

Pruning Chinese Trees

An
Experimental
and
Modelling
Approach

Bo Zeng

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Pruning Chinese Trees – an experimental and modelling approach

ISBN: 90-393-2839-0

Keywords: biomass production, biomass partitioning, growth, leaf efficiency, modelling, pruning, subtropical China, trees

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Printed:	Print Partners Ipskamp, Enschede
Cover:	Pieter van Dorp van Vliet
Layout:	Bo Zeng
Photos:	Marinus J. A. Werger

Pruning Chinese Trees

An Experimental and Modelling Approach

Bomen snoeien in China
Een experimentele en modelmatige benadering

(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad
van doctor aan de Universiteit Utrecht
op gezag van de Rector magnificus, Prof. Dr. W. H. Gispen,
ingevolge het besluit van het College voor Promoties
in het openbaar te verdedigen
op maandag 15 oktober 2001
des middags te 12:45 uur

door

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geboren op 21 februari 1972 te Fuling
Chongqing, China

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The studies reported in this thesis were mainly carried out at the Department of Plant Ecology, Utrecht University, the Netherlands, and at Faculty of Life Science, Southwest China Normal University, China. This thesis was financially supported by the Netherlands Foundation for the Advancement of Tropical Research (WB 84-411, WOTRO) and by the Science and Technology Commission of Chongqing Municipality, China.

To my wife

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1

General Introduction

Pruning and its applications

Pruning of trees, which results in the removal of whole branches or parts of branches, has been practiced for centuries and is even described in the Bible. Usually, pruning is applied for several purposes.

Improving timber quality

In timber production, apart from the quantity, the quality of timber is another main concern of forest managers. Two indexes are often used to evaluate the quality of timber. One is the number of knots in wood and the other is the taper of the log (Shepherd 1986; Waugh and Yang 1994).

Branches on a tree are the source of knot formation. While branches remain on the stem of a tree, the wood laid down contains knots. In industrial forestry, pruning is applied (especially to trees that poorly prune naturally) to attain knot-free timber. To this end, pruning is seldom done only once, but usually more times at short intervals (depending on the growth of species) with each pruning going successively higher up the tree until the required length of the pruned stem is reached. For instance, Vincent (1972) suggested three prunings of *Alstonia macrophylla* grown for match production. Each pruning was 3 meters high, and was done when trees were 5, 8, and 11 years old to get 9 meters of pruned stem. If pruning was postponed until the tree could be pruned at once to 9 meters, a wasteful, large core of big knots would be the result.

The diameter increment of the stem is mainly due to the accretion of xylem in the stem. At any position in the stem, the xylem present there is the aggregation of xylem vessels extending from all branches above this position, which has been described and proved by Shinozaki et al. (1964 a, b). Consequently, the stem of a tree is tapering from the basal end to the terminal end. Branch removal caused by pruning may reduce the accretion of xylem vessels in the pruned part of the stem and leads to a reduced stem taper (Kozłowski et al. 1991; Larson 1965). Stems of young trees are much more responsive to pruning as regards taper alteration than those of old trees (Kozłowski et al. 1991). This responsiveness is influenced by species, stand characteristics, and the intensity and timing of pruning (Kozłowski et al. 1991).

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Obtaining desirable plant materials

Pruning trees to get desirable plant materials was already used by our prehistoric ancestors, and has continued to the present age. Pruning can provide people with fuelwood and charcoal, fodder and forage, building and fencing materials, pulpwood, and food such as fruits and edible shoots (Evans 1992). It can also provide raw materials for weaving (Dijkman 1999), thatching (Zuidema 2000), tool making and medicine production (Evans 1992; Zhang 2001). Three of the five basic physical requirements of human beings (Evans 1992), fuel, construction materials, and food, can be obtained directly through pruning. The other two requirements are water and clothing. Even for clothing, pruning may provide raw materials, e.g. fibres and, indirectly, silk. Due to its many applications, pruning still plays an important role in the subsistence of people living in developing countries, especially the people in the poor rural areas of these countries. One example is fuel provision. In many tropical countries up to 90 per cent of all wood used is for firewood for cooking and heating (Evans 1992). Most of the needed fuel is achieved through pruning. In many developing countries, pruning trees in special plantations as well as in naturally growing forests (Evans 1992) to obtain desirable materials so as to increase income and raise living standards, is an effective means of rural development and poverty alleviation (FAO 1985a,b; Evans 1992).

Other purposes

Apart from the purposes mentioned above, pruning is also used to: (i) provide easy access into a stand for forest management; (ii) reduce the fire hazard by diminishing the chance of ground fires burning up into the crown; (iii) reduce diseases in trees (Evans 1992; Ho and Schooley 1995; Wardlaw 1996; Cooley et al. 1997; Noriega-Cantu et al. 1999). It is also applied to control flowering and fruiting (Guimond et al. 1998; Nunez-Elisea and Crane 2000), improve crown shapes (Ho and Schooley 1995) and train branches (Hinesley and Snelling 1995).

Pruning practices in China

Pruning practices in ancient times

Pruning has a long history in China. The earliest record of pruning practices is about 4700 years ago, in the time of Huang Di (Yellow Emperor, ca. 2700 BC). There are a lot of descriptions on pruning in *Shi Jing (The Book of Songs)* (before 770 BC) which is the earliest book describing the lives, social and agricultural activities of ancient Chinese people. In military affairs, pruning was widely used for camping and making various sorts of weapons. This is described in the famous book *Sun Zi Bing Fa (Military strategies and tactics)* by Sun Wu around 515 BC. In 105 AD during the Eastern Han Dynasty, Cai Lun

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invented the method of making paper. Pruning then was used as a means of getting raw materials for paper making. In 533 AD, Jia Sixie of the North Dynasties wrote a book entitled *Qi Min Yao Shu (Important Agricultural Techniques for People)*. In this book, he mentioned how to grow trees and how to prune them to meet people's needs. Other uses of pruning in activities such as making farming tools and handcrafts were invented and continue to be used till the present.

Pruning practices in modern times

Similar to other countries, in China, pruning practices are also performed. Besides its application in silvicultural management, pruning is used to obtain fuel and economic plant materials.

Before the middle of the 1990s, pruning was used commonly to collect fuel, especially by people living in rural and mountainous areas. This behaviour was once spread over the whole country at the end of the 1950s due to the unwise movement of steel manufacturing. With the economic development in China, pruning for fuel is not so common now. However, it is still practiced in remote and mountainous regions where traffic conditions are poor and the economy is not so strong. According to a book published in 1992, in the eastern parts (hilly area) of Sichuan province in China, about 66 per cent of the peasant households needed firewood as fuel for cooking (Anonymous I 1992). Most of the firewood was obtained by branch pruning from established firewood plantations, and part of it was obtained from natural forests. In Sichuan, the total area of firewood plantations was about 627,700 hectares around 1990 (Anonymous I 1992).

Planting tea (*Camellia sinensis* O. Kuntze) and mulberry (*Morus alba* L.) trees for tea and silk production is traditional in China. Now it is still being done, especially in south China. Pruning is routinely conducted in these plantations to get raw materials for the production of these two products, and is also used to invigorate the trees when they grow to a certain size.

From many tree species, such as *Ginkgo biloba* L., *Eucommia ulmoides* Oliv., *Cinnamomum petrophilum* (L.) Chao, *Magnolia officinalis* Rehd. et Wils., the branches and/or leaves have been collected and used as Chinese traditional medicines for centuries. In the past, these useful medicines were mostly obtained from naturally growing trees. As a consequence, the production of these medicines was limited. In recent years, many plantations of these species have been established in China and branches and/or leaves for medicine production are obtained through pruning. Planting these medicinal trees has become a major economic source in some regions of China, such as Shandong province and Chongqing municipality. Yancheng county of Shandong province has *Ginkgo biloba* plantations of 8000 hectares, and the farmers of this county made an income of 70 million US dollars in 2000 (Zhang 2001). In 1997, more than 40 per cent of the revenues of Shizhu county in Chongqing municipality came from the plantations of *Ginkgo biloba*. In Youyang prefecture of Chongqing municipality, growing *Eucommia ulmoides* is an important way of increasing the income of farmers (Lu 1998).

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Constraints on tree growth

Growth of a tree is the resultant of many constraints. Among them, ontogenetic, environmental, and genetic constraints are three chief ones.

Ontogenetic constraints

To put it simply, the ontogeny of a tree is the growing process of the tree from birth (small seedling) to death, together with all characteristics related to this ageing process.

During the life time of a tree, many leaves are produced but all of them are dropped along the long journey of growth. However, most of the produced wood tissue remains in the tree for its whole life. This leads to a gradual increment of stem diameter, stem height and an enlargement of the crown in a growing tree. For this reason, morphology- and architecture-related variables of a tree tend to vary with the age of the tree (Poorter 1999). These variables include leaf mass ratio (LMR, leaf mass/total plant mass), stem mass ratio (SMR, stem mass/total plant mass), leaf area ratio (LAR, leaf area/total plant mass), relative crown depth (RCRD, $100 \times (\text{stem length} - \text{height position of lowest branch}) / \text{stem length}$), crown width, crown area, leaf area index (LAI), etc. When a tree is growing, its architecture changes consequently, which results in a change in carbon balance. It is well known that the relative growth rate of trees decreases with age (Poorter 1998; Bruhn et al. 2000), because more assimilates have to be used for maintenance respiration due to the decreasing leaf mass ratio. Cornelissen (1993) showed that ontogenetic shifts from seedling to sapling affected tree growth patterns more than shifts during the later sapling stages. The ontogenetic status of a tree also affects the shoot extension growth (Centritto et al. 1999), biomass partitioning (King et al. 1999), and shoot size and number (Chazdon 1991; Ritchie and Keeley 1994).

Photosynthesis, as the ultimate driving force of growth, is affected by the ontogenetic status of a tree as well. In a study of five boreal tree species, Tjoelker et al. (1998) found that the leaf net CO₂ exchange rates of all tree species exhibited modest declines with increasing plant size through ontogeny. In studies of a mangrove species, *Rhizophora mangle* L., Farnsworth and Ellison (1996) demonstrated that seedling and sapling photosynthetic rates were significantly depressed in winter, while photosynthetic rates in leaves of mature trees did not differ between winter and summer.

Environmental constraints

Among all environmental factors influencing tree growth, two essential ones are light and temperature.

Tree growth is powered by light via photosynthesis. A tree gets net gain of carbohydrates when the light intensity is higher than the light compensation point of the

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whole plant (i.e. the total carbohydrate production of the plant is larger than the total maintenance respiration costs) (Poorter 1998). Although under some special circumstances a tree may grow by drawing on its reserves if the light intensity is lower than the light compensation point, it is unable to persist in this reserve-dependent growth.

When trees are exposed to very high light conditions, instead of utilising the high light intensity for growth, their photosynthetic production might decrease (Kozłowski et al. 1991; Cornelissen 1992; Kamaluddin and Grace 1992; Fetcher et al. 1996). Part of the reason is the damage of high light intensity to the photosynthetic apparatus (Kozłowski et al. 1991; Kamaluddin and Grace 1992).

Temperature determines the speed of biochemical reactions thereby affecting the rate of tree growth. It is one of the chief determinants controlling the length of the growing season. In comparison with the tropics, the temperate and boreal zones have lower mean annual temperatures which result in slower growth of the trees living there. Within a certain range, the growth of trees increases with the increase of temperature (Vaisanen et al. 1994; Pereira-Netto and McCown 1999; Sheu and Lin 1999). Very high temperatures do not facilitate but retard the growth of trees (McInnis and Roberts 1995).

Apart from light and temperature, some other environmental factors also play roles in the growth of trees, such as water (Kozłowski et al. 1991), nutrition (Kozłowski et al. 1991), ambient CO₂ level (Rey and Jarvis 1997; Cornelissen et al. 1999; Norby et al. 1999), wind (Cordero 1999), fire (Kozłowski et al. 1991), etc.

Genetic constraints

Any tree species has species-specific growth characteristics, which are primarily controlled by its genetic composition. Owing to these specific growth characteristics, many species can be easily recognized (Halle et al. 1978; Oldeman 1983).

According to their leaf habits and whether their seeds have covers or not, trees are classified into evergreen and deciduous species, and angiospermous and gymnospermous species, respectively. As regards the growth of evergreen vs. deciduous trees, and angiospermous vs. gymnospermous trees, there is a large body of literature (Kozłowski et al. 1991; Yokozawa and Hara 1995; Eamus 1999; Tjoelker et al. 1998; Walters and Reich 1999). Genetic constraints on tree growth are not only demonstrated in trees having large genetic distances from each other, but are also reflected in trees which are genetically similar. It is well documented that hybrids, which are genetically not very different from their parents, hold a much better or worse growth pattern than their parents (Li and Wu 1996; Schmidt-Adam et al. 2000). Even for the same species, clones coming from different provenances show differential growth (Anekonda et al. 1996; Centritto et al. 1999).

In effect, tree growth is the resultant of all constraints including ontogenetic, environmental and genetic ones. When a certain factor acts upon the growth of a tree, it may interact with some other factors.

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Pruning and tree growth

The impact of pruning on tree growth depends not only on the amount of branches and leaves removed, but also on the following factors.

Tree size

When a tree grows, it simultaneously increases its productive tissue (leaf mass) and its unproductive tissue (wood mass). Due to the decrease of leaf area ratio (leaf area/total plant mass), a relatively large proportion of assimilates produced by leaves has to be used to cover the maintenance respiration of the whole tree. Consequently, the relative growth rate of a tree decreases with its increase in size. From the perspective of the relative growth rate, the carbon budget of large-sized trees is relatively more stringent than that of smaller-sized trees. Pruning only takes away branches and leaves, without affecting the stem and root system of trees. Pruning leads to smaller leaf area ratios in large-sized trees as compared to small-sized trees, because of the large mass of remaining stem and roots. This makes the carbon budgets of large-sized trees much more stringent than that of small-sized trees after pruning. It is hypothesized that pruning of large-sized trees is more detrimental to tree growth than that of small-sized trees.

Growth habits

According to the patterns of leaf and shoot emergence during the growing season, tree growth is classified into two types: determinate growth and indeterminate growth (Sprugel et al. 1991). Trees with determinate growth only have a single annual flush of growth and their shoot extension is generally restricted to a relatively short period, like *Pinus massoniana* L. and *Ginkgo biloba*. By contrast, trees with indeterminate growth have continuous leaf and shoot growth throughout the growing season. As a result, after pruning, trees with a determinate growth habit can only rely on their remaining leaves for regrowth and maintenance. However, in addition to the assimilates produced by the remaining leaves, trees with an indeterminate growth habit are able to get more assimilate supply from the new leaves grown after the pruning. In terms of the assimilate status, trees with an indeterminate growth are predicted to be superior to trees with a determinate growth when pruning is imposed.

Pruning season and intensity

Seasonality of tree growth is a common biological phenomenon. Such seasonality could be caused either by water shortage (Eamus 1999; Poorter and Hayashida-Oliver 2000) or by low winter temperatures (Walter 1984; Kozłowski et al. 1991). Water-shortage-caused seasonality mainly occurs in the tropics as a result of the alternation of wet and dry

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seasons. Low-temperature-caused seasonality, characterized by the alternation of warm and cold seasons, can be observed in the subtropical and temperate zones. During the dry or cold seasons, trees grow slower or even stop their growth due to the reduced photosynthesis. Therefore, it is hypothesized that pruning in dry seasons or cold seasons is much less disadvantageous to tree growth than pruning in wet seasons or warm seasons.

Because heavy pruning leads to a greater removal of leaf area than light pruning, heavy pruning more strongly reduces the overall carbohydrate production of a tree. In pruning, not only the productive leaves are removed, but also some unproductive wood. This implies that pruning reduces both the production and the consumption of carbohydrates. Which of the two is reduced more is reflected by the leaf area ratio of the removed material, and will affect the carbon budget of the pruned tree. In general, branches in the lower crown of a tree have a lower leaf area ratio than those in the upper crown. If pruning is done by removing the lowest branch of a tree upwards, like most laborists and foresters do, it is hypothesized that light pruning has less detrimental effects on tree growth than heavy pruning. One reason is that the leaf area removed by light pruning is less; the other reason is that branches removed by light pruning are relatively less productive due to their lower leaf area ratios.

Pruning frequency

Generally, after pruning, tree growth is reduced due to the diminished carbohydrate production. As a consequence, the pruned tree needs some time to fully recover its growth. This time period varies with the pruning intensity and species (Møller 1960; Shepherd 1961; Uotila and Mustonen 1994). Therefore, repeated pruning prior to the full recovery of a pruned tree aggravates the reduction of growth, and it could eventually result in the death of the pruned tree.

Optimizing pruning for plant material harvest

As mentioned before, one of the main purposes of pruning is to harvest desirable plant materials. For this purpose, pruning is seldom done only once for a tree. In practice, it is important for farmers to know how to apply an appropriate pruning regime to obtain a maximal total harvest over a certain time period. Basically, the harvest is dependent on the pruning intensity applied. A higher pruning intensity results in a larger harvest. However, because high pruning intensities severely reduce the tree's regrowth, it is unlikely that a large harvest is obtained in the future when a high pruning intensity is applied. This consequently will reduce the total harvest. Intuitively, it is possible to select an optimal pruning intensity in such a way that the tree's regrowth is not heavily impaired, and the total plant material harvest over a given time period is maximized. This optimal pruning intensity for obtaining a maximal total harvest will be affected by pruning frequency, pruning season, and leaf habit.

General descriptions of subtropical China, study area, and studied species

Subtropical China

The subtropical region of China is located roughly between 22° and 32° N and 99° and 123° E (Fig. 1). It is exposed to the East Asian monsoon. In this region, the average annual temperatures are between 16 and 19 °C, the average monthly temperatures are between 3 and 8 °C in the coldest month and between 24 and 30 °C in the hottest month. Frost occurs occasionally between December and February and the frostless period is more than 250 days per year. Temperatures below –5 °C are rare. Cumulative temperatures (above 10 °C) are between 5000 and 6000 °C-sum. The average annual precipitation is between 1000 and 1700 mm and is concentrated in the period from April to September. Precipitation in winter is less. No significant drought occurs in this region (Zhong 1988; Cornelissen 1993).

Plants in subtropical China have clear seasonal growth patterns. The favourable period for growth is about nine months. In general, plants stop their growth in November and start their growth again next February (depending on the locality) (Zhong 1988).

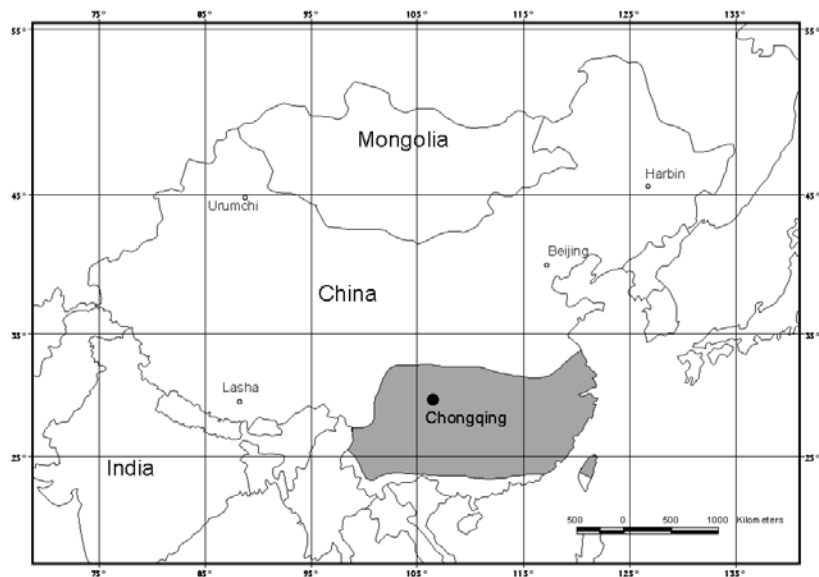


Fig. 1. China and its subtropical region (dark area). The location where the field experiments were conducted is indicated with a closed circle.

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Study area

The field work of this study was conducted in Beibei, Chongqing, China (29° 50' N and 106° 26' E) (Fig. 1).

The substrate of this area is mainly quartziferous sandstone. Soils are yellowish and acidic. Details of the temperature and precipitation of this area are given in Fig. 2 (Li 1998). Average annual relative humidity (RH) of this area is about 80%. The winters are relatively humid and the summers less so. The total duration of direct sunshine is very short in winter (due to a dense cloud cover or fog), intermediate in spring and autumn, and long in summer (Fig. 3).

Studied species and their uses

Five tree species are included in this study. They are two evergreen broadleaved species: *Ficus microcarpa* L. (Moraceae) and *Cinnamomum camphora* (L.) Presl. (Lauraceae), two deciduous broadleaved species: *Ficus virens* Ait. var. *sublanceolata* (Miq.) Cornor (Moraceae) and *Koelreuteria bipinnata* Fr. (Sapindaceae), and one evergreen conifer: *Pinus massoniana* Lamb. (Pinaceae). Trees of all five species can reach heights of more than 20 meters.

Due to their medicinal values, *Ficus microcarpa* and *Ficus virens* trees are pruned to get plant materials for medicine manufacturing. Leaves of *Ficus microcarpa* are used for the treatment of cough, dysentery, and diarrhea. Barks are used for the treatment of diarrhea, hemorrhoids, and tinea. Leaves of *Ficus virens* are used for treating rheumatism (Anonymous II 1994). Because of the shapely crown of these two species, pruning is done sometimes just for aesthetic reasons.

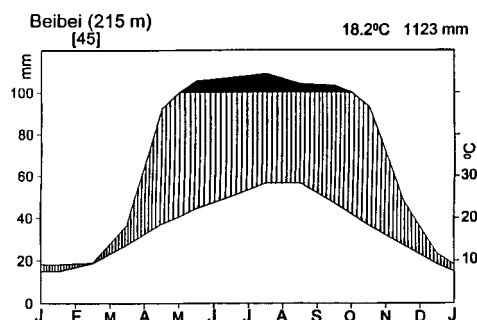


Fig. 2. Climate diagram of Beibei based on data from 1951 till 1995. Cited from Li (1998) with permission.

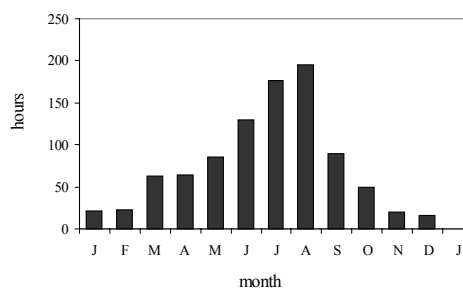


Fig. 3. Monthly total duration of direct sunshine at Beibei from 1997 till 1999 (Beibei Meteorological Station, alt. 215m).

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Cinnamomum camphora is pruned for the extraction of camphor. Leaves and branches of *Koelreuteria bipinnata* can be used for treating cough and as anthelmintics (Anonymous II 1994). *Pinus massoniana* is pruned to improve the quality of timber since it is a chief timber species in subtropical China.

Although the purpose of pruning is not completely the same for every species, pruning of trees to get fuel is a common purpose for all of them.

Aim and outline of this thesis

The aim of the thesis is to evaluate the effects of pruning on the growth and biomass production of subtropical tree species. To this end, two approaches are applied: a field experiment and modelling. In the first part of the thesis, some results based on the field experiment are presented. In the second part, a model of tree growth under a pruning regime is presented, and the simulations of branch harvests are given.

Chapter 2 investigates the biomass production and plant material harvest of several tree species associated with annually repeated pruning. Chapter 3 analyzes the biomass allocation of trees affected by pruning and their dynamics of leaf mass. Chapter 4 explores the bud activation of trees after pruning, trying to find out if the pattern of bud activation has some relations to the pattern of biomass allocation. In Chapter 5, the question is asked whether pruning changes the leaf efficiency of trees and how it does so. Chapter 6 and 7 use a growth model based on a simply formed tree to simulate the effects of pruning. Chapter 6 is the description of the mathematical structure of the model. Chapter 7 is about the simulation of branch harvests. Chapter 8 gives a summary and general discussion based on the results of this study.

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2

Effects of pruning on biomass production and plant material harvest of five subtropical Chinese tree species

Abstract

In subtropical China, trees of a variety of species are grown for harvesting branches and leaves as industrial raw materials, and as firewood for farmers. These plant materials are obtained by annually pruning the lower parts of the crowns of trees. To evaluate the effects of annual pruning on subsequent tree growth and harvests of plant materials, a pruning experiment with four pruning intensities (0%, 20%, 50%, and 70%), two pruning seasons (spring and autumn), and five subtropical Chinese tree species (two evergreen broad-leaved, two deciduous broad-leaved, and one evergreen needle-leaved species) was carried out. Pruning was conducted in three successive years.

Biomass production of pruned *Ficus microcarpa*, *Ficus virens*, and *Cinnamomum camphora* trees decreased following pruning, and this reduction was correlated with pruning intensity. Repeated pruning aggravated the decrease of biomass production. *Pinus massoniana* and *Koelreuteria bipinnata* trees did not show any reduction in biomass production after the first pruning, but their biomass production was decreased after the second and the third pruning, respectively. Higher pruning intensities led to larger harvests of plant materials in all species at the first pruning, but did not necessarily lead to larger plant material harvests at the second and the third pruning. Autumn pruning made trees realize higher biomass production, and led to a larger harvest of plant materials than spring pruning. However, with respect to the biomass production and plant material harvest, no interactions were found between pruning seasons and pruning intensities. The results indicate that the annual pruning regime can not provide enough time for pruned trees of these five species to fully recover. The strong reduction in growth of severely pruned trees may prevent sustainable high harvests of plant materials.

Keywords: biomass harvest, green pruning, pruning regime, subtropical China, tree growth

Introduction

In China, pruning of planted trees is a common practice to provide raw materials for papermaking, chemical and pharmaceutical industries, and supply firewood for farmers (Anonymous 1992). Many kinds of trees are grown for this aim. Usually, the raw materials and firewood are obtained by means of annually clipping the live branches and leaves from the lower parts of the tree canopies by local people, while leaving the upper crown of each tree intact.

Pruning leads to considerable reduction in leaf area, and this supposedly leads to an overall reduction in the assimilate production of the trees. Furthermore, while pruning takes away branches and leaves, the stem and root systems are retained. Thus, a large proportion of the assimilates produced by the residual leaf tissue after pruning (especially under intensive pruning) has to be used for the maintenance of a relatively large mass of remaining unproductive, living support tissue. As a result, assimilate investments in future photosynthetic production (via the formation of new leaf area) become smaller, and the regrowth of trees will be reduced consequently.

However, if there is sufficient recovery time after pruning, such a reduction in regrowth gradually decreases to zero (Lehtpere 1957; Uotila and Mustonen 1994) and pruned plants may resume their normal growing states (Brouwer 1962; Farnsworth and Niklas 1995). The recovery time needed is generally correlated with the severity of pruning. Repeated pruning performed before the full recovery of pruned trees, however, may be expected to cause a steady reduction in the growth of the pruned trees and therefore the potential harvest of plant materials over the years may turn out to be smaller. Some studies on pruning demonstrated that pruned trees did not gain the same growth rates as intact trees within one year after the treatment (Møller 1960; Bandara et al. 1999). However, studies on *Eucalyptus nitens* in south Australia revealed that the rates of CO₂ assimilation of three-year-old *Eucalyptus nitens* increased by up to 175% over a 16-month period following 50% crown pruning (Pinkard et al. 1998). Moreover, the stem dry mass increment of *Eucalyptus nitens* trees was not reduced after 50% crown pruning (Pinkard and Beadle 1998). In a defoliation study carried out in subtropical China, Cornelissen (1993) found that 50% defoliated saplings of *Castanopsis fargesii*, an evergreen broad-leaved tree species, achieved the same plant biomass as control saplings within ca. eight months after the treatment. Nevertheless, whether one year, constrained by annual pruning regime adopted, is sufficient for the pruned trees in subtropical China to recover from the damage remains unknown.

In China, pruning of trees is conducted irregularly in most cases. No fixed pruning season is chosen for the implementation of pruning. The favourable period for plant growth in subtropical China is relatively long, about nine months (Walter 1984), but the growth in winter is nearly zero (Cornelissen 1996). In addition, seasons of maximal growth differ between evergreen and deciduous tree species in subtropical China (Cornelissen 1996). It is likely that pruning conducted in different seasons may affect the growth of trees differently.

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The experiment was designed to investigate the effects of annual pruning on biomass production and harvest of plant materials of trees in subtropical China. Five subtropical tree species were included in the experiment: two evergreen broad-leaved, two deciduous broad-leaved, and one evergreen needle-leaved species. Four pruning intensities and two pruning seasons were adopted in the experiment. The following questions are specifically addressed:

- (1) Can pruned trees gain the same biomass production as intact trees after annually repeated pruning? Is biomass production affected by pruning intensity?
- (2) Is there a linear relation between pruning intensity and the amount of harvested plant materials at any annually repeated pruning?
- (3) Does pruning in different seasons affect biomass production and harvest of plant materials differently?

