	3.8	75	50
7	132	443	395	4.8	100	118
7	134	434	398	8.0	143	135
7	136	439	375	6.6	65	137
7	137	422	368	4.9	105	100
7	138	431	362	7.3	110	110
7	141	426	383	5.7	110	135
7	142	400	371	2.2	31	33
7	145	435	396	6.1	63	95
7	146	441	398	4.8	70	75
7	148	411	361	5.3	84	90
7	155	416	384	4.3	80	74
7	157	427	374	5.6	63	90
7	158	419	390	4.8	95	70

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
7	159	430	391	5.2	120	62
7	161	433	372	6.7	100	110
7	166	401	342	4.0	66	75
7	168	407	372	5.2	91	95
7	170	413	342	5.4	130	126
7	171	367	343	3.7	24	20
7	174	407	364	7.0	96	105
7	176	410	370	5.3	100	96
7	182	412	391	6.0	117	138
7	183	409	369	6.1	130	125
7	186	416	364	6.2	69	110
7	187	417	376	4.8	120	124
7	189	416	361	4.8	56	50
7	190	418	352	7.1	70	85
7	191	402	351	5.7	80	77
7	192	413	363	5.1	100	100
7	200	401	362	4.8	63	57
7	201	418	361	6.3	125	95
7	202	413	369	6.0	140	130
7	203	410	373	5.8	60	70
7	205	420	351	5.9	90	133
7	210	420	356	7.3	109	56
7	211	404	353	4.7	75	48
7	212	400	324	3.2	58	40
7	216	419	347	8.5	126	149
7	219	432	330	5.8	125	110
7	220	430	358	4.8	95	117
7	221	411	372	4.1	75	92
7	222	419	356	6.0	119	102
7	225	419	369	3.7	65	62
7	226	416	375	3.9	75	50
8	229	395	350	3.8	57	40
8	231	429	380	3.8	55	55

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
8	233	419	375	5.2	130	95
8	234	424	380	4.2	87	90
8	235	405	370	4.8	85	93
8	236	403	369	5.1	95	64
8	238	340	325	2.2	41	40
8	241	393	331	6.3	106	71
8	242	388	339	4.6	110	105
8	247	380	339	3.3	25	20
8	248	384	338	4.6	70	60
8	249	397	361	4.0	85	80
8	256	391	345	6.3	110	100
8	258	383	340	3.8	55	60
8	259	406	361	5.9	120	115
8	260	319	292	5.9	20	20
8	266	384	352	2.5	42	40
8	268	396	356	3.9	105	88
8	269	407	338	6.6	110	136
8	273	389	362	3.8	54	40
8	274	385	345	4.4	75	55
8	279	376	331	4.4	72	65
8	285	374	330	4.7	95	90
8	287	378	337	3.5	62	53
8	288	390	341	4.0	98	90
8	289	370	326	4.0	45	54
8	290	397	352	3.9	65	60
8	296	390	352	2.9	55	50
8	297	406	361	3.6	60	70
8	299	363	330	2.1	30	30
8	302	385	342	4.1	65	60
8	303	390	352	5.6	112	103
8	305	382	355	3.1	50	53
8	307	384	343	5.4	126	110
8	308	403	366	7.1	121	130

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
8	309	393	361	3.7	73	80
8	313	405	369	5.2	160	110
8	315	419	381	4.3	122	76
8	317	418	370	6.0	115	120
8	319	403	387	2.5	43	34
8	323	391	327	4.75	80	50
8	324	397	351	4.1	83	104
8	325	384	352	3.6	20	20
8	326	398	350	4.0	70	75
8	328	392	341	4.3	73	80
8	331	385	318	3.5	78	86
8	333	395	332	3.8	67	80
8	334	406	338	3.2	73	74
8	335	411	338	5.0	105	85
8	336	400	336	5.1	103	99
8	340	368	324	2.4	38	40
8	341	396	331	5.6	115	107
8	344	392	355	5.6	70	58
8	345	399	346	4.8	85	84
8	346	394	327	5.55	112	108
8	347	406	340	4.7	110	108
8	348	397	347	4.5	63	108
8	349	343	309	2.9	25	25
8	350	364	320	2.3	42	43
8	351	388	356	2.75	79	68
8	353	393	359	2.75	30	30
8	354	388	342	4.4	90	75
8	355	401	350	5.4	103	94
8	357	391	338	3.7	70	78
8	359	406	350	4.3	77	80
8	362	394	356	3.0	36	30
8	364	423	361	4.5	70	67
8	365	411	369	3.3	56	79

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
8	366	421	363	5.1	78	80
8	369	425	366	4.1	93	92
8	370	415	351	4.4	88	76
8	371	415	338	6.3	119	95
8	372	396	346	3.5	87	60
9	373	412	377	7.35	115	120
9	374	396	337	3.8	105	98
9	376	407	341	3.7	65	70
9	378	406	348	2.85	42	27
9	379	412	358	3.0	60	63
9	380	403	354	5.0	75	90
9	381	400	340	4.2	70	93
9	382	393	361	5.0	90	70
9	383	382	334	4.3	40	56
9	384	387	359	4.6	77	84
9	386	402	386	2.9	40	40
9	388	410	361	4.4	85	94
9	389	400	339	4.2	72	77
9	390	396	345	7.0	125	105
9	391	385	331	6.4	120	85
9	392	404	352	6.0	75	52
9	393	404	358	4.2	83	83
9	396	357	331	2.2	14	25
9	397	406	350	3.4	53	75
9	398	402	360	6.2	85	76
9	399	389	350	3.4	38	33
9	400	401	353	5.35	83	125
9	402	397	348	4.0	62	65
9	403	418	349	7.9	180	70
9	404	410	363	6.6	118	80
9	406	397	362	5.6	110	80
9	407	406	350	5.0	90	75
9	408	408	362	3.5	54	63

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
9	411	419	377	7.4	135	106
9	412	415	355	4.9	94	125
9	414	419	370	5.7	108	80
9	416	396	339	6.8	125	106
9	418	412	359	5.1	86	105
9	422	337	317	3.2	20	20
9	424	422	347	3.3	57	90
9	425	409	363	4.0	56	65
9	426	409	375	3.5	55	60
9	427	407	341	3.8	30	53
9	428	372	314	4.2	76	50
9	432	409	370	2.7	29	34
9	435	404	342	4.6	100	70
9	437	420	362	7.0	138	160
9	438	410	357	3.5	55	60
9	440	434	372	7.2	125	165
9	444	416	365	3.5	65	55
9	446	409	374	4.6	90	103
9	447	405	369	3.6	50	76
9	455	420	383	6.2	135	140
9	456	420	364	5.4	123	140
9	457	424	370	5.8	140	103
9	458	410	366	4.2	90	85
9	460	402	312	5.2	110	140
9	462	409	348	7.0	150	30
9	465	381	342	3.6	32	35
9	466	387	350	3.0	52	50
9	468	389	339	4.2	65	73
9	469	389	361	2.9	42	46
10	472	434	369	6.2	71	172
10	473	427	392	8.2	120	130
10	474	407	358	5.6	47	65
10	475	431	354	8.6	123	120

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
10	476	385	363	3.1	35	37
10	478	432	387	5.8	68	70
10	479	448	379	4.7	87	74
10	480	438	386	5.0	60	77
10	482	440	376	5.6	125	120
10	485	396	300	2.5	40	34
10	489	469	405	4.2	55	58
10	490	448	398	5.9	96	115
10	491	380	363	3.5	40	35
10	493	441	402	4.7	116	74
10	497	435	392	5.3	65	80
10	500	445	409	5.0	70	45
10	503	371	347	2.9	22	17
10	504	453	401	7.0	142	125
10	510	445	409	2.8	50	52
10	511	450	351	4.8	80	87
10	512	453	395	4.9	86	120
10	513	460	404	3.5	50	63
10	515	445	407	3.6	64	40
10	517	433	390	4.0	72	55
10	519	461	399	4.0	86	68
10	520	457	383	4.5	82	80
10	522	457	403	5.55	100	104
10	523	442	396	3.1	44	32
10	524	467	410	5.6	105	52
10	526	457	431	3.6	50	65
10	528	461	410	4.4	62	73
10	529	464	422	4.8	80	60
10	530	468	404	4.9	94	95
10	531	468	410	7.0	84	140
10	532	464	409	4.6	82	95
10	535	441	396	5.5	70	105
10	536	455	424	6.1	87	73