Materials and methods

Species and study area

The five tree species selected for the study included two evergreen broad-leaved trees, *Ficus microcarpa* L. (Moraceae) and *Cinnamomum camphora* (L.) Presl (Lauraceae), two deciduous broad-leaved trees, *Ficus virens* Ait. var. *sublanceolata* (Miq.) Cornor (Moraceae) and *Koelreuteria bipinnata* Fr. (Sapindaceae), and one evergreen conifer, *Pinus massoniana* Lamb. (Pinaceae). The leaves of *Ficus microcarpa*, *Ficus virens*, and *Cinnamomum camphora* are entire, while the leaves of *Koelreuteria bipinnata* are pinnately compound. In the four broad-leaved trees, shoot extension and leaf production occur not only in the spring flush, but also in summer and autumn (rarely in winter). By contrast, shoot extension and leaf emergence of *Pinus massoniana* are strictly confined to the spring flush. As a pioneer tree species, *Pinus massoniana* occurs naturally in stands at early successional stages in south China. However, trees of the other four species often show up in forests at late successional stages. Trees of all these five tree species are able to reach a height of more than 20 meters.

The field where trees of these five species were planted for study is situated at the foot of the Nature Reserve of Jinyun Mountain (29° 50'N and 106° 26'E), ca. 40 km north of the city of Chongqing, China. The substrate is quartziferous stone. Soils are acidic and yellowish. The climax vegetation of this region is evergreen broad-leaved forest, in which some deciduous and coniferous trees may be found. The climate in this region is monsoonal, resulting in hot, humid summers and chilly but mostly frost free winters. Details of the monsoonal climate of this region are given by Fliervoet et al. (1989), Cornelissen (1992), and Li et al. (1998).

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Tree preparation

In early 1996, 300 small trees (ca. 1.3 meter in height) of each of *Ficus microcarpa*, *Ficus virens*, and *Koelreuteria bipinnata* were planted in the selected fertile field at the foot of Mt. Jinyun. A sufficient number (ca. 300) of small *Cinnamomum camphora* trees could only be obtained and planted in early 1997. *Ficus microcarpa*, *Ficus virens*, and *Cinnamomum camphora* trees had already branched when they were planted. However, few branches occurred in *Koelreuteria bipinnata* trees until the last year of the experiment (year 1999). Trees of these four species were grown with enough spacing to avoid mutual shading during the whole experiment. Weeding, watering, and insecticide spraying were applied to all trees when needed.

300 *Pinus massoniana* small trees (ca. 0.8 meter in height) were chosen in early 1996 from an established young *Pinus massoniana* stand which was located on a hill about 10 km away from the site where other four tree species were planted. Care had been taken by foresters to keep enough spacing between trees, and no mutual shading occurred during the whole period of the experiment. The soil was yellowish sandy loam. Weeding and insecticide spraying were applied to these *Pinus massoniana* trees when needed.

Experimental design

In early 1997, after one year growth for acclimation, for each species (1998 for *Cinnamomum camphora*), 20 randomized blocks were established for pruning treatment. Environmental conditions were visually homogeneous within and between blocks. Each block contained nine trees. These nine trees were subjected to one of the following treatments: 20%, 50%, 70% pruning in spring; 20%, 50%, 70% pruning in autumn; one tree was set as control, and the remaining two trees were harvested in the spring or the autumn of 1997 (the spring or the autumn of 1998 for *Cinnamomum camphora*). Trees were assigned to treatments randomly.

Pruning was conducted in the spring (mid May) of 1997, 1998, and 1999 and in the autumn (early October) of 1997 and 1998 for all species except *Cinnamomum camphora* (not pruned in 1997) and *Pinus massoniana* (not pruned in 1999). Pruning was done by removing branches and leaves from the lower crown, leaving the top of the crown of each tree intact (Fig. 1). For all species except *Pinus massoniana*, this implied that the crown depth of each tree was reduced by 0%, 20%, 50%, and 70%, respectively. The crown depth of a tree was defined as the distance from the apical meristem of the tree to the insertion point of the lowest branch or compound leaf (*Koelreuteria bipinnata*). For *Pinus massoniana*, 0%, 20%, 50%, and 70% of the first-order branches of each tree were excised. The second and the third pruning in 1998 and 1999 were performed in the same way, after removing sprouted branches originated from activated stem buds on the lower stem parts in some pruned trees.

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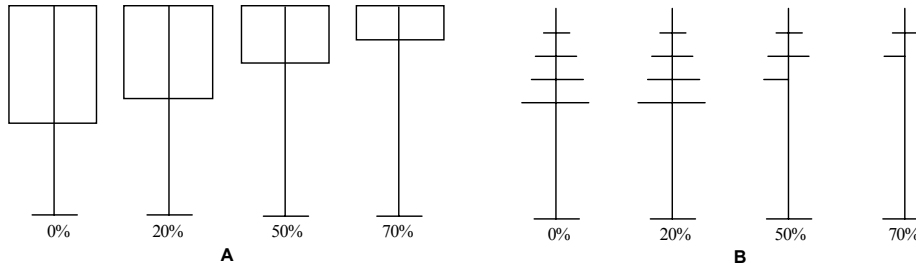


Fig. 1. Illustration of pruning intensities. A: pruning of *Ficus microcarpa*, *Ficus virens*, *Cinnamomum camphora*, and *Koelreuteria bipinnata*. B: pruning of *Pinus massoniana*. See text for details of the pruning treatments on these five tree species.

Biomass measurements

At each pruning treatment, removed branches and leaves were weighed in the field, and a subsample was returned to the laboratory for dry mass determination. Biomass samples were dried at 70°C for 96-120h. Dry weights of removed branches and leaves (which was regarded as the harvest of plant materials) were determined for each tree. Stem, residual branch and residual leaf dry weights (i.e. residual aboveground mass totally) of each tree after pruning were estimated non-destructively (see below). The sum of removed mass and residual aboveground mass was regarded as total aboveground mass. In the autumn of 1999, the aboveground parts of all trees of all species were harvested. Dry weights of the stem, branches, and leaves of each tree were determined.

Determination of stem, residual branch and residual leaf dry weight of each treated tree, after each pruning, was done non-destructively as follows.

In the spring of 1997 (the spring of 1998 for *Cinnamomum camphora*), the aboveground parts of 20 trees (one from each of the 20 blocks) of each species were harvested. For each tree, stem, branches, and leaves were weighed in the field. Length and basal diameter (ca. 10 cm above the soil) of the stem, and length and basal diameter of each first-order branch were measured, and the number of leaves (the number of leaflets for *Koelreuteria bipinnata* and the total leafy shoot length for *Pinus massoniana*) was determined. Stem, branch, and leaf dry weights were determined based on the biomass subsamples analysed in the laboratory. Regression formulas were constructed for all five tree species for stem dry weight on the product of stem length times squared stem basal diameter, and for total branch dry weight on the sum of the product of length times squared basal diameter of all first-order branches. Average dry weight per leaf, average dry weight per leaflet, and average needle dry weight per unit length of leafy shoot were determined for *Ficus microcarpa*, *Ficus virens*, *Cinnamomum camphora*, *Koelreuteria bipinnata*, and *Pinus massoniana*, respectively. With this information, the dry weights of the stem, residual branches and leaves of each spring-treated tree after the first spring pruning were

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determined. Average dry weight per leaf (or per leaflet and per unit length of leafy shoot) was also used to estimate the total dry weight of residual leaves in each spring-treated tree in the spring of 1998 and 1999.

Likewise, in the autumn of 1997 (the autumn of 1998 for *Cinnamomum camphora*), another 20 trees (from 20 blocks) of each species were harvested and analysed in the same way. With the information from harvested trees, the dry weights of the stem, residual branches and leaves of each autumn-treated tree after the first autumn pruning were estimated. Constructed regression formulas for stem dry weight based on the harvested trees were also used to estimate stem dry weights of treated trees in the spring of 1998 (the spring of 1999 for *Cinnamomum camphora*). Average dry weight per leaf (or per leaflet and per unit length of leafy shoot) based on harvested trees was used to estimate the dry weight of residual leaves in each autumn-treated tree in the autumn of 1998.

In the autumn of 1998, for all species except *Cinnamomum camphora*, 5 blocks out of 20 were randomly selected and trees in these five blocks were harvested. With these harvested trees, regression formulas for stem dry weight and branch dry weight were constructed. The dry weights of stem and branches of each treated tree of these species in the autumn of 1998 and the spring of 1999 were estimated, using these regression formulas.

Data analysis

Biomass production per tree was defined as the difference between the aboveground mass one year after pruning and the residual aboveground mass immediately after treatment (with an exception for the period from the spring to the autumn of 1999, which was in effect ca. one growing season).

For each pruning season, effects of pruning intensity and pruning year on the amounts of removed branch and leaf mass (harvest of plant materials) and biomass production were evaluated for each species by using two-way ANOVAs. Duncan's multiple range test was used to check the differences between pruning intensities in each pruning year and the differences between pruning years. Data of year 1999 were excluded when the effects of pruning season and pruning intensity on biomass production and harvest of plant materials were explored by using two-way ANOVAs, since no pruning treatment was conducted in the autumn of 1999. Logarithmic transformation was conducted to equalize variances if necessary.

Results

Biomass production

Pruning reduced biomass production of *Ficus microcarpa*, *Ficus virens*, and *Cinnamomum camphora*, in both spring- and autumn-treated trees (Fig. 2). Pruning did not reduce biomass production of spring- and autumn-treated *Pinus massoniana* trees after the first

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pruning conducted in 1997, but decreased their biomass production after the second pruning conducted in 1998 (Fig. 2). After the first and the second pruning, spring- and autumn-pruned trees of *Koelreuteria bipinnata* did not show reduced biomass production, but biomass production of these trees was reduced after the third pruning conducted in the spring of 1999 (Fig. 2). Generally, after each annual pruning, biomass production declined with increasing pruning intensities for all species except *Koelreuteria bipinnata*.

Annually produced biomass increased in unpruned trees with the years. But, in most cases, the biomass increase in repeatedly pruned trees was greatly reduced, which resulted in a steadily increasing difference in annual biomass production between unpruned and pruned trees (see the interaction between pruning year and pruning intensity in Fig. 2).

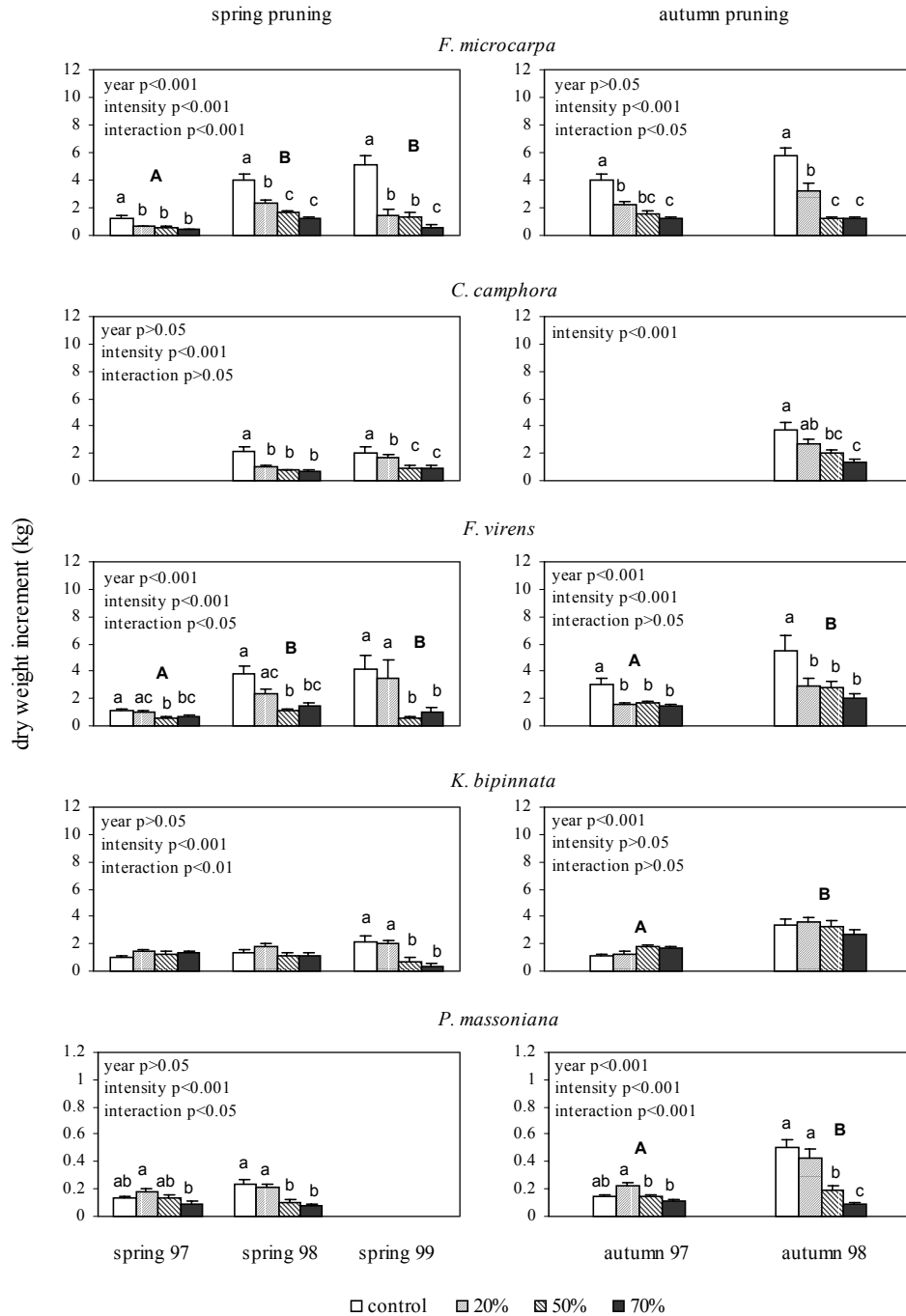
In either of year 1997 and 1998, autumn-pruned trees had higher biomass production than spring-pruned trees (Table 1, Fig. 2). No interactions between pruning season and pruning intensity on biomass production were found for all species (Table 1).

Harvest of plant materials

At the first pruning, conducted in the spring and the autumn of 1998 for *Cinnamomum camphora*, and in 1997 for the other four species, the harvests of plant materials were larger as the intensity of pruning was higher (Fig. 3). However, at the second pruning, 70% pruning did not always lead to a higher harvest of plant materials than the lower pruning intensities. *Ficus microcarpa*, *Pinus massoniana*, and spring-pruned trees of *Ficus virens* showed no difference in the harvest of plant materials between pruning intensities at the second pruning.

At the third spring pruning, which was applied only to *Ficus microcarpa*, *Ficus virens*, and *Koelreuteria bipinnata*, the plant material harvests in the 20% pruning treatments were not lower than those in the 50% and 70% pruning treatments (Fig. 3). For the *Ficus virens* trees, 20% pruning led to a higher harvest than 50% pruning, and for *Ficus microcarpa* trees, 50% pruning led to a higher harvest than 70% pruning. Although not significant, 20% spring-pruning tended to result in the largest plant material harvests in *Koelreuteria bipinnata* trees. The interactions between pruning intensity and pruning year on the harvest of plant materials were significant in all species except *Cinnamomum camphora* (Fig. 3). In either of year 1997 and 1998, autumn pruning led to a higher harvest of plant materials in all species except *K. bipinnata* (Table 1, Fig. 3). No interactions between pruning season and pruning intensity on plant material harvests were found for all species (Table 1).

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(Figure legend follows)

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Fig. 2. Biomass production (mean±se) of five subtropical Chinese tree species one year after each spring or autumn pruning (with an exception that ca. one growing season after the pruning in the spring of 1999). Pruning was done in the spring of 1997, 1998, 1999 and in the autumn of 1997, 1998 for all species except *Cinnamomum camphora* (not in 1997) and *Pinus massoniana* (not in 1999). Pruning intensities were 0% (control), 20%, 50%, and 70%. Within each pruning of each species, means which share the same lower-cased letters are not significantly different from one another. Within each pruning season of each species, different upper-cased letters are used to indicate differences in overall mean biomass production (not shown in the figure) between years. No letter-indications are shown when there are no differences between treatments.

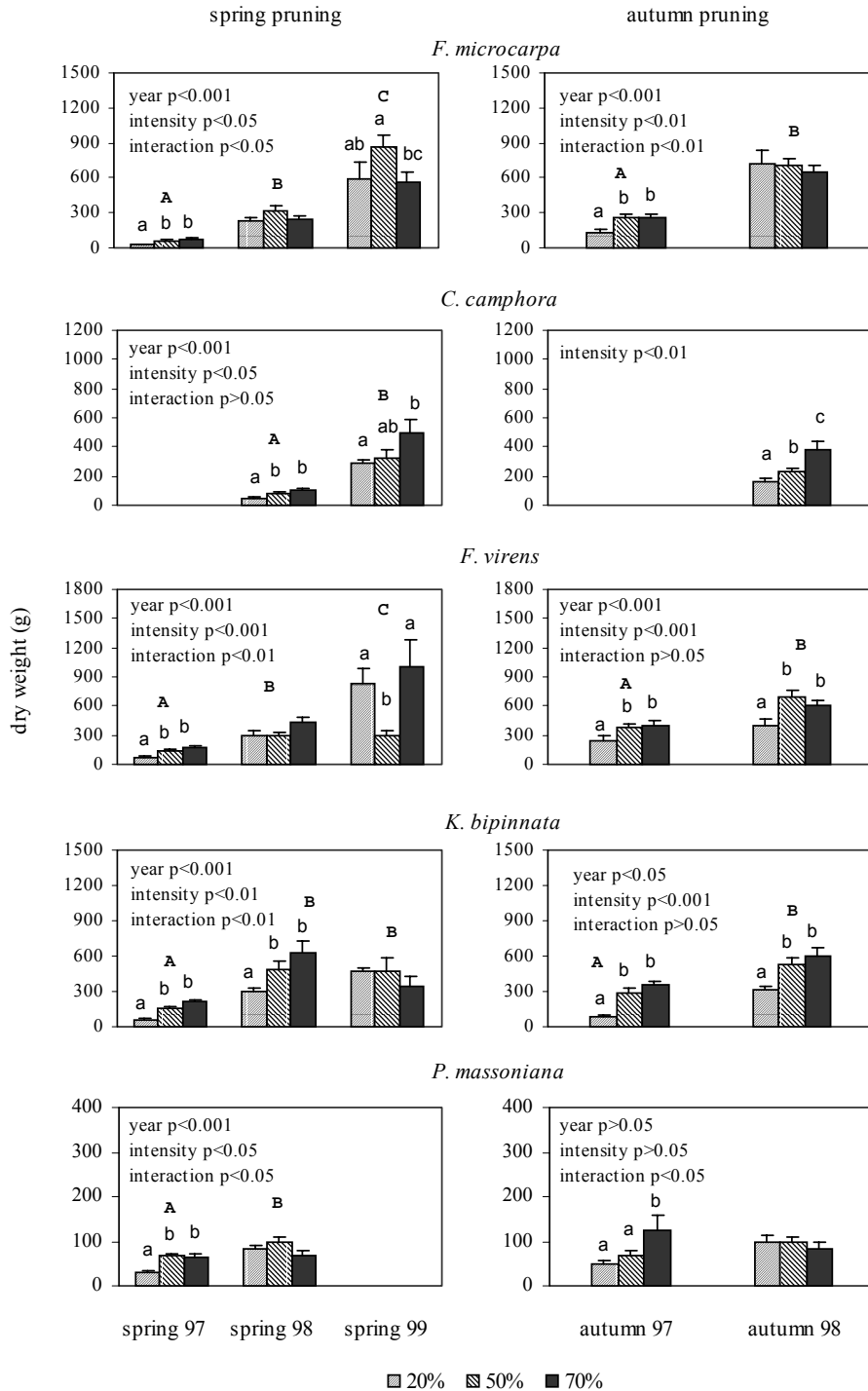
Table 1. The effects of pruning season and the interactions between pruning season and pruning intensity on biomass production and plant material harvest of five subtropical Chinese tree species. Data of year 1999 were excluded when two-way ANOVAs were applied to evaluate the effects and interactions.

species	biomass production		plant material harvest	
	season	interaction	season	interaction
<i>F. microcarpa</i>	68.65 ^a *** ^b	0.76 ns	201.62 ***	0.31 ns
<i>F. virens</i>	62.51 ***	1.06 ns	96.23 ***	1.91 ns
<i>C. camphora</i>	59.73 ***	1.02 ns	79.97 ***	0.21 ns
<i>K. bipinnata</i>	75.40 ***	0.90 ns	1.09 ns	2.05 ns
<i>P. massoniana</i>	14.86 ***	0.27 ns	4.84 *	1.48 ns

a F values.

b Significance levels: ns Not significant; * p<0.05; ** p<0.01; *** p<0.001.

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(Figure legend follows)

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Fig. 3. Amount of harvested biomass (mean±se) of five subtropical Chinese tree species at each spring and autumn pruning. Pruning intensities were 20%, 50%, and 70%, and pruning was done in the spring of 1997, 1998, 1999 and in the autumn of 1997, 1998 for all species except *Cinnamomum camphora* (not in 1997) and *Pinus massoniana* (not in 1999). Within each pruning of each species, means which share the same lower-cased letters are not significantly different from one another. Within each pruning season of each species, different upper-cased letters are used to indicate differences in overall mean harvests of plant materials (not shown in the figure) between years. No letter-indications are shown when there are no differences between treatments.

Discussion

The results clearly show that annual pruning reduced biomass production of *Ficus microcarpa*, *Ficus virens*, and *Cinnamomum camphora*, and severely pruned trees tended to produce less biomass in the year after pruning than lightly pruned trees. Similar results have been obtained by Lehtpere (1957), Møller (1960), Uotila and Mustonen (1994). Most likely, this reduction is due to the diminished overall photosynthesis of pruned trees, because pruning of branches leads to a decrease in remaining leaf area and to a decrease in the number of buds from which new branches and leaves can be produced.

In this study, the deciduous *Koelreuteria bipinnata* trees showed no difference in biomass production after the first and the second spring pruning. Only after the third spring pruning, trees began to show reduction in biomass production (Fig. 2). This remarkable response is probably due to the fact that young *Koelreuteria bipinnata* trees seldom branch: only few branches appeared in treated trees before 1999. More than 95%, sometimes even 100% of harvested biomass was leaf mass at the first and the second pruning. In a strict sense, pruning conducted in 1997 and 1998 actually was defoliation rather than pruning. Only at the third spring pruning, when the *Koelreuteria bipinnata* trees had formed some branches, branch mass began to take a bigger proportion of the total mass removed. Obviously, *Koelreuteria bipinnata* is able to recover from pure leaf loss quickly, because all buds remain on the tree after the treatment and the unaffected bud bank allows quick regrowth of leaf area and thus biomass production as in unpruned trees. When pruning also implies branch loss, a lot of buds are lost and new buds have to be produced to regenerate large leaf areas and high biomass production. This may explain why *Koelreuteria bipinnata* did not show reduced biomass production after the prunings in 1997 and 1998, but only did so after the third pruning when some branches and buds were removed.

As regards *Pinus massoniana*, the first pruning, either conducted in spring or in autumn, did not cause any reduction in the regrowth of trees. Compared with unpruned trees, 20% pruned trees of *Pinus massoniana* even tended to realize a higher biomass production one year after the first pruning, although the increase was not statistically significant (Fig. 2). It is obvious that compensatory growth occurred in pruned *Pinus*

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massoniana trees. As a response to pruning, *Pinus massoniana* trees increased the nitrogen content in their needles (data not shown), such a response was found in red maple and red oak trees (Heichel and Turner 1983), and in a birch species (Hoogesteger and Karlsson 1992). Since foliar photosynthetic capacity is positively correlated with foliar nitrogen content (Hirose and Werger 1987; Evans 1989; Hoogesteger and Karlsson 1992), this may explain why *Pinus massoniana* showed compensatory growth after pruning. In a defoliation study carried out at the same study site as ours, Cornelissen (1993) found that 50% defoliated *Pinus massoniana* trees got higher relative biomass gains than non-defoliated trees. He suggested that this compensatory growth might be partly due to the enhanced photosynthetic rates in old leaves after treatment, which is possible when nitrogen contents are elevated. It has been found that some other *Pinus* species also showed compensatory growth after severe leaf loss (Miller et al. 1978; Miller and Wagner 1989).

Generally, autumn-pruned trees realized higher biomass production than spring-pruned trees (Table 1, Fig. 2), and autumn pruning resulted in a larger harvest of plant materials than spring pruning (Table 1, Fig. 3). However, no interactions were detected between pruning season and pruning intensity for these two variables (Table 1). It seems that the effects of pruning intensity on biomass production and plant material harvest can not be influenced by pruning season.

The reduction in growth caused by leaf loss is related to the length of the time period for regrowth. If the time period is long enough, damaged trees are able to recover and eventually no sign of the damage remains (Lehtpere 1957; Uotila and Mustonen 1994; Krause and Raffa 1996). It is shown in this study that one year was not sufficient for the pruned trees in subtropical China to gain full recovery and achieve the same biomass increments as intact trees (Fig. 2), even though the trees in subtropical China have a relatively long growing season (Walter 1984). Harvests of plant material were correlated with pruning intensities at the first pruning in this study, but not correlated with pruning intensities at the second and the third pruning (Fig 3). Based on the results of this study, it appears that, in subtropical China, an annual pruning intensity of 70% was too high to sustainably provide high harvestable amounts of plant material. The optimal pruning intensity for sustainable high harvests of plant material should be considerably less than 70%, probably between 20% and 50%. However, since the regrowth of plants after damage is also affected by plant size (Pinkard et al. 1998), frequency of treatment (Whitney 1974), and times of treatment (Wagner 1952), a more accurate determination of optimal pruning intensities for sustainable maximal plant material harvests requires long-term experiments with a larger range of plant sizes. Additionally, for the accurate determination of optimal pruning intensities, application of a model taking plant growth characteristics into account would be helpful.

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Acknowledgements

I thank Prof. Marinus J.A. Werger and Dr. Heinjo During for their helpful comments on an earlier version of the manuscript. This study was funded by grant WB 84-411 of the Netherlands Foundation for the Advancement of Tropical Research to Prof. M. J. A. Werger, and partly supported by Science and Technology Commission of Chongqing Municipality, China through grant 1999 to Bo Zeng.

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3

Aboveground biomass allocation and leaf development of Chinese subtropical trees following pruning

Abstract

To evaluate the effects of pruning on aboveground biomass allocation of trees and their aboveground leaf mass ratios, a pruning experiment with four pruning intensities (0%, 20%, 50%, and 70%), two pruning seasons (spring and autumn), and four subtropical Chinese tree species was carried out. Pruning treatments were conducted in two successive years.

In contrast to the prediction based on the pipe model theory, pruned trees allocated proportionally more of their aboveground biomass to leaves and less to wood growth in most cases, irrespective of species and pruning seasons. This allocation pattern was positively correlated with pruning intensity. Pruning reduced the aboveground leaf mass ratios of trees instantaneously. However, due to the increased proportional allocation of aboveground biomass to leaves following pruning, all pruned trees reached the same aboveground leaf mass ratios as unpruned trees within one year after pruning (except for *P. massoniana* after the second pruning). This unexpected biomass allocation pattern might be attributed to the reuse of open vascular channels in stem which were formerly connected to removed branches and leaves, and the production of new branches and leaves beneath the crowns of pruned trees. The increased proportional allocation of aboveground biomass to leaves following pruning, would benefit pruned trees to alleviate negative pruning effects and recover from the damage.

Keywords: biomass allocation, leaf mass ratio, pipe model theory, pruning, trees

Introduction

The growth of trees is powered by the supply of assimilates which are chiefly produced by leaves. However, not all assimilates produced can be used for growth. In effect, a large portion of assimilates is used up by the respiration of the whole tree, in which the respiration of unproductive wood tissues takes a big proportion. Trees having larger leaf mass ratios (leaf mass/ total plant mass) can produce more assimilates per unit plant mass and invest proportionately more assimilates to growth (Poorter 1998).

Pruning is a common treatment employed in horticulture and silviculture to alter the crown shape of trees and increase the production of knot-free timber. It is also applied to obtain plant materials for food, fuel, and industrial raw materials (Shepherd 1986; Evans 1992). In China, in order to get these plant materials, trees are commonly pruned by removing leaves and branches from the lower parts of tree crowns, leaving the stems and the roots untouched. Consequently, the leaf mass ratios of pruned trees are diminished. Due to the decreased assimilate production, the growth of pruned trees is greatly reduced (Møller 1960; Uotila and Mustonen 1994; Pinkard and Beadle 1998; Pinkard et al. 1998, 1999; Bandara et al. 1999). In order to get more assimilates for growth and alleviate the negative pruning effects, one of the strategies pruned trees may adopt is to increase their leaf growth and raise their leaf mass ratios in such a way that the production of assimilates in pruned trees can be enhanced. However, whether pruned trees are able to increase their leaf growth and leaf mass ratios is greatly dependent on the allocation patterns of biomass following pruning.

The pipe model theory, derived by Shinozaki et al. (1964 a, b), has been widely used to analyze the structure and growth of roots (Tanaka et al. 1994; Arima et al. 2000), allometric relationships of plants (Chiba 1998), stand productivity (Valentine 1999), plant growth (Valentine 1985; Berninger and Nikinmaa 1997), leaf biomass and area (Waring et al. 1982; Robichaud and Methven 1992; Nygren et al. 1993), etc. According to this theory, a plant may be considered as an assemblage of many unit pipe systems, each consisting of a leaf element and a connecting pipe (Fig. 1). All leaf elements together come to be the photosynthetic structure of the plant, and all pipes together comprise the conductive system of the plant and function as supporting structure meanwhile. Growth of the plant results from the production of new unit pipe systems, which includes the occurrence of both components of the unit pipe systems simultaneously: the leaf elements and the connected pipes.