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
10	537	440	409	5.6	114	68
10	539	454	418	7.4	85	80
10	540	460	415	5.4	25	35
10	542	469	409	4.4	78	60
10	543	466	417	4.5	75	70
10	544	455	408	3.6	50	55
10	545	448	407	6.8	84	84
10	548	435	393	4.3	80	83
10	549	436	386	5.1	121	105
10	550	438	383	4.0	55	76
10	553	426	381	2.9	33	31
10	555	447	371	4.3	68	105
10	556	448	409	5.8	85	103
10	557	448	395	5.4	114	96
10	558	420	380	3.3	50	45
10	563	446	402	4.1	92	83
10	564	448	396	3.9	68	61
10	565	470	402	5.7	105	102
10	566	462	420	3.1	45	44
10	567	459	402	4.3	70	74
10	568	471	406	4.6	92	102
10	569	471	421	5.0	96	106
10	571	467	428	5.6	58	64
10	572	458	402	4.3	50	55
10	573	463	426	5.4	138	74
10	576	418	387	4.3	65	40
11	577	472	412	4.5	91	74
11	578	457	368	6.1	103	85
11	579	460	402	6.0	81	88
11	580	469	406	5.2	94	103
11	581	463	406	5.1	80	154
11	583	444	405	3.7	48	46
11	584	461	404	6.3	95	75

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
11	585	440	424	3.0	22	32
11	586	475	413	5.4	90	70
11	588	468	423	4.9	88	105
11	589	467	430	4.2	62	40
11	590	466	419	7.8	102	136
11	591	472	417	6.8	115	98
11	593	463	409	5.4	100	111
11	598	437	411	5.3	35	30
11	600	461	416	4.2	94	104
11	603	448	402	7.2	124	83
11	604	426	373	3.1	50	48
11	605	441	385	4.5	118	104
11	609	465	386	3.6	85	80
11	610	458	413	5.4	120	105
11	611	451	404	5.1	95	90
11	612	463	419	6.2	107	140
11	616	467	409	3.6	60	72
11	617	472	409	4.3	94	83
11	622	475	399	5.6	110	106
11	623	470	389	9.1	160	190
11	626	469	423	3.1	44	42
11	628	466	422	4.4	119	80
11	630	478	435	4.3	95	50
11	633	454	407	5.0	82	95
11	636	437	410	2.9	55	60
11	638	453	380	6.8	160	92
11	642	453	407	4.3	98	115
11	643	202	155	1.8	52	65
11	644	444	404	4.0	82	83
11	647	444	385	4.2	105	72
11	649	444	388	4.3	90	94
11	654	442	412	5.1	102	104
11	655	433	396	5.3	35	40

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
11	658	441	402	7.6	113	121
11	659	451	412	5.1	92	63
11	660	447	395	5.5	100	80
11	661	420	374	8.0	140	92
11	671	457	414	5.0	58	80
11	675	404	308	3.2	90	60
11	676	436	401	4.8	76	123
11	677	452	402	4.0	82	74
11	678	447	406	4.5	90	75
11	682	463	414	4.4	109	117
11	683	460	410	5.6	74	114
11	687	466	420	3.5	58	61
11	689	475	419	6.4	105	130
11	691	468	418	7.6	123	155
12	695	476	399	4.55	80	75
12	696	466	399	7.2	110	192
12	698	471	423	4.3	80	53
12	699	420	386	2.9	18	20
12	716	451	426	3.9	30	20
12	717	440	397	4.9	50	75
12	718	457	409	4.4	70	60
12	720	434	402	3.4	43	30
12	722	447	394	3.5	43	50
12	724	447	416	4.0	42	36
12	725	450	418	5.0	100	60
12	728	453	396	4.8	88	40
12	730	445	408	4.9	90	107
12	731	451	396	4.1	75	63
12	732	440	394	3.6	34	52
12	734	453	415	6.9	58	54
12	736	453	407	3.9	42	53
12	747	438	388	4.1	78	50
12	748	428	383	3.2	70	36

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
12	749	428	394	4.4	50	54
12	750	417	390	4.0	66	30
12	751	437	406	4.5	50	50
12	758	445	411	5.2	70	90
12	759	392	376	2.8	20	23
12	763	461	394	4.6	66	70
12	764	448	399	6.9	85	74
12	765	441	399	5.3	68	77
12	767	414	375	4.6	70	90
12	768	421	394	3.1	30	25
12	769	442	405	5.3	80	86
12	771	469	410	6.4	110	80
12	772	460	417	3.4	31	45
12	775	456	402	5.2	80	110
12	781	449	402	3.1	42	38
12	790	430	394	5.1	105	120
12	791	402	356	3.6	30	22
12	793	445	391	5.3	78	90
12	794	455	397	5.3	75	110
12	795	436	400	3.65	53	70
12	800	419	347	7.9	110	130
12	801	430	387	8.25	90	135
12	804	417	365	3.9	47	55
12	812	423	347	5.9	105	100
12	814	452	397	5.8	100	70
12	816	382	357	2.85	20	20
12	818	373	330	2.7	30	20
12	819	432	372	5.6	105	130
12	821	413	364	5.0	110	46
12	827	426	385	4.0	50	45
12	840	413	371	4.7	54	55
12	845	437	391	4.5	65	55
12	848	418	385	6.1	110	100

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
12	851	420	372	5.1	75	70
12	861	424	381	5.0	75	100
12	867	428	389	5.0	63	70
12	868	420	390	4.3	75	60
12	869	428	396	5.6	115	65
12	872	442	386	5.6	76	75
12	873	451	399	4.4	90	80
12	874	465	407	4.75	70	60
12	875	450	402	4.7	82	60
12	876	439	368	5.4	100	70
12	878	438	356	3.1	30	55
12	883	422	392	3.9	74	86
13	892	464	418	5.8	125	118
13	901	435	367	4.1	40	30
13	902	438	399	6.7	130	106
13	904	432	388	4.82	90	50
13	905	411	370	3.9	18	20
13	906	422	391	4.3	92	55
13	908	429	380	4.5	40	45
13	918	443	388	6.3	125	119
13	931	446	409	5.1	105	50
13	932	423	388	3.7	44	62
13	934	428	400	4.2	40	70
13	937	425	397	5.8	55	65
13	938	421	375	6.0	110	80
13	945	415	350	7.2	150	90
13	946	414	378	4.2	96	50
13	948	410	363	3.7	46	45
13	949	399	371	4.4	42	63
13	950	421	382	4.7	53	60
13	952	420	408	4.1	55	60
13	953	438	388	7.86	170	140
13	975	434	367	4.4	70	125

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
13	977	431	397	6.0	82	85
13	979	422	390	5.1	75	68
13	980	437	390	5.13	90	100
13	981	432	393	6.52	123	160
13	982	436	409	3.7	60	65
13	983	434	405	5.05	77	97
13	986	443	403	6.0	90	85
13	987	438	402	4.7	50	70
13	988	390	320	3.2	30	38
13	989	409	388	4.1	55	75
13	990	435	402	4.5	100	65
13	991	439	345	7.3	130	115
13	995	405	381	3.0	35	35
13	997	426	380	4.1	67	60
13	999	422	385	4.9	55	58
13	1000	460	410	4.6	46	53
13	1002	423	363	4.0	45	54
13	1004	395	376	3.8	55	45
13	1005	441	380	5.35	95	85
13	1007	426	412	4.0	25	30
13	1008	428	397	4.8	60	78
13	1009	450	417	4.4	84	65
13	1010	449	416	3.6	33	34
13	1012	449	409	4.3	90	45
13	1013	433	405	3.9	28	30
13	1014	456	402	5.2	63	50
13	1015	448	395	6.2	96	108
13	1016	440	402	7.6	65	60
13	1017	439	411	7.4	92	123
13	1020	441	394	5.6	95	100
13	1021	433	397	3.5	35	45
13	1022	441	399	4.8	58	60
13	1023	430	402	4.0	42	47

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
13	1024	435	354	3.7	44	45
13	1025	447	398	6.1	105	83
13	1026	449	411	5.3	85	83
13	1028	440	397	5.2	70	95
13	1029	456	423	4.9	71	82
13	1030	459	408	5.2	108	85
13	1031	456	393	5	90	100
13	1032	465	408	5.3	90	107
13	1033	467	422	6.5	120	85
13	1034	458	413	6.3	105	120
14	1122	465	357	3.5	37	30
14	1124	465	424	6.3	88	90
14	1125	455	402	9.1	145	150
14	1134	458	410	6.8	106	76
14	1139	457	378	5.4	125	85
14	1142	445	400	4.5	50	42
14	1144	451	402	6.2	66	77
14	1145	463	405	4.9	60	77
14	1150	468	420	4.7	63	54
14	1151	446	426	2.55	25	30
14	1154	463	411	4.2	40	36
14	1155	455	393	6.5	55	57
14	1156	451	392	4.4	60	45
14	1157	460	404	4.3	54	68
14	1158	464	396	6.2	110	60
14	1159	453	415	7.7	70	65
14	1161	450	417	4.6	56	33
14	1162	449	409	5.8	70	65
14	1165	462	403	4.5	76	74
14	1166	474	425	7.4	85	117
14	1170	460	406	5.1	63	44
14	1173	459	403	5.6	93	86
14	1175	465	428	3.5	50	40

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
14	1176	467	425	4.6	56	72
14	1179	456	430	2.8	30	25
14	1180	473	403	8.5	160	135
14	1181	453	403	7.6	123	56
14	1182	448	415	4.3	70	40
14	1183	465	409	5.2	83	130
14	1184	439	400	7.1	130	129
14	1187	431	408	3.3	36	45
14	1190	447	413	4.15	60	60
14	1191	444	402	4.4	48	36
14	1192	456	418	3.6	36	38
14	1193	459	371	6.0	46	71
14	1194	466	429	4.3	62	60
14	1195	464	406	5.0	106	64
14	1196	461	410	4.2	102	93
14	1197	453	409	5.2	110	103
14	1198	457	418	8.6	105	110
14	1205	467	424	7.9	125	94
14	1206	471	419	4.45	59	53
14	1209	456	402	5.4	110	88
15	1210	453	410	5.4	68	72
15	1212	453	411	4.4	52	55
15	1213	475	410	5.6	86	85
15	1214	461	427	4.1	67	54
15	1216	468	415	5.4	131	83
15	1217	443	390	4.1	54	37
15	1219	454	402	6.6	85	98
15	1221	427	398	4.1	62	70
15	1222	435	407	6.3	76	110
15	1223	457	406	7.6	77	113
15	1224	459	382	6.2	87	74
15	1226	457	394	6.6	70	92
15	1227	446	401	6.1	104	95

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
15	1227A	447	411	5.0	51	60
15	1227B	435	382	5.0	51	33
15	1230	448	405	4.7	86	67
15	1231	436	382	4.8	47	50
15	1232	441	400	5.8	92	85
15	1233	443	381	6.6	160	122
15	1234	431	372	5.5	82	61
15	1235	415	371	4.8	51	41
15	1237	421	385	4.2	50	55
15	1238	417	384	4.7	65	75
15	1239	443	402	6.4	95	68
15	1240	423	381	4.9	74	43
15	1244	427	395	5.7	78	92
15	1246	431	390	6.1	95	90
15	1247	435	421	5.3	52	70
15	1248	438	383	6.6	96	110
15	1252	423	387	3.3	21	26
15	1254	450	412	5.4	110	70
15	1255	457	402	5.4	118	77
15	1257	448	403	4.5	75	61
15	1258	449	410	5.3	81	52
15	1259	417	386	2.7	35	23
15	1260	429	402	6.4	94	55
15	1261	430	400	5.7	110	115
15	1262	429	383	4.6	70	82
15	1263	430	410	3.85	33	40
15	1264	432	394	5.7	125	84
15	1268	418	381	5.15	139	85
15	1269	423	379	5.25	126	95
15	1271	433	387	4.2	120	94
15	1275	423	376	4.7	56	92
15	1276	424	396	4.4	62	112
15	1278	434	388	4.5	98	61

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
15	1280	424	366	4.8	54	67
15	1281	425	390	4.5	76	86
15	1282	418	385	3.0	53	40
15	1285	422	377	5.1	46	39
15	1286	426	378	6.3	107	123
15	1287	424	375	5.9	113	47
15	1288	439	383	5.6	110	86
15	1292	439	377	5.1	115	90
16	1293	417	371	5.5	45	38
16	1294	431	376	6.85	112	110
16	1295	431	383	5.4	120	110
16	1296	422	376	4.8	65	54
16	1298	420	340	6.3	108	100
16	1302	417	387	5.2	85	92
16	1303	422	389	3.9	71	75
16	1304	420	375	7.8	110	145
16	1306	428	394	4.4	51	71
16	1308	409	376	4.0	67	75
16	1310	429	382	4.6	57	103
16	1311	423	378	2.8	43	75
16	1312	429	363	4.4	73	46
16	1313	423	395	4.6	75	74
16	1319	414	380	2.65	30	27
16	1320	416	369	3.5	55	57
16	1322	424	383	4.6	80	73
16	1328	423	374	3.5	75	63
16	1330	411	372	6.3	122	95
16	1332	422	359	5.5	85	115
16	1334	413	373	5.6	100	85
16	1335	422	375	5.2	108	81
16	1336	427	378	9.3	148	103
16	1338	404	360	6.0	88	56
16	1339	402	370	6.7	108	105

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
16	1340	415	365	5.6	64	58
16	1340	415	365	5.6	64	58
16	1342	411	350	5.6	66	61
16	1343	302	260	2.8	17	40
16	1344	393	355	3.8	24	35
16	1345	411	357	4.5	82	55
16	1346	410	346	4.9	60	59
16	1347	418	372	4.1	64	61
16	1348	400	375	2.8	43	35
16	1351	408	348	6.2	85	96
16	1353	404	371	6.4	98	114
16	1355	420	378	5.9	70	73
16	1357	359	291	3.8	31	35
16	1358	414	367	5.5	85	110
16	1365	424	359	4.8	57	66
16	1366	415	353	6.0	56	115
16	1367	419	361	5.7	80	120
16	1373	417	378	4.3	52	63
16	1375	432	357	6.8	83	91
16	1377	435	372	7.25	110	124
16	1378	413	386	6.2	41	67
16	1382	409	351	3.65	53	64
16	1383	419	356	4.2	55	63
16	1387	405	355	5.4	100	64
16	1388	403	363	4.8	85	66
16	1389	396	347	4.55	64	29
16	1390	406	365	4.35	45	42
16	1394	412	357	5.4	77	75
16	1397	408	361	6.4	93	87
16	1399	413	360	5.7	83	106
16	1400	411	374	5.2	73	78
16	1401	404	364	3.35	35	87
16	1402	415	354	7.55	110	135

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
16	1404	425	381	7.0	112	114
16	1405	427	376	6.9	97	106
17	1410	419	380	3.9	50	51
17	1411	418	367	7.55	90	92
17	1412	392	357	6.2	90	81
17	1416	421	394	4.4	36	45
17	1418	417	371	6.4	92	67
17	1419	416	385	7.3	87	112
17	1421	412	372	4.5	65	52
17	1423	386	351	4.3	35	35
17	1424	423	385	5.1	71	55
17	1425	408	346	5.6	65	45
17	1426	412	376	3.7	63	48
17	1429	419	372	6.6	93	92
17	1431	420	380	6.3	110	77
17	1432	415	383	4.6	35	50
17	1433	403	375	4.2	40	39
17	1434	410	346	5.6	94	63
17	1436	413	366	2.6	23	30
17	1437	414	377	4.9	55	90
17	1439	414	371	5.0	83	77
17	1440	414	363	5.7	92	55
17	1441	377	343	3.5	23	24
17	1447	430	382	3.7	41	47
17	1450	410	353	6.5	73	80
17	1451	419	366	5.9	67	100
17	1452	449	402	7.1	85	112
17	1453	440	377	6.75	97	68
17	1454	432	378	4.2	37	38
17	1455	434	381	4.3	70	60
17	1456	434	395	4.3	38	40
17	1457	415	377	4.65	75	58
17	1458	424	334	9.5	85	118