In the context of trees, basically, the aboveground part of the pipe of each unit pipe system consists of a horizontal section and a vertical section (Fig. 2). Collectively, all horizontal sections of unit pipe systems in a tree comprise the branches, and all vertical sections constitute the stem. The length of each pipe is determined by the crown characteristics of the tree and the location of the leaf element with which the pipe is connected. Theoretically, leaf elements in the upper crown of a tree are connected with longer pipes than leaf elements in the lower crown, as long as the crown depth: width ratio of the tree is not smaller than one, regardless of the crown shape (Fig. 2). Assuming the

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construction cost per leaf element and per unit length of pipe is constant, respectively, the production of a leaf element in the upper crown with its associated pipe will be more costly than that of a leaf element lower in the crown. In other words, the proportion of investments allocated to the construction of leaf elements in the upper crown will be smaller than that of leaf elements in the lower crown.

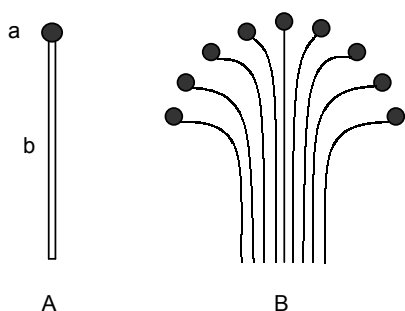


Fig. 1. Schematic illustration of the pipe model theory. A: a unit pipe system consisting of a leaf element (a) and a pipe (b); B: assemblage of unit pipe systems which together form a plant (from Shinozaki et al. 1964a).

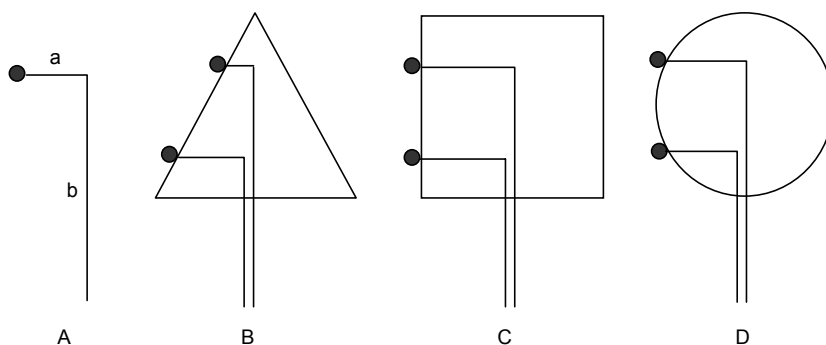


Fig. 2. Schematic illustration of the length of pipes in relation to crown shape and the location of leaf elements in the crown, indicating that pipes connecting with leaf elements in the upper crown are longer than pipes connecting with leaf elements in the lower crown, when the depth: width ratio of the crown is not smaller than one, regardless of the crown shape. A: a unit pipe system consists of a leaf element and a pipe comprising a horizontal section (a) and a vertical section (b); B: unit pipe systems in the upper and the lower part of a crown having conical shape; C: unit pipe systems in the upper and the lower part of a crown having cylindrical shape; D: unit pipe systems in the upper and the lower part of a crown having spherical shape.

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Pruning changes the structure of tree crowns dramatically. Due to the way of pruning applied in China, branches are primarily harvested from the lower crown of a tree, leaving the upper crowns of the tree intact. As a consequence, the crown of a pruned tree is not only reduced in size, but also is shifted to a higher elevation. Because the production of new leaves mainly occurs in the crown of a tree, the pipe model theory would predict that pruned trees following pruning have to allocate proportionately more biomass to the production of wood (viz. branches and stem which are composed of pipes), and less to the leaves. Moreover, this allocation pattern may be intensified in severely pruned trees and repeatedly pruned trees.

The present study aims to investigate the impact of pruning on patterns of aboveground biomass allocation and dynamics of the aboveground leaf mass ratio (ALMR; leaf mass/total aboveground mass, in g g^{-1}) of trees. Specifically, the following working hypotheses are addressed:

- (a) Conforming to the pipe model theory, pruned trees will allocate proportionally less of their aboveground biomass to the production of leaves, and more to the production of wood following pruning. In addition, this allocation pattern is intensified by severe pruning and repeated pruning.
- (b) Pruned trees consistently have a lower ALMR than unpruned trees during their growth after pruning, due to the diminished proportional allocation of aboveground biomass to leaves.

A pruning experiment with four subtropical Chinese tree species, four pruning intensities, two pruning seasons and two repeated pruning treatments was carried out to test these hypotheses.

Materials and methods

Species and study area

Four indigenous tree species from subtropical China were selected for this study: the evergreen broad-leaved species *Ficus microcarpa* L. (Moraceae) and *Cinnamomum camphora* (L.) Presl. (Lauraceae), the deciduous broad-leaved species *Ficus virens* Ait. var. *sublanceolata* (Miq.) Cornor (Moraceae), and the evergreen conifer *Pinus massoniana* Lamb. (Pinaceae). The crown depth: width ratio of naturally growing trees is about one in *F. microcarpa*, and larger than one in *F. virens*, *C. camphora*, and *P. massoniana*. Leaves of the broad-leaved species are entire. Trees of all these four species can reach a height of more than 20 meters. *P. massoniana* is a pioneer species, and occurs mainly in early successional forests. It is hardly found in the climax vegetation of subtropical China which is characterized by broad-leaved forests. However, trees of the other three broad-leaved species occur naturally in late successional forests (Zhong 1988).

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The study site is situated at the foot of the Nature Reserve of Jinyun Mountain (29° 50' N, 106° 26' E), which is about 40 km north of Chongqing Municipality, China. The climate of this region is predominantly monsoonal, resulting in hot, humid summers and chilly but mostly frost-free winters (Cornelissen 1992; Zeng and Zhong 1997; Li et al. 1998). Monthly average temperatures increase gradually from January to August, and decrease gradually from August to January. Based on the climatic data from 1951 to 1995, the annual average temperature of this region is 18.2 °C. The average temperature of the coldest month (January) and the hottest month (July) are 7.5 °C and 28.6 °C, respectively (Zeng and Zhong 1997; Li et al. 1998). The annual precipitation is 1123 mm, which mainly falls in spring and summer. Rainfall in winter is uncommon. The substrate of this region is quartziferous, and soils are acidic and yellowish (Zeng and Zhong 1997; Li et al. 1998).

Plant preparation

In early 1996, 300 saplings (ca. 1.3 meter in height) of each of *F. microcarpa* and *F. virens* were planted in a fertile field at the foot of Mt. Jinyun. A similar number of *C. camphora* saplings were obtained and planted in early 1997. Plants of these three species were grown with enough spacing to avoid mutual shading during the whole experiment. In 1996, about 300 saplings (ca. 0.8 meter in height) were chosen from a *P. massoniana* plantation on a hill which was ca. 10 km away from the fields where the other three broad-leaved species were planted. Care was taken by foresters to keep enough spacing between these coniferous saplings when they were planted. Weeding, watering, and insecticide spraying were applied to saplings of all species when needed during the whole study period.

Pruning treatments and biomass measurements

After one year of growth and acclimation, 20 blocks were established in each of the *F. microcarpa*, *F. virens*, and *P. massoniana* stands in early 1997, and 20 blocks were established in the *C. camphora* stand in early 1998. Each block contained 9 trees. These 9 trees were subjected to one of the following treatments: 20%, 50%, or 70% pruning in spring (May); 20%, 50%, or 70% pruning in autumn (October); one tree was set aside as control; the remaining two trees were harvested in the spring and the autumn of 1997 (the spring and autumn of 1998 for *C. camphora*), respectively. Trees in each block were assigned to the treatments randomly. *F. microcarpa*, *F. virens*, and *P. massoniana* were pruned in 1997 and 1998, but *C. camphora* were only pruned in 1998. For the three broad-leaved species, pruning intensities of 20%, 50%, and 70% meant that branches and leaves were removed from the lower part of the crown, and the crown depth (the distance from the apical meristem to the insertion point of the lowest branch) was reduced by 20%, 50%, and 70%, respectively. For *P. massoniana*, the pruning scheme meant that 20%, 50%, and 70% of total first order branches of the treated tree were removed from the lower crown, respectively; this was equivalent to a crown depth reduction of ca. 25%, 60%, and 80% on

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average, respectively. Side crowns which had emerged on the lower stem parts of some pruned trees were removed before carrying out the second pruning.

For each tree at each pruning event, the removed branches and leaves were weighed separately in the field, and their dry weights were assessed based on the dry weight/ fresh weight ratios of subsamples analyzed in the laboratory. Dry weights of the stem, residual branches, and residual leaves (viz. residual aboveground biomass) of each pruned tree were determined non-destructively as described below. The sum of removed biomass and residual aboveground biomass was regarded as the total aboveground biomass of the tree. In the autumn of 1999, all trees were harvested, and the dry weights of the stem, branches, and leaves of each tree were determined.

In the spring of 1997 (spring of 1998 for *C. camphora*), the aboveground parts of 20 trees (one from each of 20 blocks) of each species were harvested. For each tree, stem, branches, and leaves of each harvested tree were weighed in the field. Length and basal diameter (ca. 10 cm above the soil surface) of the stem, and length and basal diameter (ca. 1 cm from the base) of each first-order branch were measured. The number of leaves (the total leafy shoot length of *P. massoniana*) was determined. Stem, branch, and leaf dry weights of each harvested tree were determined based on the biomass subsamples analyzed in the laboratory. Regression formulas were constructed for all species for stem dry weight on the product of stem length times squared stem basal diameter, and for total branch dry weight on the sum of the product of length times squared basal diameter of all first-order branches. Average dry weight per leaf was determined for the three broad-leaved species and average needle dry weight per unit length of leafy shoot was determined for *P. massoniana*. With this information, the dry weights of the stem, residual branches and leaves of each tree after the first spring pruning were determined. Average dry weight per leaf (or per unit length of leafy shoot for *P. massoniana*) was used also to estimate the total dry weight of leaves in each tree of species *F. microcarpa*, *F. virens*, and *P. massoniana* in the spring of 1998 and of 1999, and of species *C. camphora* in the spring of 1999.

Similarly, in the autumn of 1997 (autumn of 1998 for *C. camphora*), another 20 trees (from 20 blocks) of each species were harvested and analyzed in the same way. The dry weights of stem, residual branches, and residual leaves of trees after the first autumn pruning were estimated. Constructed regression formulas for stem dry weight and total branch dry weight were also used to estimate the dry weights of the stem and residual branches of each pruned *F. microcarpa*, *F. virens*, *P. massoniana* tree in the spring of 1998, and of each pruned *C. camphora* tree in the spring of 1999. Average dry weight per leaf (or per unit length of leafy shoot for *P. massoniana*) was used also to estimate the total dry weight of leaves in each tree of species *F. microcarpa*, *F. virens*, and *P. massoniana* in the autumn of 1998.

In the autumn of 1998, for all species except *C. camphora*, 5 blocks out of 20 were randomly chosen and the trees in these five blocks were harvested. Regression formulas for stem dry weight and branch dry weight were again constructed for each species and applied to estimate the dry weights of stem and residual branches of each autumn-treated tree after

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the second autumn pruning. They were also used to estimate the dry weights of stem and branches of each tree in the spring of 1999.

Data analysis

The aboveground biomass production of each tree after each pruning over one year was calculated as the difference between the aboveground biomass of the tree one year after pruning and the residual aboveground biomass instantaneously after pruning. The allocation of aboveground biomass to leaves and wood was calculated as the proportion of produced leaf and wood mass to the total aboveground biomass production.

Statistical analysis was carried out with SPSS 8.0 (SPSS Inc. 1997). Effects of pruning on the biomass allocation to leaves and wood were investigated for each species by using the GLM module with repeated measures. Interactions between pruning intensities and repeated pruning treatments were evaluated. Effects of pruning on aboveground leaf mass ratios were examined with one-way ANOVAs. Differences between trees subjected to different pruning intensities were investigated with Duncan's multiple range test. Data were checked for equality of variance, and arcsine transformation or square root transformation was applied to equalize variances if necessary.

Results

Aboveground biomass allocation to leaves and wood

For all species after all pruning treatments, none of pruned trees showed significant decrease in the proportional aboveground biomass allocation to leaves. On the contrary, in most cases, the aboveground biomass allocation to leaves was increased after pruning (Fig. 3). After spring pruning, pruned trees of *F. microcarpa*, *F. virens* and *C. camphora* increased their biomass allocation to leaves with increasing pruning intensity. The first autumn pruning had no effects on the proportional biomass allocation to leaves in trees of *F. microcarpa*, *F. virens*, and *C. camphora*. However, the second autumn pruning increased the allocation to leaves in these trees. The proportional allocation to leaves in *P. massoniana* trees was not altered after the first spring pruning, but increased after the second spring pruning. The first autumn pruning also increased the allocation to leaf growth in *P. massoniana*. Interactions on allocation of aboveground biomass to leaf growth between pruning intensities and repetition of pruning were significant in *F. microcarpa* and *F. virens* after autumn pruning, and in *P. massoniana* after spring pruning (Fig. 3). This implies that repeated pruning intensified the increase in proportional biomass allocation to leaf growth in these trees.

As the aboveground mass was the sum of wood and leaf mass, the proportional allocation of aboveground biomass to wood production was just the opposite to the allocation of aboveground biomass to leaves (data not shown).

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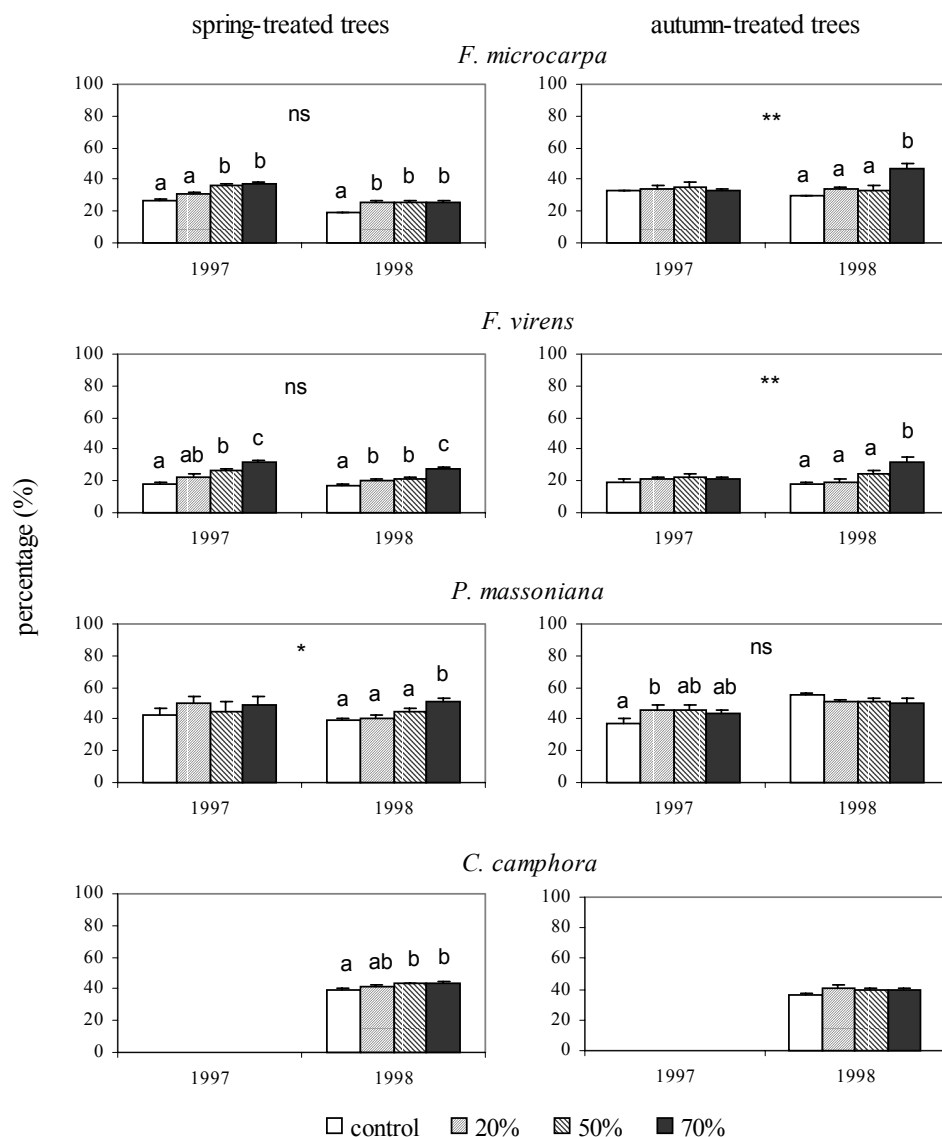


Fig. 3. Proportional allocation of new produced aboveground biomass to leaves one year following pruning in four tree species (mean±se). Pruning was conducted in spring or autumn, and it was done in 1997 and 1998 for *F. microcarpa*, *F. virens*, and *P. massoniana*, and only in 1998 for *C. camphora*. Pruning intensities were 0% (control), 20%, 50%, and 70%. For each species, after each pruning treatment, means sharing the same letter do not differ (Duncan's multiple range tests). For each species pruned in each season, the interactions on allocation to leaves between pruning intensities and repetition of pruning were shown with symbols ns (not significant), * ($p < 0.05$), and ** ($p < 0.01$) (GLM with repeated measures).

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Aboveground leaf mass ratio

Pruning, conducted in either spring or autumn, led instantaneously to a reduction in the aboveground leaf mass ratios of all tree species. This pattern remained the same after both the first and the second pruning treatment (Fig. 4). However, the aboveground leaf mass ratios of all pruned trees of *F. microcarpa*, *F. virens*, and *C. camphora* increased over the time period following pruning, and they were not smaller than those of unpruned trees one year later. The aboveground leaf mass ratios of pruned *P. massoniana* trees were the same as those of unpruned trees one year after the first pruning, but lower after the second pruning.

Discussion

The essence of the pipe model theory is that a plant is an aggregation of many unit pipe systems, each made up of a leaf element and an associated pipe extending from the leaf element to the root system of the plant. The pipe model theory was experimentally confirmed by Sachs (1981), who discovered that outgrowing buds induced the formation of complete vascular strands starting from the growing buds to the roots of the plant, and there were no direct transverse vascular contacts between branches developed from these buds. Based on the pipe model theory, it is reasonable to predict that, proportionally, pruned trees would increase aboveground biomass allocation to wood (which is the aggregation of pipes) and decrease aboveground biomass allocation to leaves, since newly grown leaves in “elevated crowns” of pruned trees need relatively longer vascular channels to connect with the roots.

However, this prediction was not confirmed by the experimental results of the study. In all investigated tree species, pruning did not increase the proportional allocation of new standing aboveground biomass to wood, and never decreased the proportional allocation of new standing aboveground biomass to leaves either, regardless of pruning season, pruning intensity, and repetition of pruning. On the contrary, all tree species proportionally decreased the allocation of their aboveground biomass to wood and increased that to leaves after pruning, even though this was not always shown after every pruning treatment (Fig. 3). The results imply that the allocation pattern of aboveground biomass in pruned trees can not be satisfactorily explained by the pipe model theory; some other processes seem to be involved.

Pruning removed some leaves and branches from the trees, but the vascular channels in the stems which formerly ran to the removed branches and leaves were not affected and still remained in the stems. The more leaves and branches were removed, the more of these open vascular channels existed in the stems of the pruned trees. It has been found in annual plants that after the removal of an organ, the vascular channels which once connected with this organ can be taken over later by other newly formed organs (Sachs 1981; Sachs and

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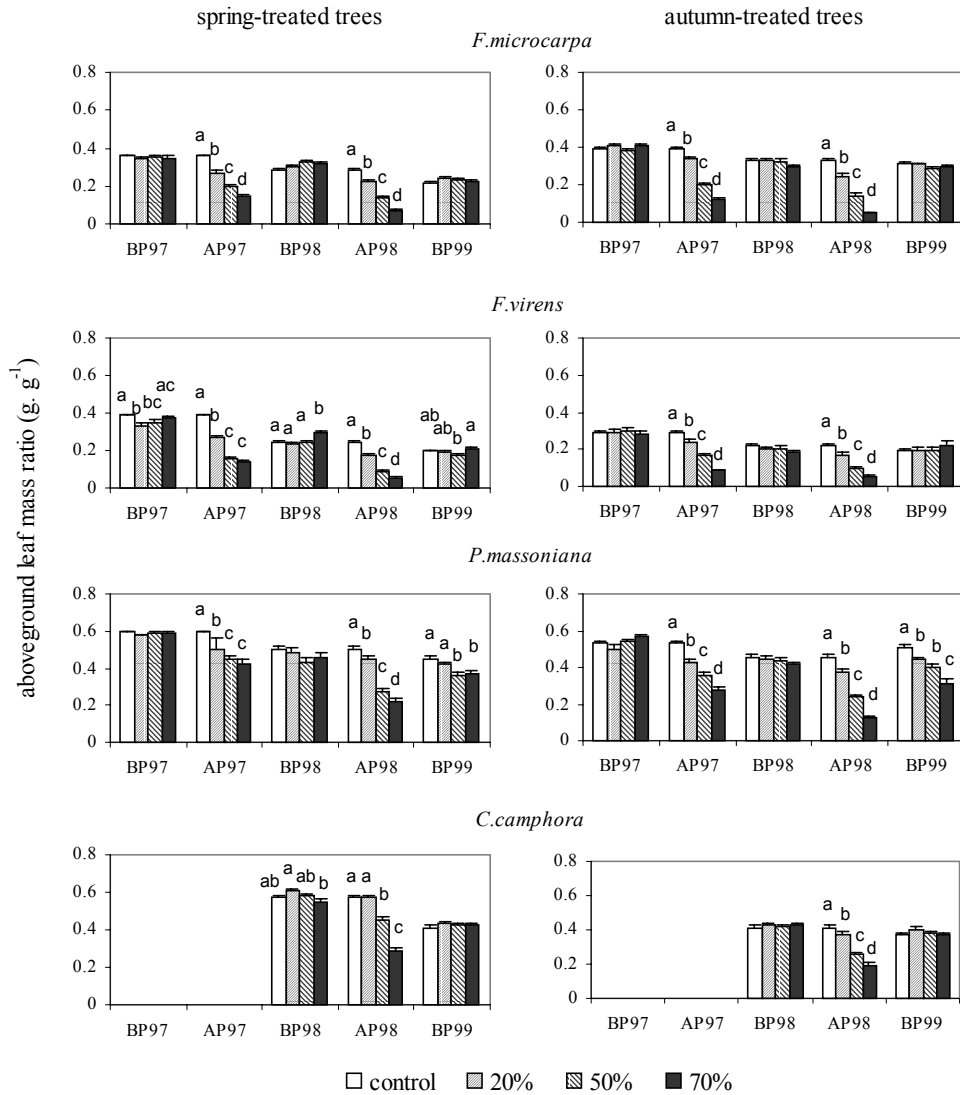


Fig. 4. The aboveground leaf mass ratios (ALMR, g·g⁻¹) (mean±se) of four tree species immediately after pruning and one year later. Pruning was conducted in spring or autumn, and it was done in 1997 and 1998 for *F. microcarpa*, *F. virens*, and *P. massoniana*, and only in 1998 for *C. camphora*. Pruning intensities were 0% (control), 20%, 50%, and 70%. BP97: ALMR before pruning in 1997; AP97: ALMR just after pruning in 1997; BP98: ALMR one year after pruning in 1997 and before pruning in 1998; AP98: ALMR just after pruning in 1998; BP99: ALMR one year after pruning in 1998. For each species, at each measurement, means sharing the same letter do not differ (one-way ANOVA, Duncan's multiple range tests).

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Novoplansky 1997). This finding may explain the unexpected allocation patterns of aboveground biomass in pruned trees found in the present study. Presumably, open vascular channels in the stems caused by pruning did not simply go to waste, but were reused and kept on functioning. As a result, for some growing buds in pruned trees, it was not necessary to form complete vascular channels starting from the growing buds to the roots. What needed to be done was only to construct some new short vascular channels, and connect them with the vascular channels left open by pruning. Only when all open vascular channels had been used up, pruned trees would then start to construct complete long vascular channels, running from the growing buds to the roots. Such investment into the construction of short vascular channels may have led to a proportional decrease in the allocation of new standing aboveground biomass to wood in pruned trees and consequently to an increase in allocation to leaves. Moreover, as severe pruning led to the forming of more and longer open vascular channels, this allocation pattern could be strengthened by the severe pruning (Fig. 3). In another pruning study carried out with *Eucalyptus nitens*, Pinkard and Beadle (1998) found similar results. They reported that more aboveground biomass in pruned *E. nitens* trees was allocated to leaves and less to stems and/or branches, and this allocation pattern was intensified with increasing pruning intensity.

The allocation pattern of aboveground biomass in pruned trees shown in the present study may not only be affected by the reuse of open vascular channels, but also by the production of leaves and branches on the lower parts of stems under remaining crowns of pruned trees. The production of new branches underneath the crowns was observed in pruned *F. microcarpa*, *F. virens*, and *C. camphora* trees. The number of these new branches increased with pruning intensity, and the mass proportion of them to all branches in the trees also increased with pruning intensity (data not shown). Since leaves on these new branches grown beneath the crowns need relatively shorter vascular channels in comparison with other leaves grown in the crowns, the production of leaves and branches on the stem parts below crowns of pruned trees may strengthen the particular aboveground biomass allocation patterns found in pruned trees.

Pruning led to an instantaneous reduction in the aboveground leaf mass ratios of all trees, but no tree consistently maintained that reduced aboveground leaf mass ratio (Fig. 4). Pruned *P. massoniana* trees had the same aboveground leaf mass ratios one year after the first pruning as unpruned *P. massoniana* trees. Although the aboveground leaf mass ratios of pruned *P. massoniana* trees one year after the second pruning did not match those of unpruned *P. massoniana* trees, they were much closer to those of unpruned trees than the values instantaneously after pruning. The failure of twice-pruned *P. massoniana* trees to obtain the same aboveground leaf mass ratios as unpruned trees may be due to the relatively slow growth of *P. massoniana*, which also means a relatively low leaf production rate, as compared to the broad-leaved species (Zhu 1980). With this slow growth, a pruned *P. massoniana* tree could not obtain the same leaf mass ratio as an unpruned tree within one year, which was constrained by the annual pruning regime. All pruned trees of broad-leaved species started to adjust their aboveground leaf mass ratios soon after pruning, and managed to reach the same values as unpruned trees within one year. The aboveground

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biomass allocation patterns and the aboveground leaf mass ratio dynamics of pruned trees shown in this study indicates that, after pruning, pruned trees are able to adjust their leaf production and re-establish aboveground leaf mass ratios similar to those of unpruned trees. This reaction would be beneficial to the regrowth and recovery of pruned trees following pruning.

Acknowledgements

I am grateful to Prof. Marinus J.A. Werger and Dr. Heinjo During for their stimulating discussions and helpful comments on previous versions of the manuscript. The study was funded by Netherlands Foundation for the Advancement of Tropical Research (WOTRO) through grant WB 84-411 and partly supported by a grant to BZ from Science and Technology Commission of Chongqing Municipality, China.

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4

Leaf emergence and shoot production of two subtropical Chinese *Ficus* tree species following pruning

Abstract

Previous studies revealed that after pruning of the lower branches, more of the newly produced aboveground biomass of two *Ficus* tree species, *F. microcarpa* and *F. virens*, was allocated to the growth of leaves. To investigate whether leaf density (leaf number per unit axis length) and shoot production patterns after pruning are involved in the alteration of biomass allocation, data from a pruning experiment with two pruning seasons and a series of pruning intensities were analyzed. It is shown that pruning, regardless of pruning intensity and pruning season, had no effect on the leaf density of new shoots. Shoot production of lateral branches of both species was not affected by pruning and the location of lateral branches in the crown. However, the shoot production on the main stem was position-dependent in both *F. microcarpa* and *F. virens* trees. Pruning, conducted either in spring or in autumn, did not affect the number and density of new shoots on the newly grown upper stem parts and the branched stem parts within the residual crown, but facilitated the shoot production on the bare stem parts beneath the residual crown in terms of both shoot number and density. Shoot production on the bare stem parts increased with pruning intensity. Autumn pruning led to a stronger emergence of shoots from the bare stem parts than spring pruning. Some mechanisms which could be involved in these results are discussed. Based on the experimental results, it is suggested that among all investigated variables, only the enhanced shoot production on the bare stem parts may have contributed to the increased biomass allocation to leaves in a pruned tree.

Keywords: *Ficus microcarpa*, *Ficus virens*, leaf density, pruning, shoot production, subtropical China

Introduction

Ficus microcarpa L. and *Ficus virens* Ait. var. *sublanceolata* (Miq.) Cornor (Moraceae) are two fig tree species which are naturally distributed in south China. Due to their medicinal values and shapely crowns, trees of these two species are widely planted in this region. Pruning, as a means of getting plant materials for medicine manufacturing, obtaining branch cuttings for vegetative multiplication, and improving crown shape for aesthetic purpose, is often applied by local people to trees of these two species. Generally, the common pruning mode adopted in this region is to remove branches and leaves from the lower crown, leaving the upper parts of trees untouched.