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
17	1459	411	376	6.5	67	85
17	1460	347	263	2.6	33	35
17	1461	395	345	2.35	28	23
17	1463	418	390	4.4	80	81
17	1465	419	373	4.6	93	82
17	1467	415	379	4.3	56	55
17	1469	415	355	4.25	73	58
17	1470	425	253	7.5	85	100
17	1471	416	373	6.8	95	110
17	1473	418	382	5.6	87	112
17	1474	414	367	3.6	58	45
17	1476	389	347	2.4	22	22
17	1477	402	362	3.8	40	36
17	1478	391	357	3.3	37	40
17	1481	414	374	3.9	50	46
17	1482	426	377	4.9	62	73
17	1484	405	366	6.73	65	46
17	1484A	412	380	4.7	54	50
17	1484B	384	335	3.1	38	36
17	1484C	376	353	3.3	17	16
17	1491	435	383	5.5	76	79
17	1493	438	383	4.0	75	60
17	1494	432	386	4.8	63	65
17	1495	431	389	7.3	115	82
17	1497	422	383	3.4	39	35
17	1498	437	391	4.3	72	70
17	1499	441	402	4.2	42	41
17	1500	435	380	3.95	57	50
18	1501	444	406	5.1	65	80
18	1503	401	373	3.5	35	24
18	1504	433	370	4.1	65	50
18	1506	435	397	5.3	103	70
18	1507	402	371	3.0	23	23

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
18	1507A	440	391	3.85	60	55
18	1509	402	380	3.4	30	30
18	1510	438	398	3.9	45	43
18	1511	436	405	5.1	72	55
18	1512	400	381	2.25	16	21
18	1513	421	388	5.2	92	120
18	1513A	428	397	3.9	75	65
18	1514	426	352	4.5	60	57
18	1515	426	378	4.1	78	45
18	1516	437	374	6.6	100	112
18	1517	427	383	6.55	105	95
18	1517A	426	385	4.5	51	50
18	1519	440	399	5.5	92	75
18	1522	447	401	4.5	83	123
18	1524	425	381	2.3	65	46
18	1526	442	387	4.4	67	85
18	1531	441	392	4.5	52	47
18	1531A	425	382	4.83	75	71
18	1532	421	385	4.6	62	86
18	1536	439	385	6.45	100	134
18	1536A	430	385	4.0	54	47
18	1538	410	377	4.4	55	88
18	1539	426	390	5.25	117	82
18	1540	427	390	3.8	43	45
18	1541	418	379	6.4	76	110
18	1542	371	349	3.0	32	28
18	1544	428	375	6.5	102	132
18	1545	427	364	5.45	75	78
18	1548	428	379	5.6	85	93
18	1549	431	391	3.0	46	45
18	1550	432	388	4.35	63	27
18	1551	426	393	5.35	46	44
18	1552	440	385	3.9	58	59

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
18	1554	439	402	4.5	74	54
18	1555	443	398	4.45	72	76
18	1556	438	402	3.8	45	44
18	1557	434	395	3.6	35	43
18	1558	442	384	5.9	75	97
18	1561	410	391	2.5	21	21
18	1563	443	354	4.9	67	100
18	1564	440	402	4.6	53	62
18	1564A	437	404	4.8	42	43
18	1565	455	420	5.1	50	62
18	1566	441	388	4.9	83	65
18	1567	441	392	4.65	43	61
18	1569	461	378	7.1	125	69
18	1570	441	388	5.8	86	76
18	1572	431	394	3.9	44	56
18	1573	438	381	3.6	38	55
18	1575	425	392	6.8	94	64
18	1575A	426	385	4.4	53	64
18	1576	422	391	5.4	87	65
18	1577	435	372	5.6	85	72
18	1578	429	389	4.7	42	56
18	1580	424	391	3.2	30	32
18	1581	409	373	4.4	65	76
18	1582	420	363	4.4	35	30
18	1583	421	388	2.5	22	20
18	1585	423	375	5.0	48	62
18	1586	421	379	3.2	24	30
18	1587	418	388	3.7	40	36
18	1588	438	399	4.4	73	65
18	1589	431	392	5.6	113	94
18	1590	421	369	3.0	34	34
19	1593	408	380	3.8	42	40
19	1595	437	405	4.4	47	61

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
19	1597	421	392	4.7	78	70
19	1600	432	395	5.1	85	52
19	1601	428	391	4.7	72	46
19	1603	436	386	4.5	52	53
19	1603A	446	389	4.0	93	50
19	1605	417	383	3.6	70	54
19	1606	389	350	4.3	30	40
19	1607	442	381	5.7	91	68
19	1609	411	387	3.8	52	55
19	1616	433	390	7.2	110	85
19	1617	426	375	6.1	107	115
19	1618	401	368	4.9	43	49
19	1619	437	377	6.6	90	110
19	1620	429	391	7.1	90	92
19	1621	439	388	7.2	68	85
19	1622	434	402	5.2	81	68
19	1625	431	379	4.2	60	53
19	1627	394	354	2.7	32	29
19	1628	399	356	3.3	42	43
19	1629	448	411	4.7	83	82
19	1633	455	414	3.5	43	28
19	1634	456	381	8.2	115	110
19	1635	437	384	4.35	110	82
19	1636	442	402	6.1	62	103
19	1637	452	410	8.8	122	163
19	1640	464	417	6.0	92	85
19	1641	442	406	4.6	63	86
19	1646	454	414	5.0	68	63
19	1648	429	409	3.05	31	30
19	1649	448	394	6.25	110	90
19	1650	446	391	4.35	75	65
19	1651	425	389	5.0	54	70
19	1652	429	387	5.1	75	60

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
19	1654	419	392	3.3	23	21
19	1656	435	380	5.4	54	73
19	1657	427	395	6.1	74	68
19	1657A	431	383	4.4	51	30
19	1658	432	383	5.5	75	83
19	1660	433	378	4.2	44	70
19	1661	439	370	4.9	61	65
19	1661A	431	386	4.85	90	67
19	1662	445	385	4.6	95	83
19	1664	458	405	4.2	75	73
19	1665	455	385	6.4	100	110
19	1666	453	406	7.0	115	94
19	1668	449	409	5.0	44	65
19	1669	445	406	5.35	75	74
19	1672	450	413	5.5	85	84
19	1673	445	366	6.7	115	105
19	1674	449	404	4.9	72	120
19	1675	453	409	4.5	58	87
19	1678	425	394	5.5	32	56
19	1678A	388	371	4.4	20	17
19	1678B	443	394	4.8	91	65
19	1680	427	389	3.5	37	38
19	1685	427	380	5.4	101	120
20	1686	434	387	7.7	105	114
20	1686A	420	376	5.2	71	63
20	1686B	433	375	7.2	192	88
20	1687	435	380	9.4	176	125
20	1689	445	390	7.8	147	133
20	1690	440	394	3.8	46	50
20	1691	437	402	3.8	63	44
20	1692	447	400	5.2	55	60
20	1693	403	378	3.5	42	32
20	1696	432	371	6.2	105	48

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
20	1696A	430	388	4.7	91	86
20	1696B	428	386	4.1	107	70
20	1697	449	397	4.2	84	77
20	1698	441	386	7.1	90	84
20	1699	430	395	7.35	94	102
20	1699A	425	398	4.6	75	80
20	1699B	405	366	3.9	25	24
20	1700	446	397	9.3	121	111
20	1701	453	415	5.9	93	61
20	1702	459	396	4.65	61	84
20	1704	451	402	4.1	51	52
20	1707	418	373	6.3	35	51
20	1708	422	366	6.5	152	114
20	1708A	418	379	4.2	51	44
20	1708B	427	380	4.6	44	52
20	1710A	415	376	3.8	54	44
20	1711	422	357	6.3	86	47
20	1712	429	368	6.8	171	112
20	1712A	428	381	5.6	72	100
20	1713	429	388	8.8	115	125
20	1714	422	375	3.8	55	50
20	1716	407	371	4.3	28	34
20	1717	423	381	3.25	119	168
20	1719	427	376	5.1	40	46
20	1720	433	381	5.2	73	105
20	1720A	431	383	7.8	75	85
20	1722	425	382	5.2	55	56
20	1723	418	382	5.8	36	33
20	1724	401	384	3.0	22	25
20	1726	415	381	5.7	92	96
20	1728	427	382	5.3	96	100
20	1730	425	374	5.9	107	110
20	1733	442	391	4.2	75	93

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
20	1734	430	390	4.9	88	90
20	1736	420	379	6.1	95	80
20	1737	435	395	5.2	34	43
20	1739	431	389	3.68	33	36
21	1740	442	397	5.2	62	45
21	1741	430	378	7.3	95	123
21	1745	411	379	6.9	95	154
21	1746	419	371	4.5	113	82
21	1747	414	384	6.7	104	92
21	1747A	390	361	4.6	19	26
21	1748	416	380	6	130	112
21	1750	429	385	5.3	75	88
21	1751	423	397	4.6	55	53
21	1753	438	404	6.4	84	58
21	1754	415	389	4.9	55	65
21	1755	420	380	4.2	75	68
21	1756	432	406	5.6	95	140
21	1757	424	349	6.5	50	40
21	1759	441	382	5.4	110	58
21	1761	442	389	4.8	70	108
21	1763	449	336	5.8	90	110
21	1764	446	345	7.9	118	110
21	1766	437	386	3.7	45	44
21	1768	420	381	5.9	60	92
21	1771	422	353	3.3	52	40
21	1772	439	394	5.55	108	86
21	1773	434	397	5.0	104	88
21	1774	391	363	3.5	42	38
21	1775	433	386	6.35	67	103
21	1775A	432	396	5.55	102	95
21	1778	432	395	5.3	41	36
21	1780	395	374	3.6	34	60
21	1781	433	394	4.9	147	80

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
21	1784	430	381	7.75	123	147
21	1784A	444	300	5.4	84	128
21	1785	419	376	7.5	58	72
21	1786	441	364	7.4	116	155
21	1788	406	379	3.0	23	35
21	1789	435	356	5.8	88	126
21	1790	430	380	6.2	51	48
21	1790A	431	394	4.3	61	65
21	1792	430	390	6.25	178	96
21	1793	417	377	4.0	50	46
21	1796	449	411	6.2	121	120
21	1797	442	370	7.3	125	82
22	1799	449	400	5.4	92	108
22	1800	435	394	6.8	74	128
22	1802	426	393	6.4	44	40
22	1802A	436	395	5.6	94	114
22	1803	449	402	6.2	104	105
22	1804	443	397	11.2	140	136
22	1805	422	391	3.8	45	28
22	1806	440	394	5.6	104	96
22	1807	419	387	4.6	42	60
22	1810	426	402	3.2	25	20
22	1811	433	399	6.2	82	88
22	1812	432	394	4.1	52	36
22	1818	428	404	4.7	45	38
22	1819	432	394	4.8	64	82
22	1821	428	388	3.7	56	36
22	1824	445	379	6.1	82	50
22	1826	438	392	6.4	131	102
22	1830	448	406	4.7	75	88
22	1831	385	349	3.0	60	84
22	1832	443	404	5.1	81	86
22	1834	466	402	7.0	122	115

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
22	1835	459	419	4.7	72	89
22	1836	450	416	3.7	48	51
22	1838	459	421	6.7	76	90
22	1839	466	428	4.9	47	49
22	1843	468	406	5.7	105	80
22	1844	459	400	4.6	110	64
22	1845	456	411	5.5	78	54
22	1846	448	402	4.7	114	70
22	1848	467	405	8.5	128	100
22	1848A	447	408	4.3	67	66
22	1849	454	404	4.9	92	66
22	1850	453	403	5.8	97	107
22	1851	451	405	5.1	73	79
22	1851A	438	403	4.8	52	43
22	1851B	447	406	4.5	42	38
22	1852	437	398	6.1	96	82
22	1853	451	403	5.3	100	58
22	1858	444	404	7.6	94	91
22	1860	402	370	3.7	26	55
22	1862	430	371	5.8	40	81
22	1863	450	387	8.0	125	130
22	1865	463	412	5.0	90	82
22	1866	458	400	4.6	86	78
22	1867	407	370	2.9	56	50
22	1870	469	418	4.9	70	84
22	1871	443	402	3.6	52	26
22	1872	396	362	4.5	30	20
22	1875	465	406	6.7	110	138
23	1876	461	413	4.3	84	95
23	1878	447	391	4.3	51	73
23	1879	459	411	6.0	152	156
23	1879A	452	406	4.1	40	62
23	1880	460	401	6.15	118	110

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
23	1881	446	406	4.8	38	28
23	1882	449	404	5.3	88	90
22	1884	454	406	4.6	92	84
23	1885	443	406	5.3	92	86
23	1887	459	407	6.7	148	112
23	1888	450	420	4.5	48	54
23	1888A	445	404	4.4	78	73
23	1889	459	409	6.2	112	76
23	1892	447	403	5.1	76	64
23	1893	451	418	3.7	40	42
23	1894	447	417	4.9	70	76
23	1896	465	440	3.2	38	52
23	1898	451	402	5.6	86	95
23	1900	461	403	5.7	80	106
23	1901	478	409	5.8	115	98
23	1903	484	428	7.5	120	98
23	1904	452	417	7.1	122	100
23	1906	477	433	4.6	54	76
23	1907	466	443	3.8	30	35
23	1909	457	401	5.8	102	116
23	1910	466	425	4.3	66	74
23	1912	461	411	7.2	136	78
23	1912A	452	420	4.0	70	40
23	1913	473	421	6.8	116	112
23	1916	475	419	5.2	94	99
23	1918	443	407	3.4	44	58
23	1919	460	419	5.0	80	98
23	1920	464	424	5.1	96	86
23	1921	447	390	4.4	38	58
23	1924	461	412	4.8	86	78
23	1925	450	409	5.4	118	97
23	1927	476	417	7.0	132	132
23	1928	460	407	3.8	45	46

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
23	1931	451	406	6.0	80	124
23	1932	470	418	6.2	74	98
23	1936	459	407	6.2	94	100
23	1937	464	406	6.2	130	88
23	1938	449	410	4.9	98	58
23	1941	448	415	5.3	82	80
23	1942	453	428	4.0	46	64
23	1943	445	404	3.8	48	52
23	1944	456	415	6.7	94	94
23	1945	478	417	5.5	80	78
23	1945A	435	408	5.2	64	45
23	1947	461	430	5.0	54	80
23	1948	467	421	5.5	92	68
23	1949	450	407	4.6	54	51
24	1950	479	430	5.7	110	124
24	1951	464	416	6.2	96	174
24	1951A	482	442	4.65	80	92
24	1951B	477	437	6.4	174	104
24	1952	454	415	6.65	92	82
24	1953	445	414	4.4	64	56
24	1954	456	418	5.7	84	118
24	1956	446	374	4.1	46	48
24	1957	464	401	5.6	108	104
24	1957A	462	415	5.1	74	102
24	1959	466	420	6.7	164	154
24	1960	463	403	6.0	88	118
24	1961	454	417	5.8	96	98
24	1962	446	403	4.3	76	48
24	1963	465	411	5.4	117	98
24	1964	458	416	7.8	186	150
24	1965	452	401	5.4	82	64
24	1968	450	412	5.7	64	58
24	1969	462	401	5.8	118	80