In a previous study, we demonstrated that the biomass allocation patterns of *F. microcarpa* and *F. virens* were significantly affected by pruning treatment implemented either in spring or in autumn: more of the newly produced aboveground biomass had been allocated to the growth of leaves and less to the production of wood. Moreover, this pattern was intensified with pruning intensity (see Chapter 3). As regards the biomass allocation of trees, many factors might be involved, one of which is leaf density (number of leaves per unit shoot length). In these two *Ficus* tree species, bud burst leads to the emergence of new shoots which simultaneously accommodate many new leaves. Obviously, the biomass allocation to leaf growth can be increased if newly grown shoots have higher leaf densities. Some studies have revealed that the leaf density of new shoots can be raised by leaf and/or shoot removal caused by defoliation and shoot clipping (Cornelissen 1993; Bell et al. 1995; Heuvelink and Buiskool 1995; Remphrey and Davidson 1994). Pruning treatments as applied in south China, which cause a large loss of leaves and shoots, might affect the leaf density of new shoots in *F. microcarpa* and *F. virens* trees as well.

A plant may be envisaged as an aggregation of many basic structural units, each of them consisting of a module (defined as the axis initiated from a bud, Prévost 1967) and some appending vessels extending to the roots (Franco 1985; Sachs 1991; Sprugel et al. 1991). According to this structural unit theory, which has been developed based on the pipe unit concept of Shinozaki et al. (1964a,b) and the integrated physiological unit concept of Watson and Casper (1984), modules which are nearer to the base of a plant tend to have shorter appending vessels. Thus, units with modules nearer to the base of a plant are relatively cheaper in construction costs, and more resources in the plant can be allocated to leaf production when units of this type are constructed. For a tree subjected to pruning, it is likely that its biomass allocation to leaves will be increased if the production of modules (which can be regarded as shoots actually) on the stem and in the lower crown is enhanced after pruning.

The present experiment was designed to investigate whether pruning has effects on the leaf emergence and shoot production patterns of *F. microcarpa* and *F. virens* trees. To get a better understanding of the response of these two *Ficus* tree species to pruning in respect of leaf emergence and shoot production, a series of pruning intensities and two pruning seasons were incorporated in the experiment. Specifically, the following questions are addressed:

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- (1) Is the leaf density of new shoots increased by pruning?
- (2) Does pruning decrease the production of shoots in the upper crown and increase it in the lower crown?
- (3) Is the shoot production on the main stem enhanced by pruning?
- (4) Are the traits mentioned in (1) – (3) affected by pruning season and pruning intensity?

Materials and methods

Study area and species

This study was conducted in an experimental garden (ca. 210 m a.s.l.) established at the foot of the National Nature Reserve of Jinyun Mountain (29° 50' N, 106° 26' E), which is ca. 40 km north of Chongqing city, China. The climate of this region is predominantly monsoonal, resulting in hot, humid summers and chilly but mostly frost-free winters (Cornelissen 1992; Zeng and Zhong 1997; Li et al. 1998). Details of the climate in this region are given in Zeng and Zhong (1997), and Li et al. (1998). Soils in this region are loamy, acidic and yellowish (Zeng and Zhong 1997; Li et al. 1998).

Ficus microcarpa and *Ficus virens* are broad-leaved tree species with entire leaves; the former is evergreen and the latter is deciduous. Individuals of both species can reach a height of 20 meters (Botany Institute of Chinese Academy of Science, 1980). In the Chongqing region, trees of these two species start their growth in early spring (early March), and new leaves and shoots can occur during the whole growing season. No apparent growth in these species can be observed during winter. Production of aerial roots is a common phenomenon for these two species. Due to the high propensity of cut branches to root, it is quite easy to vegetatively propagate these two species.

Tree preparation and pruning treatment

In early 1996, 300 small trees (ca. 1.3 meter in height) of each of *F. microcarpa* and *F. virens* species were planted in the experimental garden. Trees of these two species were grown with enough spacing to avoid mutual shading during the whole experiment. Weeding, watering, and insecticide spraying were applied to trees of both species when necessary.

In early 1997, after one year of growth and acclimation, 20 blocks were established in both the *F. microcarpa* and the *F. virens* stand. Each block contained 7 trees, one of which was subjected to each of the following treatments: 0% (control); 20%, 50%, or 70% pruning in spring; 20%, 50%, or 70% pruning in autumn. Trees in each block were assigned to the treatments randomly. Pruning treatment was conducted in May 1997 for spring-treated *F. microcarpa* and *F. virens* trees after their spring flush and in October 1997 for autumn-treated *F. microcarpa* and *F. virens* trees before the natural leaf shedding of *F. virens* trees. To simulate the pruning mode usually adopted by local people in

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subtropical China, trees were pruned by removing branches from the lower crown, leaving the upper crown untouched. As a result, pruning reduced the crown depths (the distance of the apical meristem to the insertion point of the lowest branch) of trees by 0%, 20%, 50%, and 70%, respectively. Consequently, pruned trees had longer bare stem parts without any lateral branches. Henceforth, the stem parts within and beneath the residual crown of each tree after pruning treatment are referred to as branched stem parts and bare stem parts, respectively. The elongated upper stem parts produced after the pruning treatment are referred to as new stem parts.

Determination of leaf emergence and shoot production

For both *F. microcarpa* and *F. virens* trees, the crowns of 0%, 20%, 50%, and 70% pruned trees, just after pruning, were visually separated into 4, 3, 2, and 1 layers, each layer having approximately equal depth. Layers from the top of the crown downwards were labelled as I, II, III, IV for the 0% pruned trees (control); I, II, III for the 20% pruned trees; I, II for the 50% pruned trees; and I for the 70% pruned trees. The height and the light environment of any crown layer with the same label (I, II, or III) were approximately similar in all trees, regardless of pruning intensity. In each of I, II, and III layers of all trees, one vigorous first-order lateral branch (starting from the stem) was chosen and marked. Thus, each of the 0%, 20%, 50%, and 70% pruned trees had 3, 3, 2, and 1 marked first-order lateral branches, respectively. Leaf emergence and shoot production on the main axes of all marked lateral branches were followed for one year after pruning. The elongation of the main axes was measured. The numbers of new leaves and new shoots (viz. second-order twigs) on the newly elongated parts of the lateral branches were recorded, and their densities (number of new leaves or new shoots per meter axis) were calculated. Similarly, the growth of the main stem was also followed for one year after pruning. The number and density of newly grown shoots on the newly elongated, the branched, and the bare stem parts of the main stem were recorded. New leaves and shoots were counted if they were longer than 1 (leaf blade length) and 3 cm, respectively.

Data analysis

For the elongation of the main axes of lateral branches, and the densities of new leaves and new second-order shoots on the main axes of lateral branches, one-way ANOVAs were used to check the effects of crown layer. Since the data of the crown layers did not differ from each other, data of all crown layers in a tree were pooled and two-way ANOVAs were used to evaluate the effects of pruning intensity and pruning season on the above-mentioned traits.

The number and density of newly emerged shoots on the elongated new stem parts, the branched, and the bare stem parts of treated trees were explored by applying two-way ANOVAs (factors are pruning season and pruning intensity). Differences in these two traits between different pruning intensities were evaluated with Duncan's multiple range test.

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Logarithmic transformation was performed if needed to improve the equality of variances prior to statistical analysis.

Results

For both *F. microcarpa* and *F. virens*, the density of new leaves on the elongated main axes of lateral branches did not differ between crown layers and was not affected by pruning intensity and season (Table 1). Similarly, the density of new shoots on the elongated main

Table 1. Density of new leaves (mean±se) (number · m⁻¹) on the elongated parts of main axes of marked lateral branches (n=11) in different crown layers (I, II, and III downwards) of pruned *Ficus* trees. Pruning was done in spring or autumn by removing branches from the lower tree crown, at the intensities of 0% (control), 20%, 50%, 70%. Two-way ANOVAs were applied to evaluate the effects of pruning intensity and pruning season by using pooled data of all crown layers in each tree since no effect of crown layer was found (p>0.05, one-way ANOVA).

		pruning intensity			
		control	20%	50%	70%
<i>F. microcarpa</i>					
spring	I	45.3±9.1	63.3±5.9	50.5±6.2	62.6±7.1
	II	55.8±9.4	57.0±18.0	49.9±6.1	
	III	48.5±8.3	64.4±6.8		
autumn	I	48.7±7.8	69.0±11.0	56.9±8.3	53.7±5.6
	II	47.1±10.2	51.7±9.7	67.1±6.7	
	III	62.7±7.3	62.6±7.9		
pruning intensity: p>0.05; pruning season: p>0.05; interaction: p>0.05					
<i>F. virens</i>					
spring	I	29.9±6.1	41.5±10.8	38.1±10.4	69.6±19.2
	II	35.1±6.2	47.5±11.1	40.3±5.5	
	III	37.5±6.5	45.0±6.9		
autumn	I	38.0±8.4	96.7±34.5	73.5±42.3	37.5±5.0
	II	33.8±8.1	41.7±9.9	56.5±11.8	
	III	32.3±8.7	39.6±9.2		
pruning intensity: p>0.05; pruning season: p>0.05; interaction: p>0.05					

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axes of lateral branches was not affected by crown layer, pruning intensity and pruning season (Table 2). Crown layer and pruning did not affect the elongation of the main axes of lateral branches (data not shown).

The number and the density of newly emerged shoots on the new stem parts of both *F. microcarpa* and *F. virens* trees were not affected by pruning, either conducted in spring or in autumn (Fig. 1). No shoot sprouted from the branched stem parts of pruned *F. microcarpa* and *F. virens* trees one year after pruning. However, some shoots sprouted from the bare stem parts of pruned trees in these two species (Table 3), and their number and density increased with pruning intensity in both *F. microcarpa* and *F. virens* trees

Table 2. Density of newly emerged second-order shoots (mean±se) (number · m⁻¹) on the elongated parts of marked lateral branches (n=11) in different crown layers (I, II, and III downwards) of pruned *Ficus* trees. Pruning was done in spring or autumn by removing branches from the lower tree crown, at the intensities of 0% (control), 20%, 50%, 70%. Two-way ANOVAs were applied to evaluate the effects of pruning intensity and pruning season by using pooled data of all crown layers in each tree since no effect of crown layer was found (p>0.05, one-way ANOVA).

		pruning intensity			
		control	20%	50%	70%
<i>F. microcarpa</i>					
spring	I	9.8±3.2	15.8±1.2	16.7±2.4	16.5±3.2
	II	14.8±2.6	13.3±4.1	15.6±3.0	
	III	17.4±4.4	15.8±2.4		
autumn	I	14.3±3.3	15.2±5.0	15.8±5.3	9.2±2.5
	II	16.5±4.5	15.8±2.0	17.5±2.7	
	III	13.5±3.0	20.8±2.8		
pruning intensity: p>0.05; pruning season: p>0.05; interaction: p>0.05					
<i>F. virens</i>					
spring	I	31.5±20.8	12.5±6.5	3.4±2.3	5.9±2.4
	II	12.1±2.6	6.0±2.4	11.5±3.2	
	III	9.9±3.3	6.3±1.7		
autumn	I	13.3±3.8	6.7±2.3	17.4±10.7	12.9±2.7
	II	13.9±3.6	7.2±2.1	10.8±2.6	
	III	7.5±1.8	11.1±2.8		
pruning intensity: p>0.05; pruning season: p>0.05; interaction: p>0.05					

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(Table 3, Fig. 2). Autumn-pruned trees of both species had larger numbers and higher densities of sprouted shoots on the bare stem parts than spring-pruned trees ($p < 0.001$).

Discussion

In contrast to our expectations, leaf density of new shoots produced in both *F. microcarpa* and *F. virens* was not affected by pruning treatment, conducted either in spring or in autumn (Table 1). This result is different from what has been found in some defoliation and shoot clipping studies (Cornelissen 1993; Bell et al. 1995; Heuvelink and Buiskool 1995; Remphrey and Davidson 1994). Apparently, for these two species, the enhanced biomass allocation to leaf growth found in our previous study (see Chapter 3) could not be ascribed to a higher leaf density of newly produced shoots in the remaining crown of pruned trees.

As regards the shoot production of lateral branches in the remaining crown of both species, in terms of either the density or the number of shoots, no difference was detected between pruned trees at any crown layer (Table 2). Pruned trees did not present lower shoot production in the upper crown and higher shoot production in the lower crown as expected. Moreover, no effect of crown layer on shoot production was found in trees subjected to any pruning intensity (Table 2).

Table 3. The number of sprouted shoots (mean±se) on the bare stem parts (beneath the residual crown) of two *Ficus* tree species within one year after pruning treatments (n=20). Pruning was done in spring or autumn, at the intensities of 0% (control), 20%, 50%, 70%. Two-way ANOVAs were applied to evaluate the effects of pruning season and pruning intensity. For trees pruned either in spring or in autumn, means followed by the same letter do not significantly differ with each other (Duncan’s multiple range test).

species	pruning intensity			
	control	20%	50%	70%
<i>F. microcarpa</i>				
spring	0.0±0.0 (a)	0.25±0.20 (a)	1.05±0.22 (b)	2.4±0.51 (b)
autumn	0.0±0.0 (a)	0.95±0.29 (a)	4.95±0.91 (b)	13.8±1.69 (c)
pruning intensity: $p < 0.001$; pruning season: $p < 0.001$; interaction: $p < 0.001$				
<i>F. virens</i>				
spring	0.0±0.0 (a)	0.55±0.28 (a)	2.35±0.69 (b)	4.25±0.91 (c)
autumn	0.0±0.0 (a)	3.3±0.80 (a)	6.85±1.0 (b)	12.2±1.75 (c)
pruning intensity: $p < 0.001$; pruning season: $p < 0.001$; interaction: $p < 0.01$				

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Shoot production on the tree stem of these two *Ficus* species was position-dependent. Pruning, either conducted in spring or in autumn, had no effect on the number and density of newly emerged shoots on the newly grown upper stem parts of both species (Fig. 1). No new shoots emerged on the stem parts within the residual crown in pruned *F. microcarpa* and *F. virens* trees during one year after the pruning treatment. However, on the bare stem parts beneath the residual crown of both pruned *F. microcarpa* and *F. virens* trees, some dormant buds broke and developed into shoots within one year after pruning, their numbers increasing with pruning intensity (Table 3). Many studies have revealed that apical meristems (Rinne et al. 1993; Wang et al. 1997; Sundberg and Uggla, 1998) and young leaves (Rinne et al. 1993; Wang et al. 1997; Kotov and Kotova, 2000) are able to produce auxin, which is transported downwards (Sundberg and Uggla, 1998; Kotov and Kotova, 2000) and plays an important role in the exertion of apical dominance. The quantity of auxin is thought to be related to the degree of apical dominance (Romano et al. 1993; Cline 1997). Some studies have demonstrated that removal of apical meristems frees

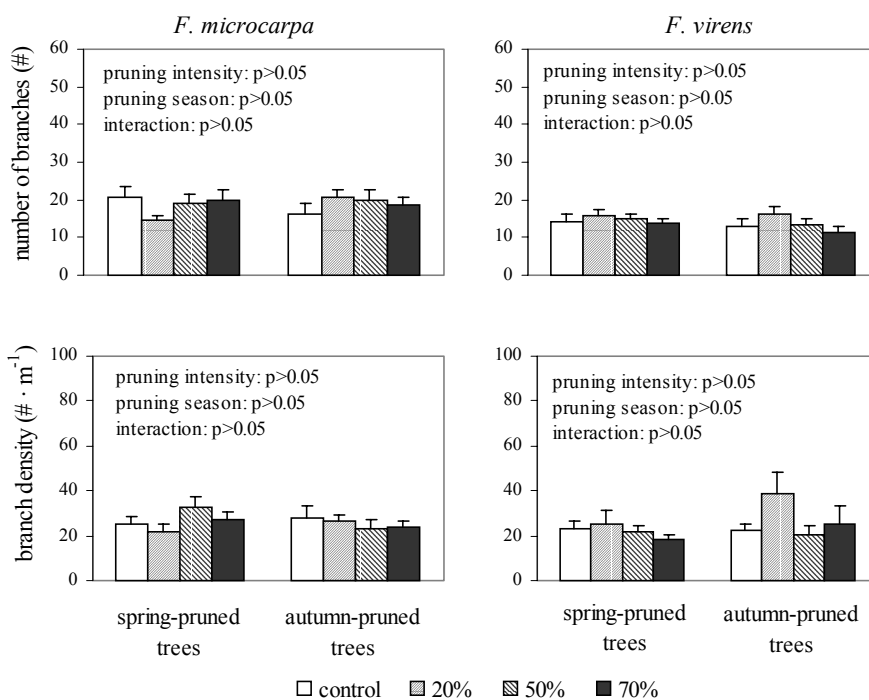


Fig. 1. Number and density of newly emerged branches (mean±se) on the new stem parts of *F. microcarpa* and *F. virens* trees one year after pruning treatment (n=10-13). Pruning was done in spring or autumn by removing branches from the lower tree crown, at the intensities of 0% (control), 20%, 50%, and 70%. The effects of pruning season and pruning intensity were evaluated with two-way ANOVAs.

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the lower (proximal) axillary buds from apical dominance (Ouellette and Young 1994; Chaar et al. 1997; Lortie and Aarssen 1997; Venecz and Aarssen 1998). A bud on the main stem of a tree is influenced by the confluent auxin produced by all apices and vigorous leaves above it, which are located on both the lateral branches and the stem. In our experiment, pruning only led to the removal of lower branches from the stem without touching the upper branches. As a consequence, the flux of auxin in the stem parts within the residual crown (viz. branched stem parts) after pruning would not have been altered. In contrast, the flux of auxin to buds on the bare stem parts beneath the residual crown after pruning would be diminished compared to buds in similar positions on control trees, because pruning had removed part of the sources of auxin. The differential bud burst pattern of different stem parts found in this study seems due to this altered auxin flux along the stem. It is obvious in this study that heavy pruning created longer bare stem parts which accommodated more dormant buds. Here, a question is arising: was the stronger shoot production on the bare stem parts of heavily pruned trees simply caused by the fact that the bare stem parts of heavily pruned trees had more dormant buds than those of lightly pruned trees or by a more strongly reduced apical dominance? Since the density of new shoots on the bare stem parts increased with pruning intensity (Fig. 2), we suggest that the enhanced shoot production on the bare stem parts of heavily pruned trees was not merely caused by the larger supply of dormant buds, but was mainly caused by a stronger release of dormant buds from apical dominance, so that more dormant buds per unit length of bare stem parts were able to burst.

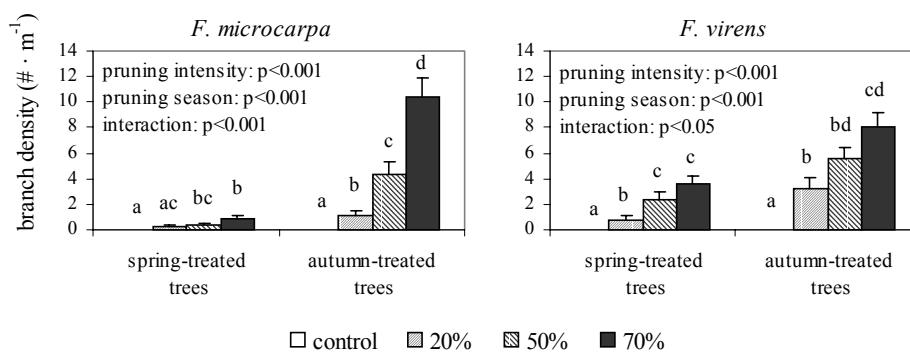


Fig. 2. Density (mean±se) of sprouted branches on the bare stem parts beneath the residual crown of two *Ficus* trees one year after pruning treatment (n=20). Pruning was conducted in spring or autumn by removing branches from the lower tree crown, at the intensities of 0% (control), 20%, 50%, and 70%. The effects of pruning season and pruning intensity were evaluated with two-way ANOVAs. For each species, at each pruning season, means with the same letter do not significantly differ from each other (Duncan's multiple range test).

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Table 4. Stem height and basal diameter (cm) (mean±se) of *F. microcarpa* and *F. virens* trees (n=20) at the time of pruning in spring or autumn. t-test was applied to evaluate the difference between trees when they were pruned in spring or in autumn.

	spring-pruned trees	autumn-pruned trees	t-test
<i>F. microcarpa</i>			
stem height	157.8±4.5	201.3±4.8	p<0.001
stem basal diameter	1.70±0.05	2.49±0.07	p<0.001
<i>F. virens</i>			
stem height	174.7±4.1	232.0±6.5	p<0.001
stem basal diameter	2.52±0.07	3.58±0.09	p<0.001

It is shown in this study that pruning season affected the shoot production on the bare stem parts. In both *F. microcarpa* and *F. virens* trees, more shoots per unit length of the bare stem parts grew out after autumn pruning as compared to spring pruning (Table 3, Fig. 2). It is likely that this difference in shoot production was not due to the different weather conditions between spring and autumn when trees were pruned, but was caused by the availability of nutrients and carbohydrates for shoot development. In this study, all autumn-treated trees were 5 months older than the spring-treated trees when they were pruned. Both the heights and diameters of autumn-treated trees were larger than those of spring-treated trees (p<0.001) (Table 4). Presumably, the enhanced shoot production on the bare stem parts of autumn-pruned trees could be caused by the larger nutrient and carbohydrate reserve in the roots and stems of the trees at the time of pruning.

Because the leaf density of new shoots, and the shoot production of lateral branches in the remaining crown of pruned *F. microcarpa* and *F. virens* trees were not affected by the treatments, it appears that, as regards leaf and shoot production, only the enhanced shoot production on the bare stem parts may have contributed to the increased biomass allocation to leaf growth in pruned *F. microcarpa* and *F. virens* trees reported previously (Chapter 3). Comparatively, less carbohydrates are needed for shoots emerging directly from the main stem than for shoots emerging from the lateral branches (Cannell et al. 1988; Ford et al. 1990), due to the shorter appending vessels to the roots. Therefore, with a given amount of carbohydrates for new growth, more of it can be invested in leaf growth if new shoots emerge from the main stem rather than from the lateral branches.

Ficus microcarpa and *Ficus virens* are different in leaf habits: the former is an evergreen species, and the latter is deciduous. However, as regards the leaf density and shoot production patterns, these two species responded similarly to pruning, either conducted in spring or in autumn. This implies that leaf habits are not crucial in affecting the response of leaf density and shoot production to pruning, as least for these two studied species.

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Acknowledgements

I am grateful to Prof. Marinus J.A. Werger, Dr. Heinjo During, and Dr. Frank Sterck for their helpful comments on an earlier version of the manuscript.

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5

Leaf efficiency of subtropical Chinese tree species following pruning

Abstract

The effects of pruning on the leaf efficiency of the evergreen tree species *Ficus microcarpa* and the deciduous tree species *Ficus virens* in subtropical China were investigated. The pruning experiment included four pruning intensities (0%, 20%, 50%, and 70%) and two pruning seasons (spring and autumn). The leaf efficiency of both species was increased after pruning. Heavily pruned trees tended to have higher leaf efficiencies than lightly pruned trees. Leaf efficiency was affected by pruning season: trees of both species pruned in autumn had higher leaf efficiencies than trees pruned in spring. The increase in leaf efficiency between autumn- and spring-pruned trees was larger in *Ficus virens* than in *Ficus microcarpa*.

Key words: *Ficus microcarpa*, *Ficus virens*, growth, leaf efficiency, pruning, subtropical China

Introduction

Leaf efficiency, which indicates the net productive capacity of leaf, has a close relation to stand production (Waring 1983; Smith and Long 1989) and tree vigor (Waring 1983; Blanche et al. 1985). Because of this close relation, it has been used as a means to evaluate the effects of silvicultural practices (Waring et al. 1981). Pruning, as a common silvicultural treatment, is applied extensively to trees for many purposes (Shepherd 1986; Evans 1992). In subtropical China, to improve wood quality, reduce pathogen attack, and obtain plant matter as industrial raw materials and fuel, trees of a variety of species are pruned by local people by means of removing living branches and leaves from the lower crown of a tree, leaving the upper parts intact. Owing to diminished overall assimilate production because of the reduced leaf area, the efficiency of leaves becomes crucial to the

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future growth of pruned trees. Undoubtedly, the diminution of assimilate production in pruned trees due to the reduced leaf area can be compensated to some extent by an increase in leaf efficiency.

Since the pruning mode in subtropical China only leads to the removal of branches and leaves without touching the stem and root systems, pruned trees have a disproportionately large mass of unproductive tissues (wood) relative to productive tissues (leaves). This imbalance is strengthened with pruning intensity. Much of the assimilates produced by a relatively small amount of leaves has to be used to maintain the unproductive tissues and consequently, the quantity of assimilates which can be invested in the tree's growth decreases.

In subtropical China, the growth of plants is seasonal. In spring and summer, plants grow very fast, but no apparent growth occurs during winter (Cornelissen 1996). Hence, the timing of pruning is critical to the trees' growth. It can be envisaged that pruning conducted in the fast-growing seasons may damage the trees' growth more than pruning performed in slow-growing seasons such as autumn.

Trees pruned in subtropical China include both evergreen and deciduous species. Deciduous trees, dropping their leaves in autumn, have less maintenance costs over winter. It is expected that deciduous trees have higher leaf efficiencies than evergreen trees, since more assimilates in deciduous trees can be used for growth.

In this paper, my aim is to assess the effects of pruning on leaf efficiency. Specifically, the following hypotheses are tested:

- (1) the leaf efficiency of trees decreases after pruning, and the decrease is stronger with pruning intensity;
- (2) the leaf efficiency of trees pruned in autumn is higher than that of trees pruned in spring, and this season-related difference is larger in deciduous trees than in evergreen trees.

To test these hypotheses, two related tree species were studied: *Ficus microcarpa* L. and *Ficus virens* Ait. var. *sublanceolata* (Miq.) Cornor. The former is evergreen, and the latter is deciduous.

Materials and methods

Species and study area

Ficus microcarpa and *Ficus virens* of the family Moraceae are indigenous tree species in subtropical China. Both of them can grow to a height of more than 20 meters (Botany Institute of Chinese Academy of Science 1980). Due to their shapely crown and medicinal values (China Medicinal Materials Company 1994; Li and Kuo 1997, 1998; Chiang and Kuo 2000), they are extensively planted in this region. In order to get cuttings for

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vegetative propagation and raw materials for pharmaceutical production, pruning of these two species is often conducted.

This study was carried out in subtropical China. The study site is situated at the foot of the Nature Reserve of Jinyun Mountain (29° 50' N, 106° 26' E), which is about 40 km north of Chongqing city, China. The climate of this area is predominately monsoonal, resulting in hot, humid summers and chilly but mostly frost-free winters (Cornelissen 1992; Zeng and Zhong 1997; Li et al. 1998). According to the climatic data from 1951 to 1995, the annual average temperature of this area is 18.2 °C; the average temperature of the coldest month (January) and the hottest month (July) is 7.5 °C and 28.6 °C, respectively (Zeng and Zhong 1997; Li et al. 1998). The frostless period per year is 334 days (Zeng and Zhong 1997). The annual precipitation is 1123 mm, which chiefly falls in spring and summer. Rainfall in winter is uncommon. The substrate of this region is quartziferous, and soils are acidic and yellowish (Zeng and Zhong 1997; Li et al. 1998).

Tree preparation

In early 1996, trees (ca. 1.3 meter in height) of *F. microcarpa* and *F. virens* were planted separately in an experimental garden at the foot of Jinyun Mountain. They were grown with enough spacing to avoid mutual shading during the whole experiment. Weeding, watering, and insecticide spraying were applied to trees of both species when needed.

Pruning experiment and biomass measurement

Four pruning intensities were applied: 0% (control), 20%, 50%, and 70%. This meant that branches and leaves were removed from the lower parts of the crown, and the crown depth (the distance from the apical meristem to the insertion point of the lowest branch) was reduced by 0%, 20%, 50%, and 70%, respectively. Pruning was done in spring or autumn for both species.

After one-year of growth and acclimation, 20 blocks were established for each of the *F. microcarpa* and *F. virens* stands in early 1997. Each block included 9 trees of one species which were subjected to one of the following treatments: 20%, 50%, or 70% pruning in the spring (May) of 1997; 20%, 50%, or 70% pruning in the autumn (October) of 1997; one tree was set aside as a control; each of the remaining two trees was harvested in the spring and the autumn of 1997, respectively. Trees in each block were assigned to the treatments randomly.

For each tree at each pruning, the removed branches and leaves were weighed in the field. Meanwhile, the length and basal diameter (ca. 10 cm above soil surface) of the stem, and the length and basal diameter (ca. 1 cm from the base) of all residual first-order branches were measured, and the number of all residual leaves of each treated tree were counted. Subsamples of removed branches and leaves were returned to laboratory. Dry weight and leaf area (Delta-T Area Meter, Cambridge, U. K.) of removed leaves and the residual leaves, and dry weight of removed branches were determined based on the analysis

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of these subsamples. Dry weights of the stem and the residual branches of each treated tree were determined non-destructively as described below. Information on leaf subsamples was used to estimate the dry weight and the area of all leaves on each tree in 1998.

In the spring and the autumn of 1997, the aboveground parts of 20 trees (one from each of the 20 blocks) of each species were harvested. For each tree, stem and branches were weighed in the field. Length and basal diameter of the stem, and length and basal diameter of each first-order branch were measured. Stem and branch dry weights of each harvested tree were determined based on the biomass subsamples analyzed in the laboratory. Regression formulas were constructed for the two species for their stem dry weight on the product of stem length times squared stem basal diameter, and for their total branch dry weight on the sum of the product of length times squared basal diameters of all first-order branches. With this information, the dry weights of the stem and residual branches of each tree after the spring and autumn pruning were determined. The constructed regression formulas of trees in the autumn of 1997 for stem dry weight and total branch dry weight were also used to estimate the dry weights of the stem and branches of each spring-treated tree in the spring of 1998.