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
24	1970	448	412	5	86	140
24	1971	466	402	5.7	80	106
24	1972	462	406	3.6	68	58
24	1973	457	416	6.2	114	118
24	1975	451	387	4.25	68	56
24	1977	457	409	5.1	106	58
24	1978	471	403	7.3	170	140
24	1979	458	400	3.8	48	54
24	1982	452	416	4.0	40	30
24	1987	459	433	3.5	56	66
24	1988	464	416	4.7	80	60
24	1989	470	412	6.8	110	120
24	1990	463	404	7.5	156	150
24	1991	476	413	5.1	98	110
24	1997	459	410	8.15	136	154
24	1998	444	408	6.4	103	120
24	1999	468	401	7.0	110	170
24	2000	431	403	3.9	50	45
24	2001	443	389	5.4	78	90
24	2001A	467	391	6.75	126	138
24	2004	480	425	6.3	160	118
24	2004B	497	433	7.8	110	90
24	2004A	475	416	5.7	113	101
25	2007	466	415	4.0	73	67
25	2008	463	409	6.1	120	96
25	2017	471	409	5.3	95	104
25	2019	461	409	7.8	120	88
25	2019A	448	387	5.2	70	107
25	2020	450	397	4.0	72	64
25	2022	455	406	4.3	105	55
25	2024	452	415	3.8	80	36
25	2028	451	376	5.5	126	84
25	2030	459	399	5.5	99	100

Plot No.	Tree No.	H (cm)	H_L (cm)	$D_{0.1H}$ (cm)	R_1 (cm)	R_2 (cm)
25	2031	456	386	5.5	112	99
25	2032	464	402	5.9	125	95
25	2034	469	411	6.6	140	110
25	2034A	464	412	5.1	122	103
25	2035	471	406	4.8	104	86
25	2037	461	418	4.8	96	93
25	2039	462	419	3.8	57	63
25	2041	460	404	4.7	78	72
25	2042	463	434	3.6	30	35
25	2044	474	378	4.9	84	92
25	2048	479	436	3.25	40	30
25	2049	480	432	5.3	84	32
25	2050	491	431	5.9	1216	126
25	2052	489	414	8.2	210	190
25	2053	479	412	8.5	146	137
25	2055	488	433	7.5	114	118
25	2060	481	433	4.4	70	40
25	2062	474	420	4.6	102	66
25	2063	502	432	5.4	74	105
25	2066	468	378	4.0	66	56
25	2068	497	430	7.1	144	120
25	2069	467	422	5.9	95	76
25	2070	476	420	9.0	145	156
25	2071	476	425	5.2	74	68
25	2072	487	425	8.0	174	172
25	2074	490	423	13.8	210	204

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Plot No.	Tree No.	*H* (cm)	$D_{0.1H}$ (cm)
3	225	427	6.1
3	231	410	6.4
3	233	424	6.8
3	234	407	5.3
3	235	417	4.65
3	236	416	5.4
3	238	424	8.5
3	243	415	5.7
3	244	416	5.4
3	246	402	6.45
3	247	417	6.7
3	249	443	6.65
3	250	440	5.3
3	251	438	4.8
3	253	415	4.65
3	254	427	5.28
3	255	411	6.7
3	256	421	4.3
3	257	409	4.25
3	258	425	5.1
3	260	431	5.2
3	262	429	6.7
3	263	411	6.5
3	265	414	7.9
3	266	401	4
3	267	418	4.5
3	268	404	4
3	271	403	5.2
3	272	399	4.65
3	273	409	5.7

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
3	275	397	5.12
3	279	413	4.65
3	280	410	5.4
3	281	415	6
3	282	411	3.9
3	284	430	6.22
3	294	426	4.55
3	296	412	6.25
3	297	417	3.25
3	299	415	5.1
3	301	419	4.58
3	304	416	4.05
3	305	439	6.2
3	309	395	4.1
3	310	427	5.7
3	312	369	3.4
3	315	441	5.1
4	317	440	5.4
4	320	449	4.92
4	325	437	4.05
4	326	445	5.5
4	329	448	6.25
4	332	444	6.1
4	335	423	4.4
4	336	420	5.05
4	340	428	4.1
4	341	435	4.85
4	343	434	5.68
4	345	440	3.75
4	347	434	4.8
4	350	440	9.5
4	351	445	6.6
4	352	442	4.8

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
4	355	430	4.6
4	356	434	5.05
4	357	441	4
4	358	438	5.2
4	359	439	9
4	360	432	5.6
4	363	445	6.6
4	366	456	5.1
4	367	449	9.2
4	374	433	5.1
4	378	450	6.15
4	381	443	6.28
4	382	442	4.3
4	383	438	6.4
4	385	443	6.9
4	386	442	4.4
4	390	432	4
4	395	437	7
4	396	439	6.4
4	397	429	5
4	398	397	3
5	400	441	5
5	404	435	6.6
5	406	437	5
5	407	425	6.5
5	409	428	4
5	410	435	5.88
5	412	430	4.25
5	414	436	5.1
5	417	435	7.3
5	418	408	5.7
5	420	434	5.95
5	422	441	10.2

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
5	424	447	5.6
5	427	462	3.9
5	429	459	6.25
5	430	439	5.35
5	431	428	6
5	434	436	4.4
5	440	419	4.95
5	441	451	4.4
5	444	473	4.2
5	445	455	4.4
5	446	422	3.7
5	447	419	4
5	449	427	4.88
5	452	432	6.2
5	455	434	4.1
5	456	439	4.5
5	458	441	4.22
5	459	374	4
5	461	457	5.42
5	464	465	5.58
5	465	445	4.31
5	466	426	4.25
5	467	462	4.7
5	468	457	5.5
5	469	478	5
5	472	448	5.38
5	476	451	6.4
5	479	467	6.5
5	480	480	5.6
5	483	461	7
5	486	443	5.75
5	487	452	5.11
5	488	428	5.6

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
5	491	457	4.3
5	493	442	3.2
5	494	458	4.5
5	495	432	3.6
6	1	459	6.11
6	2	466	4.85
6	3	464	4.7
6	6	467	6.1
6	7	480	4.7
6	10	463	5.9
6	12	469	4.72
6	13	461	10.4
6	15	459	8.5
6	16	469	4.08
6	17	462	6.42
6	18	463	5.1
6	19	469	4.3
6	22	455	5.1
6	27	461	4.6
6	32	455	5.2
6	34	454	6
6	35	456	6.92
6	37	459	4.9
6	38	454	7.6
6	40	455	6.11
6	41	467	6.3
6	45	450	7.25
6	47	447	5.1
6	53	456	5.7
6	68	459	4.9
6	69	453	6.3
6	70	454	6
6	73	468	5.7

Plot No.	Tree No.	H (cm)	$D_{0.1\mathrm{H}}$ (cm)
6	74	391	3.5
6	75	443	5.6
6	76	442	5.3
6	83	430	4
6	84	446	4.5
6	90	445	5.9
6	95	433	3.5
6	98	431	4.32
6	107	450	6.34
6	108	440	5.65
6	109	445	5.68
6	112	441	5.71
6	114	447	6.2
6	120	448	7.65
6	121	477	4.25
6	122	446	6.28
6	123	439	6.3
6	124	355	3
7	126	463	3.9
7	127	439	5
7	129	435	6.35
7	131	442	3.81
7	132	448	4.9
7	134	445	8.1
7	136	451	6.6
7	137	424	4.9
7	138	451	7.4
7	141	439	5.81
7	142	405	2.25
7	145	442	6.1
7	146	463	4.85
7	148	421	5.35
7	155	424	4.31

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
7	157	430	5.61
7	158	432	4.8
7	159	435	5.21
7	161	448	6.7
7	166	410	4.1
7	168	415	5.32
7	170	429	5.42
7	174	410	7
7	176	416	5.3
7	182	425	6.12
7	183	409	6.1
7	186	427	6.21
7	187	419	4.8
7	189	420	4.81
7	190	423	7.3
7	191	420	5.81
7	192	425	5.11
7	200	420	4.8
7	201	432	6.3
7	202	420	6.05
7	203	420	5.8
7	205	437	6.1
7	210	428	7.4
7	211	420	4.8
7	212	420	3.4
7	216	433	8.9
7	219	435	5.82
7	220	438	4.82
7	221	432	4.21
7	222	423	6.1
7	225	432	4
7	226	426	3.92
8	229	391	3.8

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
8	231	422	3.2
8	233	428	5.3
8	234	436	4.21
8	235	438	5
8	239	387	6.1
8	241	404	6.4
8	242	410	4.7
8	247	380	3.3
8	248	399	4.75
8	249	407	4.05
8	256	405	6.45
8	258	386	3.8
8	259	414	6.08
8	268	415	3.95
8	269	410	6.62
8	274	405	4.72
8	279	388	5.52
8	285	390	4.71
8	287	389	3.57
8	288	392	4.1
8	289	375	4
8	290	413	3.95
8	296	405	2.9
8	297	412	3.65
8	302	396	4.1
8	303	405	5.65
8	305	390	3.2
8	307	405	5.45
8	208	405	7.3
8	309	407	3.8
8	313	423	5.25
8	315	437	4.32
8	323	404	4.75

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
8	324	421	4.2
8	326	417	4.1
8	328	408	4.4
8	331	406	3.51
8	333	410	3.9
8	334	408	3.3
8	335	417	5.1
8	336	415	5.35
8	340	373	2.6
8	341	420	5.62
8	344	402	5.6
8	345	418	4.92
8	346	405	5.55
8	347	426	4.72
8	348	419	4.55
8	351	403	2.75
8	353	405	2.75
8	354	410	4.4
8	355	420	5.5
8	357	405	3.7
8	359	421	4.68
8	362	396	3
8	364	443	4.55
8	365	434	3.4
8	366	438	5.5
8	369	439	4.2
8	370	429	4.7
8	371	437	6.31
8	372	405	3.5
9	373	420	7.56
9	374	405	3.8
9	376	418	3.8
9	378	408	2.92

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
9	379	405	3
9	380	408	5.1
9	381	410	4.2
9	382	414	5
9	383	407	4.3
9	384	412	4.6
9	386	409	2.9
9	388	416	4.78
9	389	410	4.3
9	390	402	7
9	391	398	6.48
9	392	408	6
9	393	422	4.5
9	397	413	3.4
9	398	412	6.2
9	399	392	3.4
9	400	417	5.35
9	402	421	4.1
9	403	423	7.91
9	404	415	7.2
9	406	414	5.6
9	407	414	5.3
9	408	420	3.6
9	411	424	7.48
9	412	434	5.5
9	414	423	5.85
9	416	407	6.95
9	418	419	5.12
9	424	428	3.5
9	425	425	4.1
9	426	422	3.57
9	427	413	4.1
9	435	415	4.6

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
9	437	431	7.1
9	438	420	3.5
9	440	441	7.25
9	444	420	3.6
9	446	416	4.7
9	447	417	3.85
9	455	430	6.28
9	456	438	5.4
9	457	432	5.8
9	458	428	4.4
9	460	412	5.32
9	462	416	7.08
9	465	388	3.71
9	466	391	3
9	468	406	4.2
9	469	399	2.9
10	472	441	6.25
10	473	440	8.3
10	474	429	5.61
10	475	444	8.82
10	478	440	5.85
10	479	459	4.79
10	480	445	5.08
10	482	449	5.61
10	489	475	4.2
10	490	456	6.1
10	493	447	4.7
10	497	448	5.3
10	500	451	5
10	504	464	7.1
10	511	459	5
10	512	455	4.9
10	513	471	3.75

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
10	515	458	3.7
10	517	451	4
10	519	467	4
10	520	459	4.58
10	522	470	5.55
10	523	453	3.1
10	524	473	5.6
10	526	470	3.65
10	528	461	4.4
10	530	481	4.9
10	531	473	7.5
10	532	474	4.6
10	535	456	5.5
10	536	459	6.3
10	537	454	5.6
10	539	458	7.5
10	540	462	5.4
10	542	478	4.5
10	543	469	4.5
10	544	467	3.7
10	545	450	6.85
10	548	447	4.38
10	549	445	5.11
10	550	449	4.05
10	553	277	2.6
10	555	456	4.3
10	556	459	5.95
10	557	461	5.6
10	563	460	4.1
10	565	474	5.71
10	566	471	3.1
10	567	471	4.31
10	568	488	4.65

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
10	569	478	5.2
10	573	467	5.4
11	577	481	4.65
11	578	467	6.1
11	579	461	6.1
11	580	473	5.3
11	581	464	5.3
11	584	471	6.42
11	586	480	5.9
11	588	481	4.96
11	589	470	4.2
11	590	476	7.82
11	591	483	6.9
11	593	472	5.55
11	600	478	4.4
11	603	460	7.26
11	604	338	3.1
11	605	456	4.7
11	609	479	3.6
11	610	464	5.55
11	611	461	5.15
11	612	479	6.22
11	616	481	3.61
11	617	462	4.4
11	622	488	5.8
11	623	474	9.22
11	628	474	4.51
11	630	478	4.4
11	633	466	5.05
11	638	458	6.83
11	642	457	4.3
11	643	204	1.8
11	644	449	4.1

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
11	647	449	4.25
11	649	448	4.4
11	654	454	5.11
11	655	435	5.3
11	658	449	8.2
11	659	454	5.1
11	660	449	5.91
11	661	431	8
11	671	461	5.1
11	675	319	3.21
11	676	442	5
11	678	453	4.8
11	682	472	4.51
11	683	468	5.6
11	689	477	6.7
11	691	474	7.85
12	695	480	4.55
12	696	469	7.31
12	698	477	4.3
12	717	445	4.99
12	718	461	4.4
12	725	458	5
12	730	455	4.94
12	731	458	4.1
12	732	452	3.6
12	734	458	6.9
12	736	455	3.9
12	749	444	4.45
12	750	427	4.05
12	751	445	4.65
12	758	456	5.2
12	763	462	4.7
12	764	451	6.91

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
12	765	451	5.41
12	767	464	4.6
12	769	447	5.32
12	771	476	6.51
12	775	465	5.2
12	790	438	5.1
12	793	447	5.35
12	794	464	5.32
12	795	449	3.7
12	800	428	8.1
12	801	440	8.25
12	804	427	3.9
12	812	436	6.13
12	814	465	5.85
12	819	443	5.7
12	821	423	5.1
12	845	437	4.55
12	848	435	6.1
12	851	433	5.15
12	861	448	5
12	867	438	5.08
12	868	436	4.4
12	869	444	5.8
12	872	461	5.7
12	873	466	4.6
12	874	481	4.75
12	875	457	4.75
12	876	449	5.4
12	883	450	4
13	892	468	6
13	902	447	6.72
13	904	437	5
13	918	450	6.4

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
13	932	435	4
13	937	438	5.8
13	938	423	6.3
13	945	429	7.6
13	946	425	4.3
13	948	426	3.9
13	949	408	4.4
13	950	431	4.9
13	952	439	4.28
13	953	445	7.9
13	975	436	4.45
13	977	445	6
13	979	436	5.1
13	980	441	5.13
13	981	440	6.7
13	982	441	3.8
13	983	443	5.1
13	986	450	6
13	987	445	4.7
13	989	417	4.1
13	990	437	4.6
13	991	441	7.7
13	997	441	4.15
13	999	424	4.9
13	1005	457	5.35
13	1007	441	4
13	1008	440	4.8
13	1009	454	4.4
13	1010	457	3.68
13	1012	461	4.3
13	1014	468	5.4
13	1016	456	7.62
13	1017	452	7.5

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
13	1020	462	5.8
13	1021	437	3.5
13	1022	448	4.8
13	1023	442	4.08
13	1024	442	3.7
13	1025	460	6.1
13	1026	459	5.5
13	1028	451	5.23
13	1029	462	4.9
13	1030	459	5.23
13	1031	458	5.15
13	1032	467	5.35
13	1033	470	6.5
13	1034	469	6.5
14	1124	472	6.31
14	1125	483	9.2
14	1134	484	7
14	1139	464	5.4
14	1144	460	6.2
14	1145	451	5
14	1150	475	5
14	1156	460	4.44
14	1157	471	4.4
14	1158	477	6.2
14	1159	462	7.7
14	1161	444	4.2
14	1162	461	5.85
14	1165	473	4.75
14	1166	489	7.4
14	1170	479	5.4
14	1173	476	5.8
14	1176	486	4.6
14	1180	483	8.7