In the autumn of 1998, 5 blocks out of 20 were randomly chosen and the trees in these five blocks were harvested. Based on the allometric information from these harvested trees, dry weights of stem and branches of each autumn-treated tree in the autumn of 1998 were determined.

Data analysis

The leaf efficiency (LE, $\text{kg}\cdot\text{m}^{-2}$) of treated trees was calculated as

$$\text{LE} = \frac{M}{0.5(A_1 + A_2)} \quad (1)$$

where M is the aboveground biomass increment of treated trees which was calculated as the difference between the aboveground biomass one year after pruning and the residual aboveground biomass (the sum of the dry weights of the stem, residual branches and residual leaves) instantaneously after pruning. A_1 is the total area of residual leaves in treated trees instantaneously after pruning, and A_2 is the total area of leaves in treated trees one year after pruning. Following Madgwick (1993), $0.5(A_1+A_2)$ is regarded as the mean total leaf area (m^2) within one year after pruning.

Three-way ANOVA was used to check the overall effects of species, pruning season and pruning intensity on the leaf efficiencies of the trees. For each species, the effects of pruning season and pruning intensity on the leaf efficiencies of the trees were evaluated by two-way ANOVAs, and the effects of pruning intensity were assessed after each pruning treatment by one-way ANOVAs. Duncan's multiple range test was applied to check the differences in leaf efficiency between trees subjected to different pruning intensities. Logarithmic transformation was applied prior to statistical analysis when necessary.

Results

The leaf efficiencies of both *F. microcarpa* and *F. virens* did not decrease after pruning. Conversely, *F. virens* increased its leaf efficiency after both spring and autumn pruning, and *F. microcarpa* increased its leaf efficiency after autumn pruning (Fig. 1, Table 1). The leaf efficiencies of both species increased with pruning intensity after autumn pruning (Fig. 1).

Pruning season affected the leaf efficiencies of both species. The leaf efficiencies of both species increased more after autumn pruning than after spring pruning (*F. microcarpa* $p < 0.05$; *F. virens*, $p < 0.0001$) (Fig. 1, Table 1). Furthermore, the difference in leaf efficiency between autumn-pruned trees and spring-pruned trees was larger in *F. virens* than in *F. microcarpa*, which is indicated by the significant interaction ($p < 0.0001$) between species and pruning season (Table 1).

Discussion

Leaf efficiency is defined as biomass or volume increment of the whole plant, or of some special parts of plants (e.g. stem), over a certain time period per unit leaf area (Waring 1983; Velazquez-Martinez et al. 1992; Bandara et al. 1994; Shi and Cao 1997; Gilmore and Seymour 1996; Kuuluvainen and Sprugel 1996; Maguire et al. 1998). Chiefly, there are two ways to calculate leaf efficiency. One uses the leaf area at the beginning of the time period (Velazquez-Martinez et al. 1992), and the other uses the averaged leaf area over the entire time period (Bandara et al. 1994). The advantage of the former is that the leaf area at

Table 1. The effects of species, pruning season, pruning intensity and their mutual interactions on leaf efficiency, statistically evaluated by three-way ANOVAs. Two species (*F. microcarpa* and *F. virens*), two pruning seasons (spring and autumn), and four pruning intensities (0%, 20%, 50%, and 70%) were included in the analysis. Significance levels are: ****, $p < 0.0001$; ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

EFFECTS	SIGNIFICANCE LEVELS
Main effects	
species (SP)	****
season (SE)	****
pruning intensity (P)	***
Interactions	
SP × SE	****
SP × P	*
SE × P	***
SP × SE × P	*

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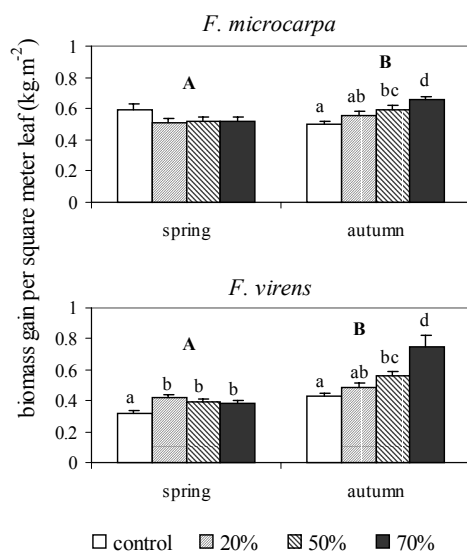


Fig. 1. Leaf efficiencies (mean±se) of two *Ficus* tree species after pruning. Pruning was conducted in spring or autumn, with intensities of 0%, 20%, 50%, and 70%. Different bold capitalized letters indicate the differences in leaf efficiencies between spring- and autumn-pruned trees. For each species, after each pruning, means which share the same lower-cased letters do not differ (Duncan's multiple range test).

the beginning of the time period can be determined quite accurately, but the disadvantage is that leaves grown during that time period, which also have contributed to the plant biomass increment, are not taken into consideration. The advantage of the latter method is that it is more realistic since leaves grown over the time period are considered, but the method is not very accurate as it just makes an estimation of the total leaf area during the time period. In our experiment, we did pruning in spring and autumn. After the autumn pruning, the leaves on the trees, especially those on deciduous trees, did not photosynthesize much due to the coming winter. The strongest contribution to the biomass increment of autumn-pruned trees was made by leaves grown during the next growing season. In order to be able to compare the leaf efficiencies of both spring- and autumn-pruned trees on a common basis, we chose the averaged leaf area for the calculation of leaf efficiency (see formula (1)).

In contrast to what we expected, pruning, either in spring or in autumn, did not decrease the leaf efficiency of the trees (Fig. 1). This implies that, though the maintenance loads on leaves following pruning were augmented, on average, each leaf in the pruned tree still provides at least an equal amount of assimilates for growth compared to a leaf in an unpruned tree. Many studies have shown that the strength of assimilate demand can affect the photosynthetic rates of source leaves (Wareing et al. 1968; Geiger 1976; Gifford and Evans 1981). The net CO₂ assimilation of leaves is usually enhanced by a high sink: source ratio of the plant (Fujita et al. 1994; Layne and Flore 1995; Suwignyo et al. 1995; Laporte and Delph 1996; Jeschke and Hilpert 1997), which is due to the raised export rate of photo-assimilates (mainly consisting of soluble sugar) (Jeannette et al. 1995) and the consequently relieved feedback inhibition of photosynthetic reactions (Layne and Flore 1995; Myers et al. 1999). In this study, pruning took many leaves away from a tree, leaving the stem and the root systems unaffected. This imbalance between productive and

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unproductive tissues created in the trees resulted in a larger sink: source ratio, and imposed a strengthened assimilate demand on the remaining leaves. Probably, the increase in leaf efficiency in both *F. microcarpa* and *F. virens* after pruning is caused by increased leaf photosynthetic rates, as it has been shown before that defoliation (Hodgkinson 1974; Alderfer and Eagles 1976; Bassman and Dickmann 1982; Wallace et al. 1984; Morrison and Reekie 1995) and pruning (Tschaplinski and Blake 1995; Pinkard and Beadle 1998; Pinkard et al. 1998, 1999) can enhance foliar photosynthetic rate.

Conform to our expectations, for both species, leaf efficiency of trees pruned in autumn was higher than that of trees pruned in spring (Fig. 1, Table 1). This means that trees pruned in autumn grow more efficiently than trees pruned in spring. Thus, in regions where the growth of plants is seasonal, like subtropical China, selection of the pruning season is important for the regrowth of trees. Our results suggest that autumn pruning is less detrimental to the growth of trees due to the resulting higher leaf efficiency. Moreover, it appears that deciduous trees are even less negatively affected by autumn pruning than evergreen trees, because the increase in leaf efficiencies between autumn-pruned and spring-pruned trees was much larger in *F. virens* than in *F. microcarpa* (Fig. 1, Table 1).

Acknowledgements

I thank Prof. Marinus J. A. Werger and Dr. Heinjo During for their useful comments on an earlier version of the manuscript.

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6

Modelling tree growth as affected by pruning

with Feike Schieving and Heinjo During

Abstract

In this chapter, a tree growth model is constructed. This model can be used to analyse the effects of pruning on the growth and morphology of trees.

The model tree has a conical crown form. Leaves, branches, and the stem of the tree are clearly related to each other. The status of the tree is well specified by the height of its crown, with a given height of the basal stem below the crown, a given top crown angle, and a given leaf element density.

Tree growth in the model is carbon dependent. Two versions of carbon-dependent growth of tree are formulated. In the first one, tree growth directly relies on the net photosynthetic production of the tree, no carbon storage is considered. The tree can not grow if its net photosynthetic production is zero. In this version, seasonal growth of the tree is modelled and the effect of pruning on tree growth is analysed. The second version is developed from the first one. In this version, the growth of the tree is not directly related to the tree's net photosynthetic production, but depends on the tree's internal carbon concentration. Whether the net photosynthetic production is positive or not, the tree can grow in height as long as the carbon concentration is high enough. In this version, the effects of changes in the crown/root ratio as a consequence of pruning on tree growth and biomass allocation, and the negative feed-back effect of carbon concentration on photosynthesis are incorporated.

Keywords: carbon balance, crown form, modelling, pruning, tree growth

Introduction

Pruning of trees is extensively used to improve timber quality (Shepherd 1986; Kozlowski et al. 1991), increase fruit production and quality (Nunez-Elisea and Crane 2000), improve crown shape (Ho and Schooley 1995), and obtain fuel and other desirable plant materials

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(Evans 1992). Pruning often is implemented by removing branches from the lower crown of a tree, especially when its purpose is to improve timber quality and obtain branches and leaves as fuel and industrial raw materials.

Because of the leaf removal, the growth of a tree may be affected by pruning. The effect of pruning on tree growth varies with pruning intensity, pruning frequency, pruning season, and tree size (Møller 1960; Kozłowski et al. 1991; Uotila and Mustonen 1994; Guimond et al. 1998). One of the often-asked questions in pruning practice is how to prune trees properly so that people's needs can be well met. Undoubtedly, to answer this question, experimental study may play an important role. However, because of practical constraints such as time and finance limitation, in field studies, only a few levels of each of the investigated factors can be tested experimentally. To get a more complete understanding of the effects of pruning on tree growth and to assess the consequences of pruning regimes, the development of a tree growth model would be helpful.

In this chapter, our aim is to construct a tree growth model and use this model to investigate the effect of pruning on tree growth. In the next chapter, we will use this model structure to simulate the effects of pruning intensities and frequencies on different types of trees in different pruning seasons.

Model

1 The form of the tree

In this section, based on the conical crown form, the leaf, branch, and stem part of the tree are formulated.

The tree we are working with is viewed as a conical crown "carried" by a stem (Fig. 1), i.e. for the moment we ignore the root part of the tree. The form of the crown is characterised by its height h_t^0 and its (constant) top angle α' (with $\alpha = \tan(\alpha')$). The total height h_t^p of the tree is given by the sum

$$h_t^p = h_t^0 + h^1$$

with h^1 the height of the basal stem part below the crown (Fig. 1). Throughout we view h^1 as a constant, except for section 3, where we view h_t^1 as a function of time.

At any time t , the surface area A_t^0 of the conical crown is given by

$$A_t^0 = \pi \alpha \sqrt{1 + \alpha^2} (h_t^0)^2$$

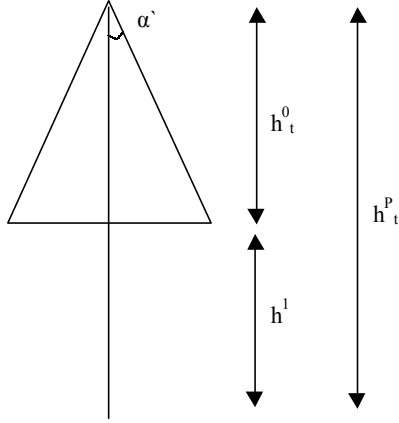


Fig. 1. Schematic illustration of the tree. h_t^0 and h_t^p denote the crown height and the total tree height at time t , respectively. α' is the top angle of the crown, h^1 is the height of the basal stem part.

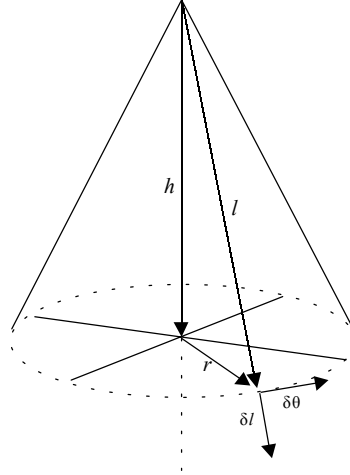


Fig. 2. Schematic illustration for deriving the surface area and the volume of the crown. h , l , and r denote the height of the crown, the side length of the crown, and the radius of the crown base, respectively.

To derive this relation we use Fig. 2. The conical surface is parameterised in terms of the pair of coordinates (θ, l) with $\theta \in [0, 2\pi]$ and $l = \sqrt{h^2 + h^2\alpha^2} = h\sqrt{1 + \alpha^2}$. The size of the infinitesimal area elements $\delta A^0(\theta, l)$ on the conical surface is given by

$$\delta A^0(\theta, l) = (r \cdot \delta\theta) \times (\delta l) = (\alpha h \delta\theta) \times (\sqrt{1 + \alpha^2} \delta h) = \alpha \sqrt{1 + \alpha^2} h \delta\theta \delta h$$

Hence the surface area of the conical crown of height h is given by

$$A^0(h) = \int_0^{2\pi} d\theta \int_0^h \alpha \sqrt{1 + \alpha^2} h' dh' = 2\pi \alpha \sqrt{1 + \alpha^2} \cdot (h^2/2) = \pi \alpha \sqrt{1 + \alpha^2} \cdot h^2$$

Shinozaki et al. (1964a,b) hold that a plant is an assemblage of many pipe units, each unit consisting of a leaf element and a pipe element. Each pipe is composed of a horizontal “branch” part and a vertical “stem” part. Due to the accretion of pipes, the stem increases in diameter from its top to the base (Fig. 3). We use this pipe model for our tree. We put the leaves of the crown on the conical surface and we assume that the leaves are distributed in a uniform way over that surface. At every time t , we assume a uniform leaf element density λ_t^p over the crown surface (viz. number of leaf elements per unit area). Then, the number of leaf elements on the surface of a crown with height h , $L_t(h)$, is given by

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$$L_t(h) = \lambda_t^P A_t^0(h) = \lambda_t^P \pi \alpha \sqrt{1 + \alpha^2} h^2$$

Each leaf element is connected to a pipe. If a_p denotes the cross section area of a pipe, then in terms of vertical pipes, the volume of living stem in the disc δh at height h in the crown is given by

$$\delta h \lambda_t^P a_p A_t^0(h) = \delta h \lambda_t^P a_p \pi \alpha \sqrt{1 + \alpha^2} h^2$$

If m_p is the specific pipe mass per unit volume, the amount of living stem mass in that crown of height h , $S_t^0(h)$, becomes

$$S_t^0(h) = \int_0^h dh \lambda_t^P a_p m_p \pi \alpha \sqrt{1 + \alpha^2} h^2 = \lambda_t^P a_p m_p \pi \alpha \sqrt{1 + \alpha^2} h^3/3$$

In order to calculate the total living stem mass S_t , we calculate the stem mass S_t^0 in the crown and the mass S_t^1 in the stem segment below the crown. In case of an unpruned tree, this stem-mass S_t^1 is given by

$$S_t^1 = L_t \cdot h^1 a_p m_p = \lambda_t^P a_p m_p A_t^0$$

To determine the total amount of living branch mass $B_t(h)$ in a crown of height h , we reason as follows: In the conical surface ring at height h and of width δh , the number of pipe ends in the crown surface band with width δh at height h is

$$2\pi \alpha \sqrt{1 + \alpha^2} \lambda_t^P h \delta h$$

and the total associated living branch pipe mass in the ring δh at height h is

$$(2\pi \alpha \sqrt{1 + \alpha^2} \lambda_t^P h \delta h) \cdot (\alpha h) \cdot (a_p m_p) = 2\pi (\lambda_t^P a_p m_p) \alpha^2 \sqrt{1 + \alpha^2} h^2 \delta h$$

Thus, the total living branch mass in a crown of height h is given by

$$B_t(h) = \int_0^h 2\pi (\lambda_t^P a_p m_p) \alpha^2 \sqrt{1 + \alpha^2} h^2 dh = 2\pi/3 (\lambda_t^P a_p m_p) \alpha^2 \sqrt{1 + \alpha^2} h^3$$

To summarize,

$$\begin{aligned} L_t &= \text{number of leaf elements in the crown with height } h_t^0 = \\ &= \pi \lambda_t^P \alpha \sqrt{1 + \alpha^2} (h_t^0)^2 = \alpha_L \lambda_t^P (h_t^0)^2 \end{aligned}$$

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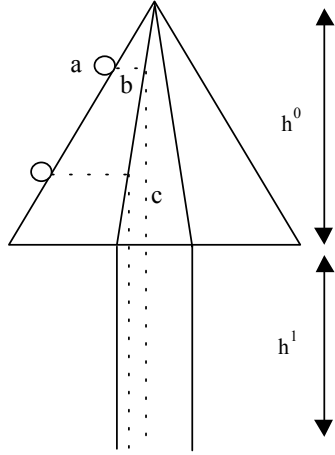


Fig. 3. Architecture of a tree based on the pipe model theory. Due to the accretion of pipes, the stem increases in diameter from the crown top to the base. The leaf element, the horizontal pipe, and the vertical pipe are denoted by a, b, and c, respectively. h^1 and h^0 indicate the crown height and basal stem height, respectively.

$$B_t = \text{amount of living branch mass in a crown with height } h_t^0 = \\ = 2\pi/3 (\lambda_t^P a_p m_p) \alpha^2 \sqrt{1 + \alpha^2} (h_t^0)^3 = \alpha_B \lambda_t^P (h_t^0)^3$$

$$S_t^0 = \text{amount of living stem mass in a crown with height } h_t^0 = \\ = \pi/3 (\lambda_t^P a_p m_p) \alpha \sqrt{1 + \alpha^2} (h_t^0)^3 = \alpha_{S0} \lambda_t^P (h_t^0)^3$$

with

$$\alpha_L = \pi \alpha \sqrt{1 + \alpha^2}, \quad \alpha_B = 2\pi/3 a_p m_p \alpha^2 \sqrt{1 + \alpha^2}, \quad \alpha_{S0} = \pi/3 a_p m_p \alpha \sqrt{1 + \alpha^2}$$

To determine the total living stem mass $S_t = S_t^0 + S_t^1$ at time t , we also must know the living stem mass over the height interval h^1 , and this mass is given by

$$S_t^1 = L_t a_p m_p h^1 = \alpha_L \lambda_t^P (h_t^0)^2 a_p m_p h^1 = \alpha_{S1} h^1 \lambda_t^P (h_t^0)^2$$

with

$$\alpha_{S1} = \alpha_L a_p m_p = \pi a_p m_p \alpha \sqrt{1 + \alpha^2}$$

Thus, for an unpruned tree, the status of the tree can be completely specified by its top crown angle α , crown height h_t^0 , leaf element density λ_t^P , and basal stem height h^1 .

Furthermore, the sum of the cross-section area of all vertical pipes in the crown is

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$$\pi \lambda_t^P a_p h_0^2 \alpha \sqrt{1 + \alpha^2}$$

which is exactly the cross-section area of the stem at the crown base (provided that all pipes in the stem closely stick to each other without any openings).

Therefore, the radius (r_0) of the stem at the crown base is given by

$$r_0 = \sqrt{\frac{\pi h_0^2 \lambda_t^P a_p \alpha \sqrt{1 + \alpha^2}}{\pi}} = h_0 \sqrt{\lambda_t^P a_p \alpha \sqrt{1 + \alpha^2}}$$

This is equal to the radius of the cylindrical stem part with height h^1 under the crown (Fig. 3).

2 The growth of the tree

In this section, on the basis of the carbon balance principle, the growth of the tree is formulated. In addition, the maximal height, the maximal growth rate, and the maximal photosynthetic rate of the tree are derived.

The carbon balance equation

At any time t , the form of the tree is given by its crown height h_t^0 and the leaf/pipe element density λ_t^P in the crown. Thus, the number of leaves in the crown and the amount of branch and stem mass are given by

$$L_t = L(h_t^0, \lambda_t^P) \quad B_t = B(h_t^0, \lambda_t^P)$$

$$S_t = S(h_t^0, \lambda_t^P) = S^0(h_t^0, \lambda_t^P) + S^1(h_t^0, \lambda_t^P)$$

For the rates of change in L_t , B_t and S_t this gives

$$d_t L_t = \partial_{h_0} L_t d_t h_t^0 + \partial_{\lambda_p} L_t d_t \lambda_t^P$$

$$d_t B_t = \partial_{h_0} B_t d_t h_t^0 + \partial_{\lambda_p} B_t d_t \lambda_t^P$$

$$d_t S_t = \partial_{h_0} S_t d_t h_t^0 + \partial_{\lambda_p} S_t d_t \lambda_t^P$$

where, $d_t L_t$ denotes dL_t/dt , while $\partial_{h_0} L_t$ denotes $\partial L_t / \partial h^0$, etc.

The rate of change in crown height is given by

$$d_t h_t^0 = \pi_t^{h_0}$$

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where π_t^{h0} is viewed as a ‘‘control variable’’. The rate of change $d_t \lambda_t^p$ in leaf/pipe element density in the crown surface is given by

$$d_t \lambda_t^p = \pi_t^{\lambda p} - \tau_p \lambda_t^p$$

Here $\tau_p \lambda_t^p$ is the death rate of leaf/pipe elements per unit crown area and this death rate is taken as the product of a constant relative death rate (τ_p) times the number of pipe-ends/leaf elements per unit crown area (λ_t^p). The production rate in pipe elements per unit crown area is denoted by $\pi_t^{\lambda p}$ and is also viewed as a control variable.

To keep things simple, we assume that the tree keeps the leaf element density in the crown at a constant value λ_{p0} . This means that $d_t \lambda_t^p$ is always zero and hence the production rate $\pi_t^{\lambda p}$ in leaf elements is equal to $\tau_p \lambda_{p0}$.

Obviously, the control variables π_t^{h0} and $\pi_t^{\lambda p} = \tau_p \lambda_{p0}$ are not independent. They are related via the carbon balance equation:

Net photosynthetic rate = carbon consumption rate involved in the production of
leaf and branch/stem pipe elements

(We assume here that there is no carbon storage in the tree). We write this as

$$\begin{aligned} P_t^n &= r_{gL} \{ \partial_{h0} L \pi_t^{h0} + \partial_{\lambda p} L \pi_t^{\lambda p} \} + \\ &\quad r_{gBS} \{ \partial_{h0} B \pi_t^{h0} + \partial_{\lambda p} B \pi_t^{\lambda p} + \partial_{h0} S \pi_t^{h0} + \partial_{\lambda p} S \pi_t^{\lambda p} \} \\ &= \{ r_{gL} \partial_{h0} L + r_{gBS} (\partial_{h0} B + \partial_{h0} S) \} \pi_t^{h0} + \{ r_{gL} \partial_{\lambda p} L + r_{gBS} (\partial_{\lambda p} B + \partial_{\lambda p} S) \} \tau_p \lambda_{p0} \\ &= \{ r_{gL} \partial_{h0} L + r_{gBS} (\partial_{h0} B + \partial_{h0} S) \} \pi_t^{h0} + \{ r_{gL} L + r_{gBS} (B+S) \} \tau_p \end{aligned}$$

Here r_{gL} and r_{gBS} are the structural and respiratory carbon investments in the production of leaf elements and branch/stem mass. For branches and stems we assume that those construction costs are the same.

For the net photosynthetic rate P_t^n one can write

$$P_t^n = p_{gL} L_t - \{ r_{mL} L_t + r_{mBS} (B_t + S_t) \}$$

with r_{mL} and r_{mBS} the maintenance respiration per leaf element and per unit branch/stem mass and p_{gL} the gross photosynthetic rate per leaf element. This gross photosynthetic rate p_{gL} per leaf element per day itself is calculated as

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$$p_{t}^{gL} = \int_{tSR}^{tSS} dt' p_{t'}^{gL} = \int_{tSR}^{tSS} dt' \alpha_L \frac{p_{gmL} \Phi_{aL} i_{aL}(t')}{p_{gmL} + \Phi_{aL} i_{aL}(t')}$$

Here tSS and tSR denote the time of sunset and sunrise in a day, respectively, a_L is the area of the leaf element, p_{gmL} is the photosynthetic capacity per unit leaf area, Φ_{aL} is the quantum yield (in terms of absorbed photons) and $i_{aL}(t')$ is the rate of photon absorption per unit leaf area of the leaves as a function of time of the day. Since all leaves are located in the crown surface, we assume that all leaves experience the same light climate over the day. We also assume that all days are the same, i.e. for the moment we ignore the seasonality of the light climate.

Thus, for a tree growing with a constant pipe/leaf element density λ_{p0} in the crown, the carbon balance equation becomes

$$\{p_{gL} - (r_{mL} + r_{gL}\tau_p)\} \cdot L - (r_{mBS} + r_{gBS}\tau_p)(B+S) = \{r_{gL} \partial_{h0}L + r_{gBS}(\partial_{h0}B + \partial_{h0}S)\} \pi^{h0} \quad (1^A)$$

which specifies the height growth rate π^{h0} in terms of the height h^0_t of the crown. That is, using

$$\begin{aligned} L &= \alpha_L \lambda_{p0} (h^0)^2 & \partial_{h0}L &= 2\alpha_L \lambda_{p0} h^0 \\ B &= \alpha_B \lambda_{p0} (h^0)^3 & \partial_{h0}B &= 3\alpha_B \lambda_{p0} (h^0)^2 \\ S &= \alpha_{S0} \lambda_{p0} (h^0)^3 + \alpha_{S1} h^1 \lambda_{p0} (h^0)^2 & \partial_{h0}S &= 3\alpha_{S0} \lambda_{p0} (h^0)^2 + 2\alpha_{S1} h^1 \lambda_{p0} h^0 \end{aligned}$$

We can write the carbon balance equation 1^A as

$$\begin{aligned} &\{p_{gL} - (r_{mL} + r_{gL}\tau_p)\} \cdot \alpha_L \lambda_{p0} (h^0)^2 - (r_{mBS} + r_{gBS}\tau_p) \{ \alpha_B \lambda_{p0} (h^0)^3 + \alpha_{S0} \lambda_{p0} (h^0)^3 + \alpha_{S1} h^1 \lambda_{p0} (h^0)^2 \} \\ &= \{ r_{gL} 2\alpha_L \lambda_{p0} h^0 + r_{gBS} \cdot \{ 3\alpha_B \lambda_{p0} (h^0)^2 + 3\alpha_{S0} \lambda_{p0} (h^0)^2 + 2\alpha_{S1} h^1 \lambda_{p0} h^0 \} \} \pi^{h0} \end{aligned}$$

Cancellation of the common factor $\lambda_{p0} \cdot h^0$ results in

$$\begin{aligned} &\{p_{gL} - (r_{mL} + r_{gL}\tau_p)\} \cdot \alpha_L h^0 - (r_{mBS} + r_{gBS}\tau_p) \{ \alpha_B (h^0)^2 + \alpha_{S0} (h^0)^2 + \alpha_{S1} h^1 h^0 \} = \\ &= \{ r_{gL} 2\alpha_L + r_{gBS} \cdot (3\alpha_B h^0 + 3\alpha_{S0} h^0 + 2\alpha_{S1} h^1) \} \pi^{h0} \end{aligned} \quad (1^B)$$

i.e., the carbon balance equation can be written as

$$A_L h^0 - A_{S1} h^1 h^0 - A_{BS0} (h^0)^2 = (B_L + B_{S1} h^1 + B_{BS0} h^0) \pi^{h0} \quad (2^A)$$

with

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$$\begin{aligned} A_L &= \{p_{gL} - (r_{mL} + r_{gL} \tau_p)\} \alpha_L \\ A_{S1} &= (r_{mBS} + r_{gBS} \tau_p) \alpha_{S1} \\ A_{BS0} &= (r_{mBS} + r_{gBS} \tau_p)(\alpha_B + \alpha_{S0}) \end{aligned}$$

and

$$\begin{aligned} B_L &= 2 r_{gL} \alpha_L \\ B_{S1} &= 2 r_{gBS} \alpha_{S1} \\ B_{BS0} &= 3 r_{gBS} (\alpha_B + \alpha_{S0}) \end{aligned}$$

Hence, as a function of the crown height h^0 , the height growth rate π^{h^0} is a function of the form

$$\pi^{h^0} = \frac{A_L h^0 - A_{S1} h^1 h^0 - A_{BS0} (h^0)^2}{B_L + B_{S1} h^1 + B_{BS0} h^0} \quad (2^B)$$

Obviously, the numerator in the above expression is a ‘‘top’’ parabola with root $h^0 = 0$ and root $h^0 = h^{0,max} = (A_L - A_{S1} h^1) / A_{BS0}$. The denominator is a line with intercept $B_L + B_{S1} h^1$ and positive slope B_{BS0} . This means that h^0 reaches a stable maximum at $h^{0,max}$.

The maximum height of the tree

The maximum height of the tree is given by

$$h^0 = \frac{A_L - A_{S1} h^1}{A_{BS0}}$$

Thus,

$$h^0 = \frac{\{p_{gL} - (r_{mL} + r_{gL} \tau_p)\} \alpha_L - \alpha_{S1} h^1 \cdot (r_{mBS} + r_{gBS} \tau_p)}{(r_{mBS} + r_{gBS} \tau_p)(\alpha_B + \alpha_{S0})}$$

To simplify,

$$h^0 = \frac{\{p_{gL} - (r_{mL} + r_{gL} \tau_p)\} \alpha_L}{(r_{mBS} + r_{gBS} \tau_p)(\alpha_B + \alpha_{S0})} - \frac{\alpha_{S1}}{\alpha_B + \alpha_{S0}} h^1 \quad (3^A)$$

According to the specifications of α_B , α_{S0} , and α_{S1} in section 1, we have

$$\frac{\alpha_{S1}}{\alpha_B + \alpha_{S0}} = \frac{\pi \cdot a_p m_p \cdot \alpha \sqrt{1 + \alpha^2}}{(2\pi/3) \cdot a_p m_p \cdot \alpha^2 \sqrt{1 + \alpha^2} + (\pi/3) \cdot a_p m_p \cdot \alpha \sqrt{1 + \alpha^2}}$$

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$$= \frac{\alpha}{2\alpha^2/3 + \alpha/3} = \frac{3}{2\alpha + 1} \quad (3^B)$$

So, the maximum height h^0 is a decreasing function in h^1 , but the total tree height $h^p = h^1 + h^0$ is an increasing function in h^1 if $\{\alpha_{S1}/(\alpha_B + \alpha_{S0})\} < 1$ and that will be the case if $\alpha > 1$ (this means that the total tree height h^p will be decreasing in height h^1 if $\alpha < 1$).

The maximum growth rate in height and maximum net photosynthetic rate

Using expression (2^B) and differentiate π^{h^0} with respect to h^0 gives

$$d_{h^0}\pi^{h^0} = \frac{1}{(B_L + B_{S1}h^1 + B_{BS0}h^0)^2} \{ (A_L - A_{S1}h^1 - 2A_{BS0}h^0)(B_L + B_{S1}h^1 + B_{BS0}h^0) - (A_Lh^0 - A_{S1}h^1h^0 - A_{BS0}(h^0)^2)B_{BS0} \}$$

Thus, for h_t^0 sufficiently close to zero, the derivative $d_{h^0}\pi^{h^0}$ is positive, while for h_t^0 sufficiently close to $h^{0, \max} = (A_L - A_{S1}h^1)/A_{BS0}$, this derivative is negative. Obviously, the crown height h_t^0 at which the growth rate π^{h^0} is at its maximum, is given by the equation

$$(A_L - A_{S1}h^1 - 2A_{BS0}h^0)(B_L + B_{S1}h^1 + B_{BS0}h^0) - (A_Lh^0 - A_{S1}h^1h^0 - A_{BS0}(h^0)^2)B_{BS0} = 0$$

i.e.

$$(A_L - A_{S1}h^1 - 2A_{BS0}h^0) - (A_Lh^0 - A_{S1}h^1h^0 - A_{BS0}(h^0)^2) \frac{B_{BS0}}{B_L + B_{S1}h^1 + B_{BS0}h^0} = 0 \quad (4)$$

The “top” parabola in the numerator of (2^B) has its maximum value at $(A_L - A_{S1}h^1)/(2A_{BS0})$. Substitution of this value of h^0 in the left hand side of (4) gives a negative value. So, if the crown is at half of its maximum length, the height growth rate function is already a decreasing function of crown height h_t^0 . Therefore, the tree height at which the tree obtains its maximum growth rate must lie below half the maximum crown height.

In effect, the height growth of the tree depends on the left part of equation (1^A). Only when this part is positive, the tree grows in height (viz. $\pi^{h^0} > 0$). This part we view as the “net photosynthetic rate” P^{n^*} of the tree taking leaf shedding and pipe death into account, which is a bit different from the net photosynthetic rate $P_t^n = p_{gL} L_t - \{ r_{mL} L_t + r_{mBS}(B_t + S_t) \}$.

P^{n^*} is given by

$$\{ p_{gL} - (r_{mL} + r_{gL}\tau_p) \} \cdot L - (r_{mBS} + r_{gBS}\tau_p)(B + S) =$$

$$= \{ p_{gL} - (r_{mL} + r_{gL}\tau_p) \} \cdot \alpha_L \lambda_{p0}(h^0)^2 - (r_{mBS} + r_{gBS}\tau_p) \{ \alpha_B \lambda_{p0}(h^0)^3 + \alpha_{S0} \lambda_{p0}(h^0)^3 + \alpha_{S1} h^1 \lambda_{p0}(h^0)^2 \}$$

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$$= A_L \lambda_{p0} (h^0)^2 - A_{S1} h^1 \lambda_{p0} (h^0)^2 - A_{BS0} \lambda_{p0} (h^0)^3$$

Differentiation of P^{n^*} with respect to height h^0 gives

$$d_{h^0} P^{n^*} = 2 A_L \lambda_{p0} h^0 - A_{S1} h^1 \lambda_{p0} 2 h^0 - 3 A_{BS0} \lambda_{p0} (h^0)^2$$

and the net photosynthetic rate P^{n^*} will be at its maximum if

$$2 A_L \lambda_{p0} h^0 - A_{S1} h^1 \lambda_{p0} 2 h^0 - 3 A_{BS0} \lambda_{p0} (h^0)^2 = 0$$

$$2 (A_L - A_{S1} h^1) - 3 A_{BS0} h^0 = 0$$

$$h_0 = \frac{2(A_L - A_{S1} h^1)}{3 A_{BS0}} = \frac{4}{3} \frac{A_L - A_{S1} h^1}{2 A_{BS0}}$$

Hence, the tree crown obtains its maximum net photosynthetic rate P^{n^*} at 2/3 of its maximum height. Since the maximum growth rate is obtained at a crown height which lies below half of this maximum crown height, the point of maximum growth rate in height lies “far below” the point at which the net photosynthetic rate obtains its maximum.

3 Pruning

In this section, we assume that the height of the basal stem h^1 of the tree is a variable, not a constant. In this way, the pruning effect on growth can be simulated.

Here we specify the status of the tree in terms of its total plant height h_t^p and the height of its basal stem h_t^1 . In that case its crown height h_t^0 is given as $h_t^0 = h_t^p - h_t^1$. If the tree increases its crown, this occurs by an increase in h_t^p . If the tree prunes itself, by shedding its lower branches, then the basal stem height h_t^1 increases. Here we assume that as soon as h_t^1 is increased, the pipes in the stem, which are associated with the pruned leaves and branches, die. This means that for any tree, pruned or not, the status of the living aboveground part is given by h_t^p , h_t^1 and λ_t^p .

Thus, in this section the status of the tree is given by the three system variables λ_t^p , h_t^p and h_t^1 . Therefore the rate of changes in number of leaf elements, living branch and stem mass is given by

$$d_t L_t = \partial_{h^p} L_t d_t h_t^p + \partial_{h^1} L_t d_t h_t^1 + \partial_{\lambda^p} L_t d_t \lambda_t^p$$

$$d_t B_t = \partial_{h^p} B_t d_t h_t^p + \partial_{h^1} B_t d_t h_t^1 + \partial_{\lambda^p} B_t d_t \lambda_t^p$$

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$$d_t S_t = \partial_{hp} S d_t h_t^p + \partial_{h1} S d_t h_t^1 + \partial_{\lambda p} S d_t \lambda^p$$

We also assume that the tree grows under a constant leaf element density λ_{p0} and that the relative death rate of leaf elements and pipe elements is equal to the constant τ_p , and hence $d_t \lambda^p = 0$ and $\pi^{\lambda p} = \tau_p \lambda_{p0}$.

Using equation 1^A and 1^B from section 2, with $h^0 = h_t^0 = h_t^p - h_t^1$, we can write π^{hp} as a function of h_t^p and h_t^1 :

$$\pi^{hp} = \frac{\{p_{gL} - (r_{mL} + r_{gL} \tau_p)\} \cdot \alpha_L (h^p - h^1)}{r_{gL} 2\alpha_L + r_{gBS} \cdot \{3\alpha_B (h^p - h^1) + 3\alpha_{S0} (h^p - h^1) + 2\alpha_{S1} h^1\}} - \frac{(r_{mBS} + r_{gBS} \tau_p) \{(\alpha_B + \alpha_{S0})(h^p - h^1)^2 + \alpha_{S1} h^1 (h^p - h^1)\}}{r_{gL} 2\alpha_L + r_{gBS} \cdot \{3\alpha_B (h^p - h^1) + 3\alpha_{S0} (h^p - h^1) + 2\alpha_{S1} h^1\}} \quad (5^A)$$

or, using the abbreviations from section 2

$$\pi^{hp} = \frac{A_L (h^p - h^1) - A_{BS0} (h^p - h^1)^2 - A_{S1} h^1 (h^p - h^1)}{B_L + B_{BS0} (h^p - h^1) + B_{S1} h^1} \quad (5^B)$$

Although the above expression is very similar to the one formulated in section 2, it is not exactly the same, because here h^p and h^1 are both variables. If we differentiate π^{hp} with respect to h^1 , the expression

$$\partial_{h1} [A_L (h^p - h^1) - A_{BS0} (h^p - h^1)^2 - A_{S1} h^1 (h^p - h^1)] \cdot \{B_L + B_{BS0} (h^p - h^1) + B_{S1} h^1\} - \{A_L (h^p - h^1) - A_{BS0} (h^p - h^1)^2 - A_{S1} h^1 (h^p - h^1)\} \cdot \partial_{h1} [B_L + B_{BS0} (h^p - h^1) + B_{S1} h^1]$$

determines the sign of the derivative $\partial_{h1} \pi^{hp}$. Expansion of this expression gives

$$\{-A_L + 2A_{BS0} (h^p - h^1) - A_{S1} (h^p - h^1) + A_{S1} h^1\} \{B_L + B_{BS0} (h^p - h^1) + B_{S1} h^1\} - \{A_L (h^p - h^1) - A_{BS0} (h^p - h^1)^2 - A_{S1} h^1 (h^p - h^1)\} \{-B_{BS0} + B_{S1}\} \quad (6)$$

If we assume that both total height h^p and crown base height h^1 are small, i.e. if we assume that they are both of size ϵ , expression (6) becomes

$$\{-A_L + 2A_{BS0} \epsilon - A_{S1} \epsilon + A_{S1} \epsilon\} \{B_L + B_{BS0} \epsilon + B_{S1} \epsilon\} - \{A_L \epsilon - A_{BS0} \epsilon^2 - A_{S1} h^1 \epsilon\} \{-B_{BS0} + B_{S1}\} = -A_L B_L + O(\epsilon)$$

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and we see that, whatever the precise form of the form factors $\alpha_L, \alpha_B, \alpha_{S0}$ and α_{S1} , pruning has a negative effect on the height growth rate π^{hp} , if the tree is sufficiently small.

At steady state, the net tree photosynthetic rate P^{n^*} is zero, and expression (6) becomes

$$\{-A_L + 2A_{BS0}(h^p - h^1) - A_{S1}(h^p - h^1) + A_{S1}h^1\} \{B_L + B_{BS0}(h^p - h^1) + B_{S1}h^1\}$$

and since the second factor in the above expression is always positive, the sign of this expression, i.e. the sign of $\partial_{h^1}\pi^{hp}$, is determined by the sign of the first factor

$$\{-A_L + (2A_{BS0} - A_{S1})(h^p - h^1) + A_{S1}h^1\} \quad (7)$$

If the net photosynthetic rate P^{n^*} is zero, one can write

$$A_L(h^p - h^1) - A_{BS0}(h^p - h^1)^2 - A_{S1}h^1(h^p - h^1) = 0$$

i.e.

$$A_L - A_{BS0}(h^p - h^1) - A_{S1}h^1 = 0$$

or

$$A_L - A_{BS0}h^p + A_{BS0}h^1 - A_{S1}h^1 = 0$$

and

$$h^p = \frac{A_L + (A_{BS0} - A_{S1})h^1}{A_{BS0}} > h^1 > 0$$

So, substitution in expression (7) gives

$$\begin{aligned} & \{-A_L + (2A_{BS0} - A_{S1})(h^p - h^1) + A_{S1}h^1\} = \\ & = -A_L + (2A_{BS0} - A_{S1}) \left\{ \frac{A_L + (A_{BS0} - A_{S1})h^1}{A_{BS0}} - h^1 \right\} + A_{S1}h^1 = \\ & = -A_L + (2A_{BS0} - A_{S1}) \left\{ \frac{A_L + (A_{BS0} - A_{S1})h^1 - A_{BS0}h^1}{A_{BS0}} \right\} + A_{S1}h^1 = \\ & = -A_L + (2A_{BS0} - A_{S1}) \left\{ \frac{A_L - A_{S1}h^1}{A_{BS0}} \right\} + A_{S1}h^1 = \\ & = -A_L + (2 - A_{S1}/A_{BS0})(A_L - A_{S1}h^1) + A_{S1}h^1 = \end{aligned}$$

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$$\begin{aligned}
 &= -A_L + 2A_L - 2A_{S1}h^1 - A_{S1}/A_{BS0}(A_L - A_{S1}h^1) + A_{S1}h^1 = \\
 &= A_L - A_{S1}h^1 - A_{S1}/A_{BS0}(A_L - A_{S1}h^1) = \\
 &= (A_L - A_{S1}h^1)(1 - A_{S1}/A_{BS0})
 \end{aligned}$$

Here, $(A_L - A_{S1}h^1)$ is positive (because if P^{n^*} is zero, $\{A_L - A_{BS0}(h^p-h^1) - A_{S1}h^1\} = 0$). It depends on the ratio A_{S1}/A_{BS0} whether $\partial_{h^1}\pi^{hp}$ is decreasing in h^1 or increasing for the steady state situation $P^{n^*} = 0$.

In section 2 we defined A_L, A_{S1}, A_{BS0} by

$$A_L = \{p_{gL} - (r_{mL} + r_{gL}\tau_p)\} \alpha_L \quad A_{S1} = (r_{mBS} + r_{gBS}\tau_p) \alpha_{S1} \quad A_{BS0} = (r_{mBS} + r_{gBS}\tau_p)(\alpha_B + \alpha_{S0})$$

And the ratio A_{S1}/A_{BS0} is given by

$$\frac{A_{S1}}{A_{BS0}} = \frac{\alpha_{S1}}{\alpha_B + \alpha_{S0}} = 3/(2\alpha + 1) \quad \text{with } \alpha = \tan(\alpha')$$

We thus see that, at steady state, the effect of pruning will depend on the crown angle α' . If $\alpha = \tan(\alpha') < 1$, meaning a very narrow crown, even a single pruning in the steady state will always lead to the death of the tree. If $\alpha > 1$, meaning a flat crown, a single pruning will lead to an increase in height. However, this doesn't imply that the height can be increased by pruning always. Actually, repeated pruning will eventually lead to the death of the tree.

4 Growth of the tree in an environment with seasons

In many parts of the earth the weather conditions change in a more or less regular pattern over the year. Such areas have different seasons, which implies different conditions for growth.

To study the performance of our modelled tree, we divide the year simply in a "good" season and a "bad" season. If we want to investigate the growth of a tree in this seasonal environment, we must take the internal "carbon" status of the tree into account. This becomes clear if we assume that the calendar year is split up in a "good" season, with length Γ^+ and leaf light intensity i_L^+ and a "bad" season, with length Γ^- and leaf light intensity i_L^- (Fig. 4). In this model, we can take the light intensity i_L^- in the bad season so low, that the net photosynthetic rate P^{n^*} becomes negative and hence, the tree will die. To prevent its death during the bad season, the tree needs carbon to survive that season.

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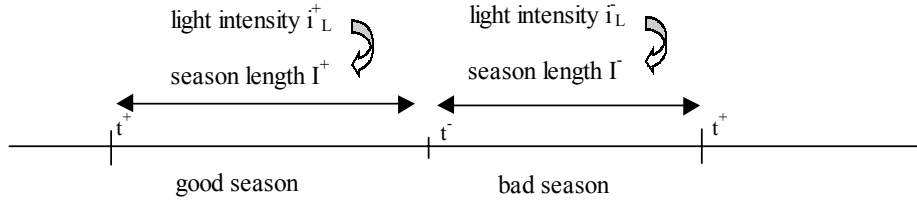


Fig. 4. Illustration of seasonality in terms of light intensity and season length. A calendar year is split up in a "good" season, starting from t^+ , with length I^+ and light intensity i_L^+ , and a "bad" season, starting from t^- , with length I^- and light intensity i_L^- .

To keep things simple, we assume that conditions during the bad season are unfavourable so that the tree does not grow during that season. Given the tree status $(h_{t^-}^p, h_{t^-}^l)$ at the beginning of the bad season, we can calculate the amount of carbon $C_{I(-)}$ needed to survive the bad season:

$$C_{I(-)} = I^- \cdot \{ (r_{mL} + r_{gL}\tau_p - p_{gL}) L_{t^-} + (r_{mBS} + r_{gBS}\tau_p)(B_{t^-} + S_{t^-}) \}$$

$$= I^- \cdot \{ (r_{mL} + r_{gL}\tau_p - p_{gL}) L(h_{t^-}^p, h_{t^-}^l) + (r_{mBS} + r_{gBS}\tau_p)(B(h_{t^-}^p, h_{t^-}^l) + S(h_{t^-}^p, h_{t^-}^l)) \}$$

Here t^- denotes the time at which the bad season begins, and t^+ denotes the time at which the next good season begins.

Two examples of simple growth strategies can be formulated:

- A over the good season I^+ : the tree first grows, up to a certain time t_a , and from time t_a on it stops growing in height and stores carbon needed to survive the bad season I^- (Fig.5).
- B over the good season I^+ , up to a certain time t_b , the tree first saves carbon needed to survive over the bad season I^- , and then grows in height after time t_b until the arrival of the bad season at time t^- (Fig. 6).

The first strategy appears to be somewhat easier to calculate. If the tree grows in height $h_{t^-}^p$, we can calculate for any tree size $h_{t^-}^p$, the net carbon gain $P^{n^+}(h_{t^-}^p, t^- - t)$ over the time interval $(t^- - t)$ and we can compare $P^{n^+}(h_{t^-}^p, t^- - t)$ with $C_{I(-)}$ (Fig. 5). We assume that for small trees, the net carbon gain over the growing season (viz. the good season) is larger than the maintenance costs needed to survive the bad season.

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Then, the calculation of t_a is well specified if the lengths of the seasons are fixed. Since an increase in tree size will lead to an increase of the survival costs $C_{I(-)}$, the tree will eventually stop growing in height, as height increase will lead to a stronger increase in survival costs than in photosynthetic gains. It is easy to see that decreasing the light intensity i_L^+ and/or i_L^- will move the switch time t_a to a point longer before the end of the good season, while increasing the light intensity i_L^+ and/or i_L^- will move the switch time t_a more towards the end of the good season.

In strategy B the tree does not grow in height during the first part of the good season. If $h_{t^+}^p$ denotes the height status at the beginning of the good season, the tree has still that same height status at the switch time t_b . We can calculate the growth in height over the time interval $(t-t_b)$. Thus, for every t_b we can calculate the amount of carbon a tree having grown to height $h_{t^-}^p$ at time t needs to survive the bad season Γ . If at a certain time, this amount of carbon is equal to the net carbon gain $P^n(h_{t^+}^p, t_b-t^+)$ over the first part (t_b-t^+) of the good season Γ^+ , this defines the switch time t_b (Fig. 6). Obviously, this switch time t_b reacts in the same way on changes in light intensities i_L^+ and i_L^- as t_a in strategy A.

The strategies A and B do not lead to the same results. We may expect the time period $(t-t_a)$ to be shorter than the time period (t_b-t^+) . The reason is that in case of strategy A, over the good season Γ^+ , the tree first starts increasing its photosynthetic area and then starts saving carbon. Starting at the beginning of the good season, a tree growing under strategy A will need less time to collect the carbon to survive the bad season than a tree growing under strategy B, and hence at the end of the good season, it will also be larger than the tree growing under the B strategy.

One may also formulate strategies A and B in terms of a ‘‘concentration’’ strategies A' and B'. For that purpose, we take a tree with initial status $h_{t_0}^p$ at the end of the good season having a carbon concentration c^* , which is needed to survive the first bad season. Given the status $h_{t^-}^p$ at the beginning of the first bad season, we can calculate the amount of carbon

$$C_{I(-)} = \Gamma \cdot \{ (r_{mL} + r_{gL}\tau_p - p_{gL}) L(h_{t^-}^p, h_{t^-}^1) + (r_{mBS} + r_{gBS}\tau_p)(B(h_{t^-}^p, h_{t^-}^1) + S(h_{t^-}^p, h_{t^-}^1)) \}$$

needed to survive this bad season. Then, given the tree status $M_{t^-} = m_L L_{t^-} + B_{t^-} + S_{t^-}$, where m_L is the mass of a leaf element, we can define the constant value of c^* by

$$c^* = \frac{C_{I(-)}}{M_{t^-}}$$

Using $h_{t^-}^0 = h_{t^-}^p - h_{t^-}^1$ one can rewrite this minimum concentration c^* , which must be reached at the beginning at the first bad season, by

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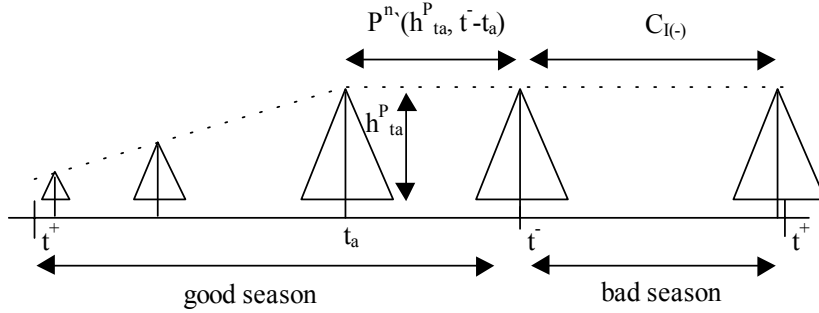


Fig. 5. Diagram of strategy A: over the good season, the tree first grows in height until time t_a , and then stores carbon over the rest time of good season needed to survive the bad season. The good season and the bad season start at time t^+ and t^- , respectively. t_a is the time at which the tree stops growing in height and starts to store carbon. h^p_{ta} is the height of the tree at time t_a . $P^n(h^p_{ta}, t-t_a)$ is the carbon storage over the time period $t-t_a$, which is equal to the carbon consumption $C_{I(-)}$ of the tree with height h^p_{ta} over the bad season.

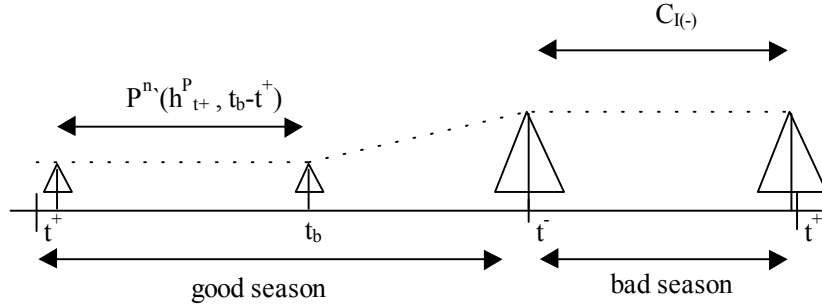


Fig. 6. Diagram of strategy B: over the good season, up to time t_b , the tree first stores carbon which is needed to survive the bad season, and then starts growing in height from t_b to t^- . The good season and the bad season start at time t^+ and t^- , respectively. t_b is the time at which the tree stops storing carbon and starts to grow in height. $h^p_{t^+}$ is the height of the tree at time t^+ , which does not change until time t_b . $P^n(h^p_{t^+}, t_b-t^+)$ is the carbon storage over the time period t_b-t^+ , which is equal to the carbon consumption $C_{I(-)}$ of the tree with height $h^p_{t^+}$ over the bad season.

$$c^* = \Gamma \cdot \frac{(r_{mL} + r_{gL}\tau_p - p_{gL})L(h_{t^-}^0) + (r_{mBS} + r_{gBS}\tau_p)(B(h_{t^-}^0) + S(h_{t^-}^0))}{m_L L(h_{t^-}^0) + B(h_{t^-}^0) + S(h_{t^-}^0)}$$

Simplifying the notation by writing $\rho_L = r_{mL} + r_{gL}\tau_p - p_{gL}$, $\rho_{BS} = r_{mBS} + r_{gBS}\tau_p$, this expression can be written as

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$$c^* m_L L(h_{t-}^0) + c^* \{ B(h_{t-}^0) + S(h_{t-}^0) \} = \Gamma \rho_L L(h_{t-}^0) + \Gamma \rho_{BS} (B(h_{t-}^0)+S(h_{t-}^0))$$

i.e.

$$(c^* m_L - \Gamma \rho_L) L(h_{t-}^0) + (c^* - \Gamma \rho_{BS}) \{ B(h_{t-}^0) + S_0(h_{t-}^0) + S_1(h_{t-}^0) \} = 0$$

Obviously, $L(h_{t-}^0)$ and $S_1(h_{t-}^0)$ are quadratic functions in h_{t-}^0 , while $B(h_{t-}^0)$ and $S_0(h_{t-}^0)$ are cubic in h_{t-}^0 . That implies that the above equation can only be guaranteed to hold for every height h_{t-}^0 , if the coefficients $(c^* m_L - \Gamma \rho_L)$ and $(c^* - \Gamma \rho_{BS})$ are both zero, which does not need to be the case. Thus, if want to work with a minimum concentration c^* , which the tree must reach at the beginning of a bad season, we have no guarantee that after that year the amount of carbon associated with this minimum concentration c^* will be sufficient to have the tree survive subsequent bad seasons. However, a simple way to guarantee this condition is by not storing the carbon in the leaves but in the stem and branches, i.e. we define the container volume M by $M=B+S$. We then can write for the concentration c^* to be reached at the beginning of the first bad season

$$c^* = \Gamma \cdot \frac{(r_{mL} + r_{gL} \tau_p - p_{gL})L(h_{t-}^0) + (r_{mBS} + r_{gBS} \tau_p)(B(h_{t-}^0) + S(h_{t-}^0))}{B(h_{t-}^0) + S(h_{t-}^0)}$$

$$= \Gamma \cdot \left\{ \frac{(r_{mL} + r_{gL} \tau_p - p_{gL})L(h_{t-}^0)}{B(h_{t-}^0) + S(h_{t-}^0)} + (r_{mBS} + r_{gBS} \tau_p) \right\}$$

In this case the term

$$(r_{mL} + r_{gL} \tau_p - p_{gL}) \frac{L(h_{t-}^0)}{B(h_{t-}^0) + S(h_{t-}^0)}$$

will be a (positively valued) decreasing function of the crown height h_{t-}^0 . If the tree grows in height over the years, this term will become smaller. Therefore, if the tree always reaches the constant value c^* at the beginning of the successive bad seasons, it will build up a surplus of carbon at the end of the bad season over the years. This also implies that, if our trees grow under strategies A` or B`, these trees will grow less in height compared to the trees growing under strategies A and B.

5 Strengthening the physiological basis of our mechanistically growing tree

The tree we modelled so far is steered very simply. It differs strongly from real-world trees which grow under a complex of physiological controls. In this section we want to increase the practical value of our model by strengthening the physiological basis of our model tree. We do this by equipping our model tree with a number of controls that are similar to the physiological controls of real-world trees.

Let us imagine the tree as a sort of “carbon” container with a “volume” characterised by its total mass

$$M_t = L_t + B_t + S_t + R_t = M^{LB}_t + S_t + R_t$$

Here, $M^{LB}_t = L_t + B_t$ is the so-called crown mass, S_t is the total stem mass and R_t is the total below-ground (root) mass. In the previous sections we defined L_t in terms of the total number of leaf elements in the crown, but here it is viewed as the total leaf mass. The leaf, branch and stem mass are completely specified by crown height h^0 , basal stem height h^1_t , and the constant leaf element density λ_{p0} . However, the root mass R_t , and its associated dynamics must still be specified. To model the growth of the roots, we reason as follows:

Let $\sigma_t = M^{LB}_t/R_t$ denote the crown/root ratio of the tree and at a certain time t^* the crown/root ratio is equal to some value σ^* . Let us assume that the tree will maintain this ratio σ^* after that time t^* . Then for any time after that time t^* , one may write

$$M^{LB}/R = \sigma^*$$

$$d_t [M^{LB}/R] = 0$$

$$1/(R)^2 \cdot \{ d_t M^{LB} R - M^{LB} d_t R \} = 0$$

$$d_t R = R/M^{LB} \cdot d_t M^{LB} = 1/\sigma^* \cdot d_t M^{LB}$$

In an imbalanced tree, in which the crown/root ratio σ is different from the set value σ^* , we assume that the above- and below-ground “growth rates” $d_t M^{LB}$ and $d_t R$ are “steered” by a function

$$\sigma \rightarrow \frac{d_t R}{d_t M^{LB} + d_t R} = \varphi^R(\sigma) = \text{MIN} \left\{ 2\varphi^{R*} \cdot \frac{\sigma^n}{(\sigma^*)^n + \sigma^n}, 1-\varepsilon \right\} \quad (8^A)$$

Here n is a non-negative integer, and usually we take n equal to 2.