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
14	1181	469	7.6
14	1182	454	4.3
14	1183	465	5.3
14	1184	471	7.1
14	1190	467	4.48
14	1191	444	4.5
14	1193	466	6
14	1194	469	4.4
14	1195	476	5.3
14	1197	473	5.5
14	1198	473	8.8
14	1205	488	7.92
14	1206	479	4.45
14	1209	467	5.45
15	1210	472	5.5
15	1212	471	4.45
15	1213	482	5.6
15	1216	475	5.71
15	1219	470	6.6
15	1221	433	4.2
15	1222	475	6.3
15	1223	473	7.6
15	1224	474	6.2
15	1226	479	6.75
15	1227	465	6.4
15	1227A	456	5
15	1230	464	4.7
15	1231	423	4.5
15	1232	450	5.8
15	1233	454	6.9
15	1234	437	5.6
15	1235	412	4.3
15	1237	434	4.2

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
15	1238	431	4.7
15	1239	459	6.6
15	1240	437	4.9
15	1244	439	5.7
15	1246	440	6.3
15	1247	423	5.3
15	1248	444	6.6
15	1254	465	5.55
15	1255	465	5.6
15	1257	458	4.5
15	1258	452	5.39
15	1260	447	6.5
15	1261	451	5.8
15	1262	444	4.6
15	1263	433	3.85
15	1264	450	6
15	1268	433	5.15
15	1269	450	5.32
15	1271	437	4.3
15	1275	444	4.72
15	1276	439	4.8
15	1278	441	4.6
15	1280	439	4.8
15	1281	432	4.58
15	1282	424	3.08
15	1285	439	5.1
15	1286	445	6.31
15	1287	441	5.9
15	1288	452	5.7
15	1292	449	5.2
16	1293	426	5.6
16	1294	446	7
16	1295	441	5.6

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
16	1296	445	4.8
16	1298	433	6.72
16	1302	422	5.4
16	1303	429	3.95
16	1304	440	7.8
16	1306	438	4.5
16	1308	418	4
16	1310	432	4.78
16	1311	437	2.9
16	1312	432	4.5
16	1313	430	4.9
16	1320	432	3.58
16	1322	431	4.6
16	1328	439	3.62
16	1330	424	6.3
16	1332	437	5.68
16	1334	419	5.62
16	1335	428	5.3
16	1336	432	9.45
16	1338	418	6
16	1339	416	6.8
16	1340	427	5.6
16	1342	416	5.68
16	1344	317	3.8
16	1345	419	4.7
16	1346	423	5
16	1347	429	4.4
16	1348	408	2.8
16	1351	414	6.2
16	1353	410	6.4
16	1355	425	5.9
16	1358	433	5.8
16	1365	425	4.9

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
16	1366	431	6.4
16	1367	433	5.7
16	1373	442	4.3
16	1375	461	7
16	1377	461	7.38
16	1378	420	6.2
16	1382	415	3.65
16	1383	420	4.2
16	1387	413	5.4
16	1388	417	5
16	1390	425	4.35
16	1394	433	5.4
16	1397	432	6.4
16	1399	425	5.7
16	1400	420	5.5
16	1401	413	3.6
16	1402	428	7.55
16	1404	425	7
16	1405	431	6.9
22	1799	467	5.5
22	1800	458	6.8
22	1802A	461	6
22	1803	470	6.25
22	1804	453	11.4
22	1805	425	3.9
22	1806	452	5.65
22	1807	420	4.6
22	1810	426	3.2
22	1811	440	6.2
22	1812	437	4.1
22	1818	428	4.7
22	1819	432	4.8
22	1824	448	6.2

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
22	1826	458	6.8
22	1830	449	4.7
22	1832	456	5.1
22	1834	471	7.1
22	1835	471	5
22	1838	467	6.7
22	1839	476	4.9
22	1843	475	5.7
22	1844	472	4.6
22	1845	457	5.6
22	1846	462	4.7
22	1848	468	8.5
22	1848A	450	4.4
22	1849	466	4.9
22	1850	467	6
22	1851	461	5.1
22	1851A	443	4.8
22	1851B	454	4.53
22	1852	450	6.1
22	1853	465	5.3
22	1858	461	7.7
22	1862	457	5.8
22	1863	467	8
22	1865	464	5
22	1866	473	4.6
22	1870	470	5.1
22	1871	443	3.6
22	1875	473	6.7
23	1876	472	4.3
23	1878	472	4.3
23	1879	473	6.2
23	1879A	460	4.1
23	1880	480	6.3

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
23	1881	460	4.8
23	1882	456	5.6
23	1884	472	4.62
23	1885	461	5.5
23	1887	485	6.75
23	1888	455	4.5
23	1888A	448	4.4
23	1889	482	6.2
23	1892	452	5.1
23	1893	459	3.7
23	1894	447	4.9
23	1898	467	5.65
23	1900	490	5.8
23	1901	480	5.1
23	1903	490	7.5
23	1904	482	7.1
23	1906	500	4.78
23	1907	484	3.8
23	1909	476	5.9
23	1910	470	4.5
23	1912	482	7.3
23	1912A	459	4
23	1913	489	6.8
23	1916	490	5.2
23	1918	443	3.4
23	1919	470	5
23	1920	475	5.1
23	1921	447	4.4
23	1924	477	4.8
23	1927	486	7.1
23	1928	465	3.8
23	1931	482	6
23	1932	473	6.2

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
23	1936	475	6.2
23	1937	483	6.4
23	1938	468	4.9
23	1941	460	5.3
23	1942	466	4
23	1943	477	3.8
23	1944	473	6.7
23	1945	484	5.5
23	1947	456	4.68
23	1948	476	5.7
23	1949	450	4.6
24	1951	485	6.4
24	1951A	496	5.1
24	1951B	488	6.5
24	1952	466	6.66
24	1953	454	4.4
24	1954	457	5.7
24	1956	454	4.1
24	1957	464	5.6
24	1957A	469	5.1
24	1959	472	6.7
24	1960	471	6.2
24	1961	474	5.8
24	1962	450	4.3
24	1963	481	5.5
24	1964	472	7.9
24	1965	456	4.45
24	1968	458	6
24	1969	489	6
24	1970	469	5
24	1971	482	5.8
24	1972	462	3.62
24	1973	474	6.32

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
24	1975	472	4.25
24	1977	479	5.3
24	1978	489	7.4
24	1987	459	3.5
24	1988	486	5.1
24	1989	494	6.9
24	1990	486	7.5
24	1991	488	5.2
24	1997	472	8.15
24	1998	449	6.4
24	1999	474	7
24	2000	441	3.91
24	2001	463	5.41
24	2001A	487	6.79
24	2004	501	7
24	2004B	503	7.8
24	2004A	505	5.9
25	2007	496	4.1
25	2008	488	6.1
25	2017	492	5.4
25	2019	489	7.83
25	2019A	467	5.28
25	2020	461	4
25	2022	467	4.3
25	2024	458	3.82
25	2028	458	5.58
25	2030	459	5.6
25	2031	471	5.5
25	2032	471	6.2
25	2034	480	6.62
25	2034A	473	5.4
25	2035	494	4.9
25	2037	466	5.1

Plot No.	Tree No.	H (cm)	$D_{0.1H}$ (cm)
25	2039	479	3.8
25	2041	466	4.7
25	2042	440	3.6
25	2044	479	5
25	2048	489	3.3
25	2049	470	5.2
25	2050	508	6.1
25	2052	500	8.2
25	2053	502	8.5
25	2055	503	7.6
25	2060	480	4.4
25	2062	494	4.75
25	2063	502	5.4
25	2066	456	3.7
25	2068	502	7.2
25	2069	489	5.9
25	2070	497	9.28
25	2071	484	5.2
25	2072	500	8.3
25	2074	500	14.3