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At crown/root ratio σ^* , the value of φ^{R*} is given by

$$\varphi^{R*} = \frac{d_t R}{d_t M^{LB} + d_t R} = \frac{\frac{1}{\sigma^*} d_t M^{LB}}{d_t M^{LB} + \frac{1}{\sigma^*} d_t M^{LB}} = \frac{1/\sigma^*}{1+1/\sigma^*} = \frac{1}{\sigma^* + 1} \quad (8^B)$$

The form of the function $\sigma \rightarrow \varphi^R(\sigma)$ is visualised in Fig. 7. The use of the value $(1-\varepsilon)$ instead of 1 in the definition of the function $\sigma \rightarrow \varphi^R(\sigma)$ guarantees that for high crown/root ratios, we can still write $d_t R$ as a function of $d_t M^{LB}$ (see below).

So, whether the plant is balanced or not, at any time t the derivatives $d_t R$ and $d_t M^{LB}$ can be related to each other by

$$\begin{aligned} \frac{d_t R}{d_t M^{LB} + d_t R} &= \varphi^R(\sigma_t) \\ d_t R &= \varphi^R(\sigma_t) \{ d_t M^{LB} + d_t R \} \\ d_t R (1 - \varphi^R(\sigma_t)) &= \varphi^R(\sigma_t) d_t M^{LB} \\ d_t R &= \frac{\varphi^R(\sigma_t)}{1 - \varphi^R(\sigma_t)} \cdot d_t M^{LB} \end{aligned}$$

For an unpruned tree with above-ground height $h^p = h^0 + h^1$, at any time t , the above-ground mass status is uniquely defined by its crown height h^0 and leaf element density λ^p . Thus, using that $d_t \lambda^p = 0$, we may write the derivative $d_t M^{LB}$ as

$$\begin{aligned} d_t M^{LB} &= d_t [L(h^0, \lambda^p) + B(h^0, \lambda^p)] = \\ &= (\partial_{h^0} L + \partial_{h^0} B) d_t h^0 + (\partial_{\lambda^p} L + \partial_{\lambda^p} B) \cdot d_t \lambda^p = \\ &= (\partial_{h^0} L + \partial_{h^0} B) \pi^{h^0} \end{aligned}$$

Since the crown is supposed to maintain a constant pipe density over the crown, and we allow a constant relative death rate τ_p for those pipes, the associated mass production rate Π^{LB} can be written as

$$\Pi^{LB} = (\partial_{h^0} L + \partial_{h^0} B) \pi^{h^0} + \tau_p M^{LB}$$

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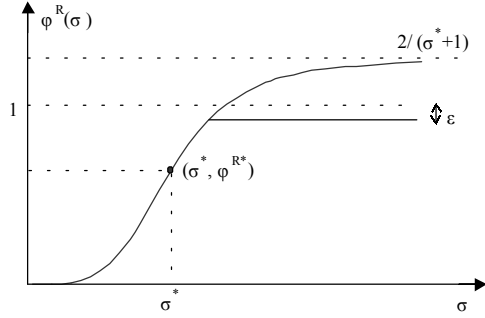


Fig. 7. Illustration of $\varphi^R(\sigma)$ as a function of the crown/root ratio σ . Mathematically, the maximum value of $\varphi^R(\sigma)$ is $2/(\sigma^*+1)$. Biologically, the maximum value of $\varphi^R(\sigma)$ should be smaller than 1, which is $1-\varepsilon$. The black dot on the curve denotes the value φ^{R*} when σ equals σ^* .

i.e.

$$\Pi^{LB} = d_t M^{LB} + \tau_p M^{LB}$$

For the mass production rate Π^R of the root we take the expression

$$\Pi^R = d_t R + \tau_p R$$

(we also assign a relative death rate τ_p to the living root mass).

This implies that the mass production rate Π^R can be written as

$$d_t R = (\Pi^R - \tau_p R) = \frac{\varphi^R(\sigma_t)}{1 - \varphi^R(\sigma_t)} \cdot d_t M^{LB}$$

$$\Pi^R = \frac{\varphi^R(\sigma_t)}{1 - \varphi^R(\sigma_t)} \{ (\partial_{h0}L + \partial_{h0}B) \cdot \pi^{h0} \} + \tau_p R$$

Let C_t denote the size of the carbon pool in the tree “container”. Given a carbon-construction cost r_{gR} , we can formulate the carbon balance equation

$$d_t C = p_{gL} L - (r_{mL} L + r_{mBS}(B+S) + r_{mR} R) -$$

$$- \{ r_{gL} \partial_{h0}L + r_{gBS} (\partial_{h0}B + \partial_{h0}S) \} \pi^{h0} - \{ r_{gL} L + r_{gBS}(B+S) \} \tau_p - r_{gR} \Pi^R$$

i.e.

$$d_t C = \{ p_{gL} - (r_{mL} + r_{gL} \cdot \tau_p) \} L - (r_{mBS} + r_{gBS} \cdot \tau_p) (B+S) - (r_{mR} + r_{gR} \cdot \tau_p) R$$

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$$- \{ r_{gL} \partial_{h0}L + r_{gBS} (\partial_{h0}B + \partial_{h0}S) + \frac{\varphi^R(\sigma_t)}{1 - \varphi^R(\sigma_t)} \cdot r_{gR} \cdot (\partial_{h0}L + \partial_{h0}B) \} \pi^{h0} \quad (9^A)$$

In order to keep the “analytic” specification of the system simple, we assume that if the leaves and branches in a tree are pruned, the associated pipes in the stem part are also removed. Thus, for convenience we assume that at every time t the amounts of living leaf elements and pipe elements in the branches and stem are completely specified by the height h_t^0 of the crown. This means that at each time t , the status of the tree is completely given by the height h_t^0 (with L_t , B_t and S_t being given functions of crown height h_t^0), the amount of root mass R_t and the size C_t of the carbon pool at that time t .

Summarizing the results so far, the growth of the tree is given by the carbon balance equation (9^A) together with the differential equations describing the rates of change d_tL , d_tB , d_tS and d_tR in leaf mass, branch mass, total stem mass and root mass,

$$d_tL = \partial_{h0}L \pi^{h0} \quad , \quad d_tB = \partial_{h0}B \pi^{h0} \quad , \quad d_tS = \partial_{h0}S \pi^{h0} \quad , \quad (9^{B,C,D})$$

$$d_tR = \frac{\varphi^R(\sigma_t)}{1 - \varphi^R(\sigma_t)} (\partial_{h0}L + \partial_{h0}B) \cdot \pi^{h0} \quad (9^E)$$

Next, let us take a closer look at the height growth rate π^{h0} . We assume π^{h0} is a function of the carbon concentration c_t (which is given by $c_t = C_t / M_t = C_t / (L+B+S+R)$),

$$c \rightarrow \pi^{h0}(\sigma, c) = \text{MIN} \left\{ k^{h0}(\sigma) \frac{c - c_{h^*}}{K_{hc} + (c - c_{h^*})} , 0 \right\} \quad (10^A)$$

(see Fig. 8). Here the factor $(c - c_{h^*}) / (K_{hc} + (c - c_{h^*}))$ formalizes the idea that the growth rate of the tree is a function of the availability of carbon. At very “low” concentrations $(c - c_{h^*})$ the tree’s growth rate must become very low simply because there is not enough carbon. The off-set $c = c_{h^*}$ guarantees that the growth of the tree will never draw the carbon concentration below some critical level. For example, the critical carbon concentration c_{h^*} might refer to the amount of carbon needed to survive the bad season I in terms of maintenance and turnover respiration. If the carbon concentration drops below this value c_{h^*} , the tree will no longer grow, but will use the remaining carbon for “survival”. The capacity k^{h0} is assumed to depend on the crown/root ratio $\sigma = M^{LB}/R$, which reflects the idea that a pruned tree will not only allocate relatively more of its carbon to the reconstruction of the damaged part (in this case the crown), but pruning will also speed up the rate at which the tree is (re)growing. It can be associated with the compensatory growth which real-world trees frequently show after pruning. As an example, visualised in Fig. 9,

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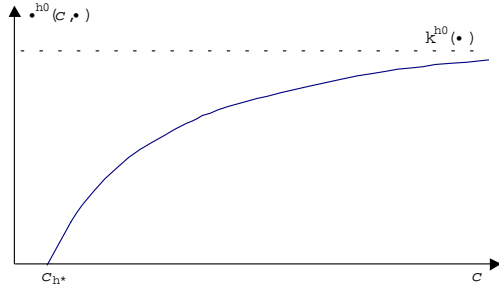


Fig. 8. Height growth rate $\pi^{h0}(c, \sigma)$ as a function of carbon concentration c . $k^{h0}(\sigma)$ is the maximum value that $\pi^{h0}(c, \sigma)$ can approach. c_{h*} is the carbon concentration below which the tree stops to grow in height.

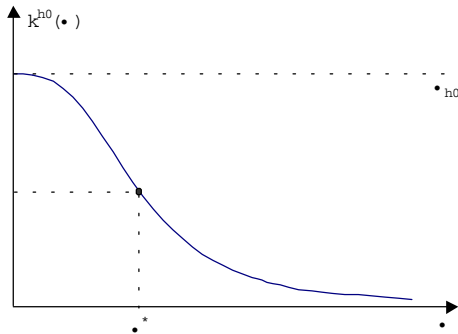


Fig. 9. Illustration of the height growth capacity $k^{h0}(\sigma)$ as a function of the crown/root ratio σ . α_{h0} is the height growth capacity at $\sigma=0$. The black dot on the curve denotes the height growth capacity at σ^* , which is $\alpha_{h0}/2$.

we may take a function $\sigma \rightarrow k^{h0}(\sigma)$ of the form

$$\sigma \rightarrow k^{h0}(\sigma) = \alpha_{h0} \frac{(\sigma^*)^n}{(\sigma^*)^n + \sigma^n} \tag{10^B}$$

with α_{h0} the maximal height growth without the limitation of the crown/root ratio. Here, n is a non-negative integer. As before, we may take n equal to 2.

Although the model now already contains a lot of “physiological details”, in one aspect it is still somewhat flawed, and that concerns the regulation of the photosynthetic capacity of the leaves by the carbon concentration in the tree. Let us assume a tree is pruned at a certain time t^P . Immediately after that time t^P there is a change in crown/root ratio and this will lead to an increase in the capacity $k^{h0}(\sigma)$ of the growth rate function $\pi^{h0}(c, \sigma)$. Because of the root/crown balance function (8), the tree will start to invest relatively more mass in the crown. However, via the carbon balance equation (9^A), the increase in the capacity $k^{h0}(\sigma)$ of the growth rate function will tend to decrease the internal carbon concentration c_t . As a result, the response of the tree to the pruning event will tend to lead to a decrease in its

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overall growth rate. To compensate for this negative effect, one could imagine, and in real-world trees this is indeed the case, that in balanced trees there might be a negative effect of the internal carbon concentration on the photosynthetic capacity p_{gmL} of the leaves:

$$c \rightarrow p_{\text{gmL}}(c) = \alpha_{\text{pm}} \left(1 - \frac{c^n}{(c_{\text{p}^*})^n + (c)^n} \right) \quad (11)$$

with α_{pm} the maximal photosynthetic rate obtained at an extremely low carbon concentration level. Again, n is a non-negative integer which we usually take to equal 2.

This shows that the consequence of a drop in the carbon concentration is that the gross photosynthetic rate p_{gL} of the leaf elements will go up, because the negative feed-back of the internal carbon concentration is relieved.

Summary and discussion

In modelling the growth of a tree, the first aspect we have to think of is to choose a suitable form for the tree to keep it manageable and computable. The tree form selected should have two characteristics. One is it should be simple, the other is it ought to be “real” enough. Based on these criteria, although many forms are available, such as ellipsoidal or cylindrical, we chose to confer the tree a conical form.

To analyse the structure and the allometric relationships between compartments in a tree, Shinozaki et al. (1964a,b) derived the pipe model theory. This theory has been successfully used to analyse leaf area and biomass (Robichaud and Methven 1992), plant growth (Berninger and Nikinmaa 1997), and stand productivity (Valentine 1999). Because the pipe model clearly depicts the structural relations between compartments of a tree, we used it in our model tree in order to analyse the effects of pruning on tree growth and allometry.

Tree growth models can be divided into architectural models (Fisher 1992) and physiological models (Loomis et al. 1979, Isebrand et al. 1990). Most architectural models are based on deterministic or stochastic rules of growth and branching, repeatedly applied to each apex (de Reffye et al. 1991) and on geometric algorithms which describes the construction of the branching system (Honda et al. 1982). These models produce realistic simulations of tree forms and can be used to describe plant morphology (Fisher 1992). However, they are not suitable for studying the growth of a tree under stress conditions, since the physiological mechanisms making a tree grow are not considered in these models. Conversely, physiological models integrate the basic physiological functions such as photosynthesis and respiration (Rauscher et al. 1990; Grossman and DeJong 1994). In these models, tree growth is powered by carbohydrates, and it is expressed as a change in mass of different compartments such as shoots and roots, instead of an iteration and accretion of

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modules. The model we have established is based on the concepts of both model types. In this model, tree growth is carbon-based; the growth rate basically depends on the amount of carbohydrates in the tree. Tree growth is reflected directly by the increase of crown height. Due to the conical tree form, this height growth of the crown can be translated into the growth of all compartments including leaves, branches, and the stem.

It should be noted that, although the tree growth in the model is carbon-based, it is formulated in somewhat different ways in the different sections. In sections 2 to 4, tree growth is dependent on the net photosynthetic rate (P^n): it occurs only if the net photosynthetic rate is positive. In section 4, even though the carbon storage is considered, this carbon storage is used for surviving “bad” seasons, not for growth. Since this amount of stored carbon is just enough to survive the bad season, the tree has no carbon storage at the end of each year. In section 5, tree growth is a function of the carbon concentration of the tree; it is not directly dependent on the net photosynthetic rate (P^n). Whether the net photosynthetic rate is positive or not, the tree can grow as long as the carbon concentration of the tree is above a critical value (c_{h*}). In this sense, even after a complete crown pruning, the tree is still able to grow, as long as its carbon concentration level is high enough. This is not true for the trees formulated in sections 2 to 4.

In sections 2 and 4, the effects of photosynthetic production and seasonality on tree growth are modelled. Based on the sections 2 and 4, section 5 is developed. It should be noted that, in comparison to the sections 2 and 4, the tree growth modelled in section 5 is more similar to the growth of a real tree. In this section, some aspects influencing tree growth as have been found in the experimental studies, were built in, including the effect of shoot damage (viz. decrease in shoot/root ratio) on biomass allocation (Fitzgerald and Hoodinott 1983; Singh and Thompson 1995), the negative feed-back effect of the carbohydrate level on the photosynthetic rate (Jeannette et al. 1995; Layne and Flore 1995; Myers et al. 1999), and the compensatory growth (Singh and Thompson 1995) due to pruning. Although these aspects are incorporated in the model, we have to admit that still a lot of factors which may influence the growth of a pruned tree are not included, for instance, the re-use of open vascular channels after pruning (Sachs 1981; Sachs and Novoplansky 1997), and the changes in water potential and leaf conductivity in the plant as a result of the changes in crown/root ratio (Blake and Tschaplinski 1986; Pinkard et al. 1998). Such factors may divert the growth behaviour of a model tree from that of a real tree. In fact, in the simulation study of the next chapter, we will incorporate the re-use of the open vascular channels after pruning by newly formed leaves, since this will have large consequences for the total amount of harvestable material.

Acknowledgements

We thank Prof. dr. Marinus J. A. Werger for his helpful comments on the earlier versions of the manuscript.

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Appendix: List of symbols

Symbols introduced in section 1

α'	Top angle of crown with $\alpha = \tan \alpha'$ and $\alpha' \in (0, \pi/2)$; see Fig. 1.
h_t^0	Crown height; see Fig. 1.
h_t^p	Total tree height.
h^1	Height of the basal stem; see Fig. 1.
A_t^0	Crown surface area.
V_t^0	Crown volume.

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λ_t^p	Density (number per unit area) of leaf/pipe elements on the crown surface.
$L_t(h)$	Number of leaf/pipe elements in a crown of height h .
a_p	Cross section area of a pipe.
m_p	Mass per unit pipe volume.
$S_t^0(h)$	Amount of living pipe mass in the stem part of a crown with height h .
S_t^1	Amount of living pipe mass in the basal stem part of the tree.
$B_t(h)$	Amount of living pipe mass in the branches of a crown of height h .
$L_t, B_t, S_t = S_t^0 + S_t^1$	Number of leaf elements, amount of branch mass and amount of total stem mass in a crown of height h^0
$\alpha_L, \alpha_B, \alpha_{S0}, \alpha_{S1}$	Scaling factor in the calculation of L_t, B_t, S_t^0, S_t^1 , i.e. $\alpha_L = \pi \cdot \alpha \sqrt{1 + \alpha^2}$, $L_t = \alpha_L \lambda_t^p (h^0_t)^2$ $\alpha_B = 2\pi/3 \cdot a_p m_p \cdot \alpha^2 \sqrt{1 + \alpha^2}$, $B_t = \alpha_B \lambda_t^p (h^0_t)^3$ $\alpha_{S0} = \pi/3 \cdot a_p m_p \cdot \alpha \sqrt{1 + \alpha^2}$, $S_t^0 = \alpha_{S0} \lambda_t^p (h^0_t)^3$ $\alpha_{S1} = \pi \cdot a_p m_p \cdot \alpha \sqrt{1 + \alpha^2}$, $S_t^1 = \alpha_{S1} h^1 \lambda_t^p (h^0_t)^2$
r_0	Radius of the stem at the crown base.

Symbols introduced in section 2

d_t	The derivative d/dt with respect to time
$\partial_{h^0}, \partial_{\lambda^p}$	The partial derivatives $\partial/\partial h^0, \partial/\partial \lambda^p$
$\pi^{h^0}_t$	The “crown-production” rate, i.e. the rate at which the crown increases in height
$\pi^{\lambda^p}_t$	The production rate per unit crown area in pipe/leaf elements
τ_p	The relative death rate of the pipe/ leaf elements
P^n_t	Net photosynthetic rate of the tree

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P_t^n	Net photosynthetic rate of the tree, taking also the leaf/pipe element turnover rate into account
r_{gL}, r_{gBS}	Amount of carbon to produce a leaf element or a unit of branch/stem mass, both structural and respiratory costs are taken into account
p_{gL}, r_{mL}	Gross photosynthetic rate and maintenance respiration rate per leaf element
a_L	Area of a leaf element
r_{mBS}	Maintenance respiration per unit branch or stem mass
$p_{gmL}, \Phi_{aL}, i_{aL}$	Photosynthetic capacity, quantum yield and rate of photon absorption by a leaf
tSR, tSS	Time point of sunrise and sunset of a day.
A_L, A_{S1}, A_{BS0} B_L, B_{S1}, B_{BS0}	Factors to simplify the carbon balance equation

$$\begin{aligned}
 A_L &= \{p_{gL} - (r_{mL} + r_{gL}\tau_p)\} \alpha_L & B_L &= 2 r_{gL} \alpha_L \\
 A_{S1} &= (r_{mBS} + r_{gBS}\tau_p) \alpha_{S1} & B_{S1} &= 2 r_{gBS} \alpha_{S1} \\
 A_{BS0} &= (r_{mBS} + r_{gBS}\tau_p)(\alpha_B + \alpha_{S0}) & B_{BS0} &= 3r_{gBS} (\alpha_B + \alpha_{S0})
 \end{aligned}$$

Symbols introduced in section 3

h_t^1	Height of the basal stem part beneath the crown as a function of time
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Symbols introduced in section 4

Γ^+, Γ^-	Length of the “good” and the “bad” seasons
i_L^+, i_L^-	Light intensities during the “good” and “bad” seasons
t^-, t^+	Time at which the “bad” or “good” season begins
$C_{I(-)}$	Amount of carbon, which the tree needs to survive the bad season Γ^-
t_a	Time in the good season Γ^+ , at which in growth strategy A the tree stops its growth in height
t_b	Time in the good season Γ^+ , at which in growth strategy B the tree starts its growth in height
c^*	A fixed reference carbon concentration in the tree, which guarantees the tree in its first year to survive the bad season.
m_L	The mass of a leaf element

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Symbols introduced in section 5

L_t	Leaf mass
M^{LB}_t	$M^{LB}_t=L_t+B_t$ = crown mass
R_t	Root mass
σ_t	Crown/root mass ratio of the tree
σ^*	Reference value for the crown/root mass ratio
$\varphi^R(\sigma)$	Function, which steers the derivatives d_tR and d_tM^{LB} of an unbalanced tree
r_{gR}	Carbon construction cost per unit root mass
$\pi^{h0}(\sigma,c)$	The height growth rate function as function of crown/root ratio and as function of the internal carbon concentration c
c_{h^*}	Carbon concentration below which the tree stops to grow in height
$k^{h0}(\sigma)$	Capacity of the height growth function; this capacity is depending on the crown/root ratio
K_{hc}	Michaelis-Menten equilibrium constant for the height growth rate function
α_{h0}	Absolute capacity of the height growth rate free from the effect of crown/root ratio
$p_{gmL}(c)$	Capacity of the gross photosynthetic rate as a function of the internal carbon concentration
α_{pm}	Absolute capacity of the gross photosynthetic rate free from the effect of the internal carbon concentration
c_{p^*}	The internal carbon concentration level at which the capacity of the gross photosynthetic rate is half of α_{pm}

7

Simulation of branch harvests

with Heinjo During and Feike Schieving

Abstract

Based on the tree growth model developed in Chapter 6, we simulated the branch harvest obtained from deciduous and evergreen trees as affected by pruning intensity, pruning interval, and pruning season. The chief results are summarized as follows:

1. An unpruned tree, evergreen or deciduous, grows fast in height when it is young, but it will stop its height growth eventually and reach a steady state. With the parameter settings used, an evergreen tree reaches a smaller height than a deciduous tree at steady state, due to its leaf maintenance costs during winters.
2. Repeated pruning decreases the maximal height a tree can reach, and drives the tree to death. A higher pruning intensity and/or a shorter pruning interval lead to a smaller tree height, and make a tree die earlier. Heavy pruning results in a larger branch harvest than light pruning in the first few pruning events, but provides a smaller branch harvest later on. Light pruning results in more pruning occasions, since a tree subjected to light pruning can live longer.
3. At short pruning intervals, the total branch harvest obtained from a young tree over its life time has a unimodal relation to pruning intensity. The total branch harvest is maximized at a certain pruning level. This level becomes higher at a longer pruning interval. Comparatively, the total branch harvest of a tree at short pruning intervals is much more sensitive to pruning level than that of a tree at long pruning intervals. At very long pruning intervals, such that a tree has already grown to approximately its maximal size, the total branch harvest tends to increase with pruning level, because the tree will die before the second pruning.
4. Compared to spring pruning, winter pruning increases the branch harvest of an evergreen tree, because it reduces the leaf maintenance costs of the evergreen tree during winter, which gives the evergreen tree a better carbon concentration status. Deciduous trees do not benefit from winter pruning, since they are leafless during winter.
5. The tree size at which pruning starts affects the total branch harvest of the tree over its life time. If pruning starts at small sizes, total branch harvest can be maximized at a certain

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pruning level. At large sizes, which are near or equal to the full size of the tree, the total branch harvest of the tree increases with pruning level.

6. Higher pruning levels and/or shorter pruning intervals lead to larger cumulative branch harvests within the first few prunings, but they do not do so later on. Compared to a small-sized tree, a large-sized tree produces a larger cumulative branch harvest before its death.

Keywords: branch harvest, pruning intensity, pruning interval, pruning season, tree size

Introduction

Pruning of trees is widely applied in China, one use of which is to harvest branches as fuel (Anonymous I 1992) and as raw materials for medicine production (Anonymous II 1994; Li and Kuo 1997, 1998). Usually, branches are obtained by pruning the lower crown of a tree.

Many factors may influence branch harvest. Pruning intensity, pruning frequency, pruning season, and tree size are four chief ones among them.

It is obvious that, for a tree, branch harvest at each pruning is dependent on the pruning intensity applied. Heavy pruning results in a large branch harvest. However, owing to a reduction in the regrowth caused by the diminished leaf area left on the tree, heavy pruning may lead to lower branch harvests in the future. Intuitively, there should exist an optimal pruning intensity at which branch harvests in the future will not be greatly reduced, and the total branch harvest from the tree is maximized.

Because of the removal of leaf area, a pruned tree needs some time to fully recover its growth and produce harvestable branches. Within a certain time period, there is a trade off between the number of pruning applications and the amount of branches available for harvesting at each pruning. More frequent pruning leaves less time for regrowth and consequently a lower branch harvest at each pruning is the result. It seems possible to select an appropriate pruning frequency at which the total branch harvest is maximized.

In China, tree growth is seasonal. In each year, trees start growing in spring. No apparent growth occurs in winter. Due to the nil growth in winter, compared to spring pruning, winter pruning may less severely affect tree growth in the next growing season. Consequently, winter pruning is expected to lead to a larger future branch harvest than spring pruning. In spring, trees spend some energy on the flush of leaves. This phenomenon is much striking for deciduous trees, since all leaves in a deciduous tree are newly grown. The energy consumed for the growth of new leaves will be paid back by the photosynthesis of these leaves later on. If spring pruning is conducted shortly after the new leaves have flushed, compared to an evergreen tree with the same leaf area, more new leaves in a deciduous tree are removed by spring pruning. As a result, the growth of the deciduous tree is presumable to be much more impaired by spring pruning than that of the evergreen tree. Considering the light effect of winter pruning on tree growth, it is

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hypothesized that the difference in branch harvest between spring and winter pruning is bigger in a deciduous tree than in an evergreen tree.

It is clear that, with a same pruning intensity applied, more branches can be harvested from a large-sized tree than from a small-sized tree. However, the disadvantage of pruning a large tree is that no branches are harvested until the tree reaches the predetermined size. The situation is reversed when a small-sized tree is pruned: branch harvesting can be started earlier but the amount of branches harvested at each pruning is less. It is hypothesized that there is an appropriate tree size at which if pruning is started, the total branch harvest is maximized.

Based on the tree growth model developed in Chapter 6, the branch harvest of a tree as affected by pruning intensity, pruning frequency, pruning season, and initial tree size is simulated, and the addressed hypotheses are tested.

The simulations

It is assumed in the model that the aboveground part of a model tree consists of a canopy and a branchless trunk (Fig. 1). Pruning implies the removal of the lower crown, which is in agreement with the pruning practiced in China. Pruning intensity (pruning level) is defined as the fraction of canopy height removed (Fig. 1). The unchanged parameter settings in the simulations are given in Table 1.

According to the model (Chapter 6), a calendar year consists of a “good” season and a “bad” season which are analogous to the spring/summer and the winter, respectively. In the “good” season, trees experience a stable good light environment, produce a lot of carbohydrates and are able to grow. In the “bad” season, light conditions are poor and trees have to rely on their carbohydrate reserve for their maintenance. For convenience, henceforth, the “good” season and the “bad” season are referred to as summer and winter, respectively.

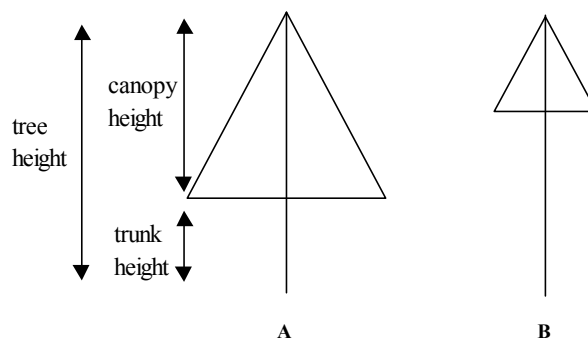


Fig. 1. Aboveground structure of a model tree. A and B illustrate the status of a tree before and after pruning, respectively. The pruning level applied is 0.5 (50 % of the canopy height is removed).

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Table 1. Unchanged parameter settings in the simulations.

Parameters	Values
α' (top angle of crown)	45°
λ_t^p (density of leaf element on the crown surface, #·m ⁻²)	2000
a_L (leaf size, m ²)	0.001
m_L (leaf mass, g·m ⁻²)	50
r_{gL} (leaf construction cost, g (carbon)·m ⁻²)	62
r_{gBS} (wood construction cost, g (carbon)·m ⁻³)	5E5
c_{h*} (minimum carbon concentration for height growth, g·m ⁻³)	5E5
α_{pm} (maximal capacity of the gross photosynthetic rate (p_{gmL}) free from the effect of the internal carbon concentration, g·m ⁻² ·hour ⁻¹)	7.2
c_{p*} (carbon concentration at which $p_{gmL} = 0.5\alpha_{pm}$, g·m ⁻³)	2E6
Φ_{aL} (quantum yield, g·mol ⁻¹ (photon))	2.0
K_{hc} (Michaelis-Menten equilibrium constant for the height growth rate function, g·m ⁻³)	1E6
α_{h0} (maximal height growth free from the effect of crown/root ratio, m·day ⁻¹)	0.006
σ^* (crown/root ratio without pruning)	1
r_{mL} (maintenance respiration of leaf, g·m ⁻² ·hour ⁻¹)	1.0
r_{mBS} (maintenance respiration of wood, g·m ⁻³ ·hour ⁻¹)	10.0
a_p (pipe cross section area, m ²)	1E-6
τ_p (relative leaf shedding rate, m ² ·m ⁻² ·day ⁻¹)	0.01
h^1 (trunk (viz. basal stem) height, m)	1

Basic model behaviour with respect to height growth and branch harvest

The simulations in this section explore the basic behaviour of the model by analyzing: (i) the canopy height and tree height of an unpruned evergreen and deciduous tree, and the temporal dynamics of their carbon concentration (analogous to carbohydrate concentration) at the end of each “good” season and “bad” season (viz. at the end of summer and winter); (ii) the effects of pruning on canopy height and tree height; (iii) the branch harvest at each pruning when a tree is repeatedly pruned.

The simulations show, that an unpruned tree, whether it is evergreen or deciduous, grows fast in tree height and canopy height when it is young. As the tree gets older, its growth rate gradually reduces and finally the maximal tree height and canopy height are reached (Fig. 2). Using the same set of parameter settings, a deciduous tree can reach a much larger tree and canopy heights than an evergreen tree. Fig. 3 shows the carbon

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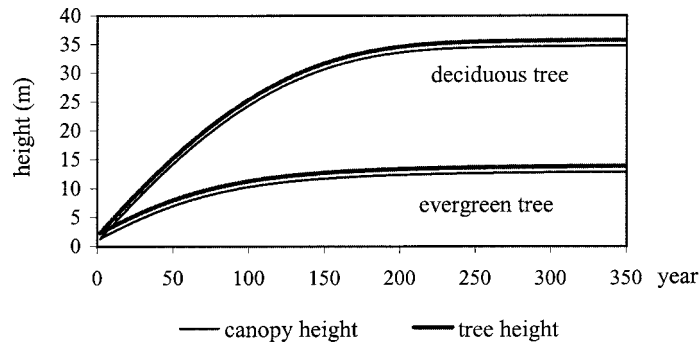


Fig. 2. The tree height and canopy height of an unpruned evergreen and deciduous tree. Parameter settings: initial canopy height=1m.

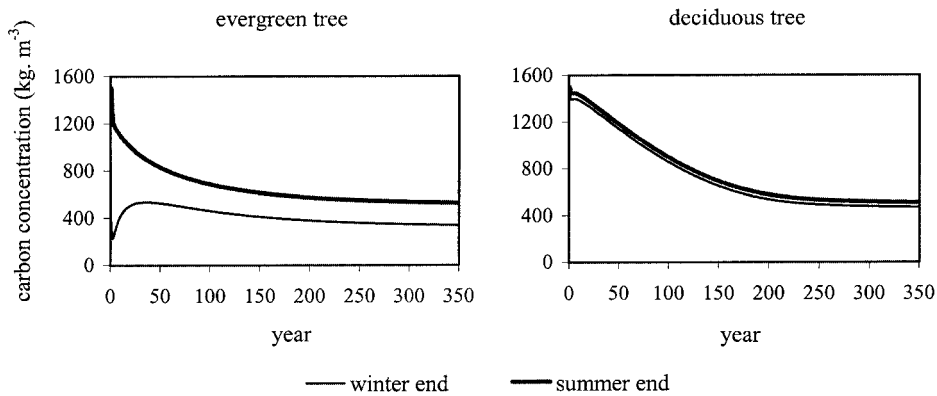


Fig. 3. Carbon concentration of an evergreen and a deciduous tree at the end of summer and winter. Parameter settings: initial canopy height = 1 m.

concentration of an evergreen and a deciduous tree at the end of each summer and winter. The difference in carbon concentration of the evergreen tree between summer ends and winter ends is much larger than that of the deciduous tree, since the evergreen tree has leaf respiration costs during winters, which does not exist in the deciduous tree. According to the model, the height growth of a tree is affected by the carbon concentration of the tree. Strong reduction in carbon concentration in an evergreen tree due to the leaf respiration during winters impairs tree growth. As a consequence, in comparison to a deciduous tree, an evergreen tree reaches a smaller maximal tree height and canopy height. According to the model, a tree can grow only when its carbon concentration is larger than a critical value (c_{h*}). For an unpruned tree, its carbon concentration decreases gradually as its grows. When

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the carbon concentration at the end of summer is equal to or below the critical value, the unpruned tree reaches its maximal height. With its maximal height, the maintenance costs of the unpruned tree can just be covered by the tree's photosynthetic production. The tree's carbon pool stays unaffected. Consequently, with its maximal height, the unpruned tree can live for quite a long time.

The simulations show that repeated pruning decreases the maximal tree height and canopy height of a tree. The higher the pruning level, the smaller maximal tree height and canopy height the tree can reach (Fig. 4). When the tree is pruned repeatedly, the difference between the tree height and the canopy height gets larger. The reduction in the height growth of a repeatedly pruned tree is caused by the impaired photosynthetic production due

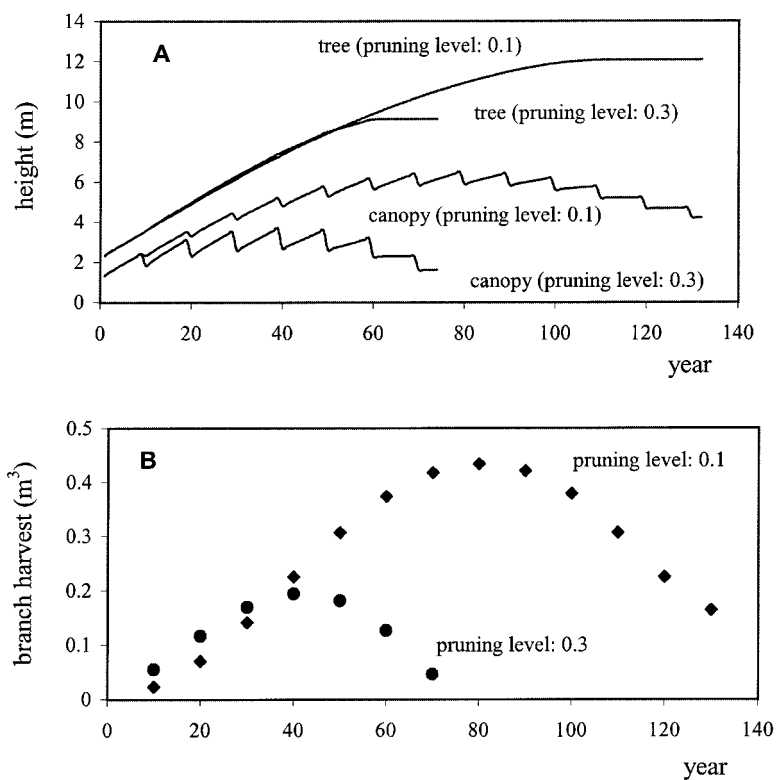


Fig. 4. Tree height, canopy height, and branch harvest at each pruning of a pruned tree. Simulations are conducted with an evergreen tree. A. temporal dynamics of tree height and canopy height growth of the tree subjected to pruning levels of 0.1 and 0.3; B. branch harvest at each pruning. Parameter settings: pruning interval = 10 years; initial canopy height = 1m.

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to the repeated removal of leaves. Furthermore, because of this continual leaf removal, repeated pruning drives a tree to death, by decreasing its carbon concentration to zero. Compared to an unpruned tree, a pruned tree lives a much shorter time period. The higher the pruning level, the earlier the tree will die. For instance, Fig. 4 shows that a tree can live for 132 years at a pruning level of 0.1, but it only lives 74 years at a pruning level of 0.3.

Basically, the branch harvest at each pruning is dependent on the canopy height. It goes up with the increase of canopy height, and begins to drop when the canopy height stops increasing (Fig. 4). A high pruning level provides a larger branch harvest than a low pruning level at the first few prunings, but results in smaller harvests later on (Fig. 4). Low pruning levels result in more pruning occasions, since a tree subjected to low pruning levels can survive for a longer period of time. In the simulations shown in Fig. 4, a tree subjected to 10 percent canopy pruning at a pruning interval of 10 years can be pruned thirteen times, but it can only be pruned seven times if 30 percent of the canopy height is removed.

Effect of pruning level and pruning interval

Simulations in this section analyze the effects of pruning level and pruning interval on the total branch harvest over a tree's lifetime. At a pruning interval of 1 year, the total branch harvest first increases to a maximum and then decreases with pruning level (Fig. 5). If the pruning interval is longer (e.g. 30, 70, and 100 years shown in Fig. 5), similar to the situation presented by the pruning interval of 1 year, the total branch harvest first increases to a maximum and then decreases. However, from a certain pruning level on, the total branch harvest begins to increase again with pruning level. If the pruning interval is so long that the tree has already grown to approximately its maximal size before the start of the first pruning (e.g. 300 and 500 years in Fig. 5), pruning levels between zero and a critical level (ca. 0.1 in Fig. 5) result in a similar total branch harvest. Above this level, the total branch harvest consistently increases with pruning level (Fig. 5). In effect, this critical pruning level is the lowest level at which a tree can only survive a single pruning (Table 2). Above this level, a higher pruning level always leads to a larger branch harvest simply because a larger part of the canopy is removed. In the simulations, pruning intervals from 30 to 500 years all exhibit this phase in which the total branch harvest starts to increase consistently with pruning level (Fig. 5). Although it is not recognizable in the picture, this phase also exists for pruning intervals of 5 and 10 years. What needs to be pointed out is, above this critical level, with the increase of pruning level, the increase in total branch harvest becomes smaller and smaller. This can be attributed to the conical form of the canopy (Fig. 1), because a canopy layer in the upper part of a conical canopy has a smaller volume than a canopy layer of the same depth in the lower canopy. Consequently, pruning a canopy layer in the upper canopy results in less branch harvest than pruning a canopy layer of the same depth in the lower canopy.

At shorter pruning intervals, the relationship between the total branch harvest and pruning level is unimodal. The total branch harvest of a tree can be maximized at a certain

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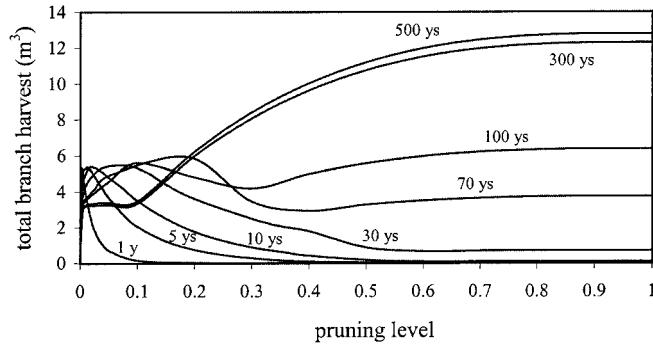


Fig. 5. Total branch harvest as affected by pruning level and pruning interval. Simulations are conducted with an evergreen tree. Parameter settings: initial canopy height=1m.

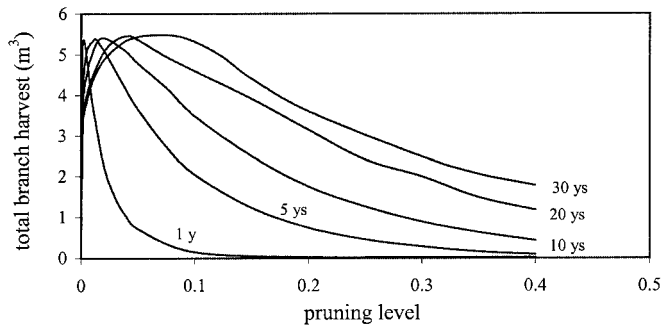


Fig. 6. Zoom-in of Fig. 5 to show the maximal total branch harvest as affected by pruning level and pruning interval.

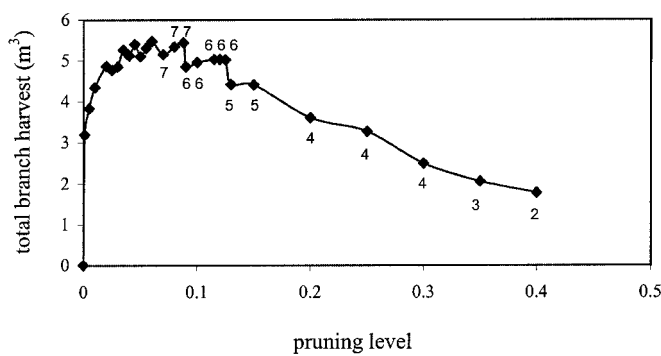


Fig. 7. Details of total branch harvest as affected by pruning level. Simulations are conducted with an evergreen tree. Parameter settings: pruning interval=30 years; initial canopy height=1m.

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Table 2. The smallest pruning levels at which a tree can only survive a single pruning. Simulations are done with an evergreen tree. Parameter settings: initial canopy height=1m.

Pruning intervals	The smallest pruning levels
5 years	0.8
10 years	0.8
30 years	0.6
70 years	0.4
100 years	0.3
300 years	0.1
500 years	0.1

pruning level (Fig. 5). Fig. 6 shows the total branch harvests at different pruning intervals up to 30 years. The simulations show that all these pruning intervals lead to a similar maximal total branch harvest, indicating that the total maximal branch harvest is not greatly affected by pruning interval. As pruning interval gets longer, the pruning level at which the maximal total harvest is obtained becomes higher. Moreover, the total branch harvest of a tree subjected to short pruning intervals is much more sensitive to pruning level than that of a tree subjected to long pruning intervals (Fig. 6). Therefore, at short pruning intervals (e.g. one year), selecting a suitable pruning level for obtaining the maximal total branch harvest should be prudent.

A close look at Fig. 5 shows that, if pruning level is below the critical level, the total branch harvest does not change smoothly with pruning level. Instead, it shows a zigzag relation to pruning level. As an example, the total branch harvest at pruning interval of 30 years is shown (Fig. 7). In Fig. 7, the values denote the number of prunings a tree can survive at a certain pruning level. For instance, value 7 means a tree can be pruned for 7 times before its death. At low pruning levels, a pruned tree recovers its growth quickly. Thus, for pruning levels which guarantee a tree to survive the same number of prunings, the higher the pruning level, the larger the total branch harvest. This is clearly illustrated by cases of surviving 6 or 7 prunings (Fig. 7). With the increase of pruning level, the growth recovery of a pruned tree becomes slower. Therefore, higher pruning levels do not necessarily lead to larger harvests (e.g. the case of surviving 5 prunings in Fig. 7). If pruning level is too high, a pruned tree can not recover its growth before the start of the next pruning at all. Consequently, higher pruning levels always lead to smaller harvests (e.g. the case of surviving 4 prunings in Fig. 7). This differential response of total branch harvest at different pruning levels explains why the total branch harvest does not change smoothly with pruning level.

In practice, people are not only interested in the total branch harvest over a tree's life time, but also want to know the cumulative amount of branch harvest changing over time. Since in many cases the latter can be dealt with more easily and seems more practical.

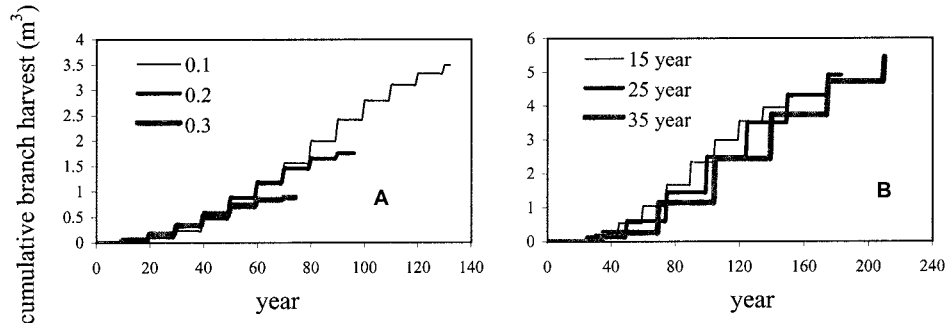


Fig. 8. Cumulative branch harvest at different pruning levels (A) and different pruning intervals (B). Simulations are conducted with an evergreen tree. In subfigures A and B, pruning levels and pruning intervals are indicated by different lines, respectively. Parameter settings for A: initial canopy height = 1 m; pruning interval = 10 years. Parameter settings for B: initial canopy height = 1 m; pruning level = 0.1.

Fig. 8 shows the cumulative branch harvest of a tree. Obviously, higher pruning levels result in larger cumulative harvests within the first few prunings. However, with the progress of time, lower pruning levels gradually proceed to realize larger cumulative harvests (Fig. 8A). With respect to pruning interval, a similar result is shown: prunings at short intervals first lead to larger cumulative harvests, but eventually, prunings at long intervals lead to larger cumulative harvests than prunings at short intervals (Fig. 8B).

Effect of pruning season

In this section, the branch harvests at each pruning of evergreen and deciduous trees subjected to spring and winter pruning are simulated.

The first set of simulations is performed based on the assumption that trees have the same size (i.e. the same canopy height) at the first spring and winter pruning. The simulations show (Fig. 9) that, for an evergreen tree, compared to spring pruning, winter pruning realizes a larger branch harvest. This enhanced harvest is caused by the increased canopy height and tree height growth after winter pruning. However, for a deciduous tree, spring and winter pruning make no difference in branch harvest at each pruning (Fig. 9), because the canopy and tree height growth of the deciduous tree do not differ between spring and winter pruning (Fig. 9). Based on the simulations, it is clear that pruning season affects the evergreen tree to a certain degree but does not affect the deciduous tree. In the model, the only difference between the evergreen and deciduous tree is that the deciduous tree is leafless but the evergreen tree retains its leaves during the winter. Because of the leaf respiration costs in winter, the carbon concentration of the evergreen tree is greatly reduced at the end of winter. By contrast, for the deciduous tree, the carbon concentration at the end of winter is only a bit smaller than that at the end of summer (Fig. 3). Winter

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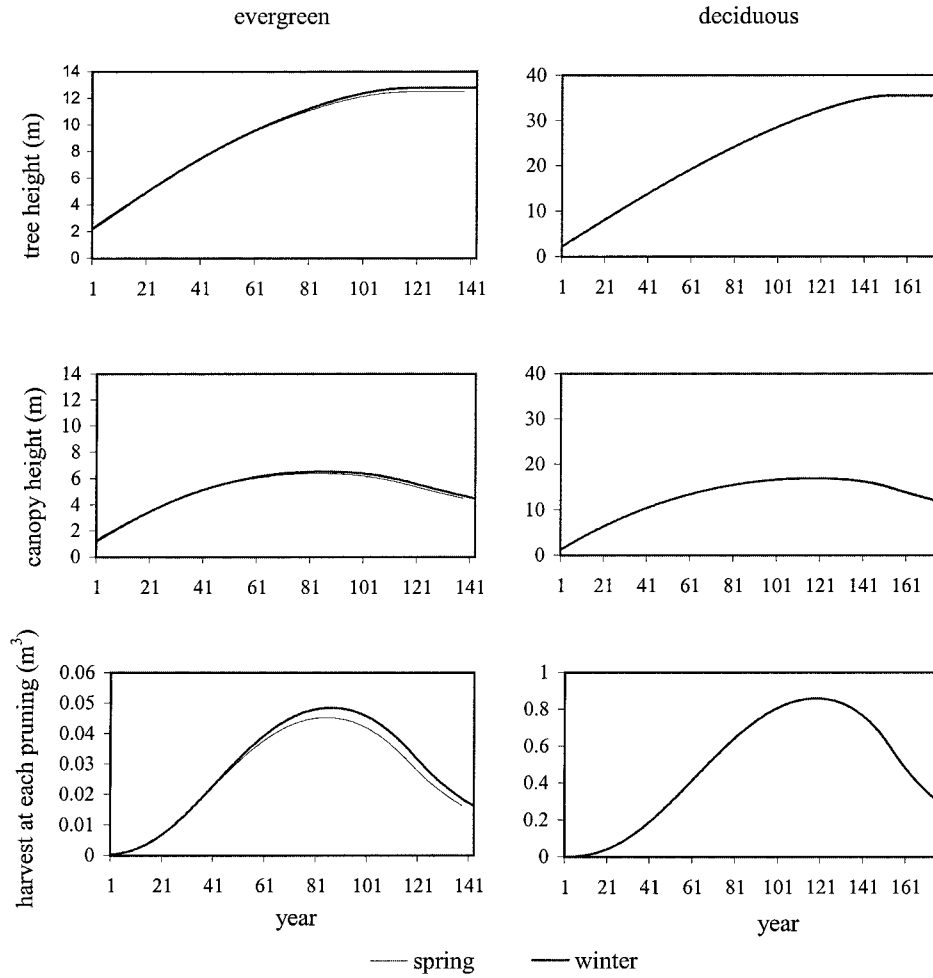


Fig. 9. Tree height, canopy height, and branch harvest of an evergreen and a deciduous tree subjected to spring and winter pruning. Trees experiencing the first spring and the first winter pruning have the same size. Tree height and canopy height at the end of each year and branch harvest at each pruning have been plotted. Parameter settings: pruning interval=1 year; pruning level=0.01; initial canopy height=1 m.

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pruning removes respiring leaves from the evergreen tree so that the respiration costs of the evergreen tree is reduced, and the carbon concentration status is improved. Comparatively, the deciduous tree can not benefit from the winter pruning because it has no leaves in winter. Since tree growth is a function of carbon concentration, the growth of evergreen trees is favoured by winter pruning. As a result, more harvestable branches are produced.

In the field experiments, trees pruned in winter were larger than those pruned in spring, because the winter-pruned trees had grown for an extra growing season. The second set of simulations is performed to explore the effect of pruning season on trees which differ in size at the first pruning. In these simulations, spring pruning and winter pruning are conducted at day 1 and day 200 of a calendar year, respectively. Trees at day 200 are larger than trees at day 1, because the former ones grow 200 days more. The simulations show that, under this circumstance, for an evergreen tree, winter pruning results in a larger canopy height (Fig. 11) and tree height (Fig. 10) than spring pruning, even though the difference is not big. As a result, winter pruning leads to a larger branch harvest than spring pruning in the evergreen tree (Fig. 10), similar to the pattern shown in Fig. 9. For a deciduous tree, winter pruning leads to a slightly lower canopy height (Fig. 11) and tree height (not shown), which consequently leads to a smaller branch harvest in the deciduous tree in its second half of the lifetime (Fig. 10).

For the convenience of narration, henceforth, pruning in the first and the second set of simulations is referred to as theoretical and realistic pruning, respectively.

The carbohydrate concentration of a tree plays a key role in determining the response of evergreen and deciduous trees to pruning. For a deciduous tree, its carbohydrate concentration decreases gradually with size (Fig. 3). Thus, in the case of realistic pruning, spring-pruned deciduous trees always grow with a higher carbon concentration than autumn-pruned trees and consequently realize a better height growth (Fig. 11). In theoretical pruning, deciduous trees experiencing the first spring pruning and the first winter pruning have the same size and they hardly differ in carbon concentration at the time of pruning. So, no differences in height growth and branch harvest appear between the theoretical spring and winter pruning (Fig.9). For evergreen trees, winter pruning removes respiring leaves and improves the carbon concentration status of the trees. In the case of realistic pruning, this increase in carbon concentration due to leaf removal can be larger than the decrease in carbon concentration due to growth. As a result, compared to spring pruning, winter pruning leads to a better height growth in the evergreen tree, and realizes larger branch harvest (Figs. 9, 10, and 11).

For a deciduous tree in its fast-growth phase, in any year, realistic spring pruning does not lead to a larger harvest than realistic winter pruning, because the realistic winter pruning is conducted one growing season later than the realistic spring pruning, so that more branches can be harvested from the tree. Only when the net canopy height growth of the tree slows down, the realistic spring pruning may come to provide a slightly larger branch harvest (Fig. 10). For the same reason, the difference in branch harvest of evergreen trees between the realistic spring and winter pruning first increases, and decreases later on (Fig. 10).

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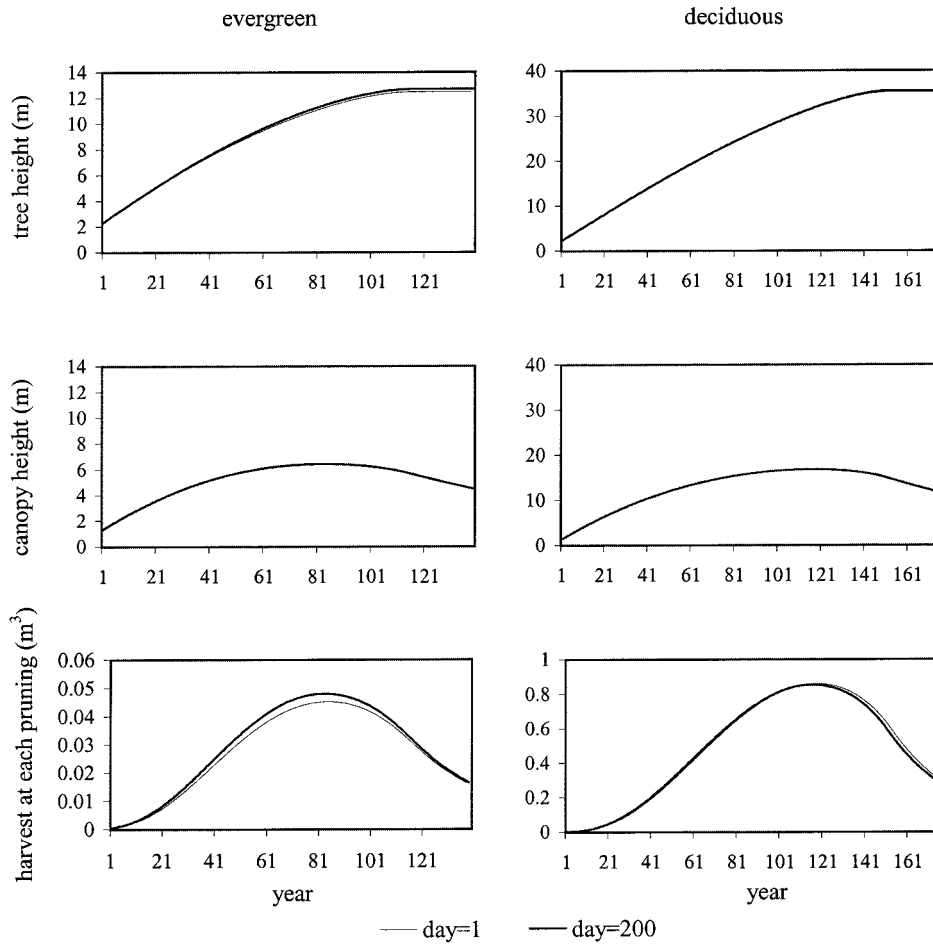


Fig. 10. Tree height, canopy height, and branch harvest of an evergreen and a deciduous tree pruned at different day in a calendar year. In the simulations, plant starts growing at day 1. Tree height and canopy height at the end of each year and branch harvest at each pruning have been plotted. Parameter settings: pruning interval=1 year; pruning level=0.01; initial canopy height=1 m.

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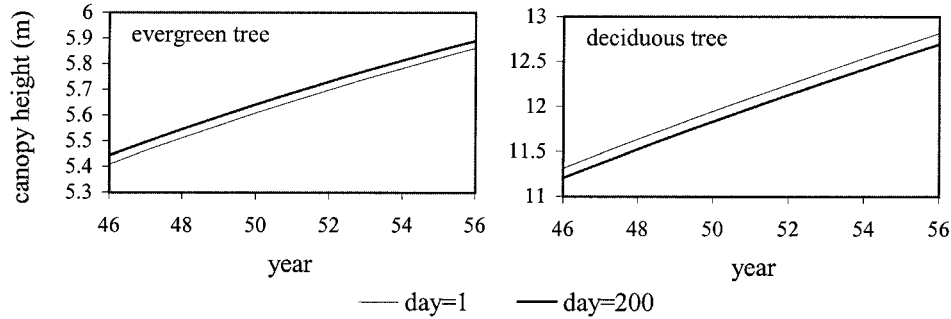


Fig. 11. Zoom-in of Fig. 10 to show the canopy height differences at the end of each year between the "realistic" spring pruning (day=1) and winter pruning (day=200)

Effect of tree size

The simulations in this section intend to explore the total branch harvest over a tree's lifetime as affected by tree size at the first pruning. Fig. 12 presents the simulations of imposing the first pruning on an evergreen tree when it is small, about half of its full size, and near its full size (viz. canopy height of 1, 5, and 12 meters; the maximal canopy height of the tree without pruning is 13 meters). The simulations show that, if pruning starts at canopy height of 12 meters, the total branch harvest tends to increase with pruning level (Fig. 12). This implies that, if pruning starts when the tree is fully grown, heavy pruning always results in a larger total harvest. However, if pruning starts when the tree is quite smaller than the full size (e.g. 1 m and 5 m), the total branch harvest is not increased by heavy pruning. For these small trees, there exists a certain low pruning level at which the total branch harvest can be maximized. This maximal total harvest is larger than the total harvest of a fully grown tree at the same pruning level (Fig. 12), even though the difference is not large. For tree sizes with such a unimodal pattern of total branch harvest, total branch harvest will always be larger in bigger trees at any pruning level (compare trees with canopy height of 1m and 5m in Fig. 12).

In addition, size effect on cumulative branch harvest over time is also analysed. Fig. 12 shows that, for small-sized trees, maximal total branch harvests are obtained at a similar pruning level. Fig. 13 shows the cumulative branch harvest of trees at pruning levels above or below this optimal pruning level (represented by 0.01 and 0.001, respectively). Whether the pruning level is above or below the optimal level, with the progress of time, a large-sized tree always provides a larger cumulative harvest than a small-sized tree. In this sense, large-sized trees are superior to small-sized trees. However, the cumulative branch harvest of a tree till its death (viz. total branch harvest over the life time in this sense) is affected by

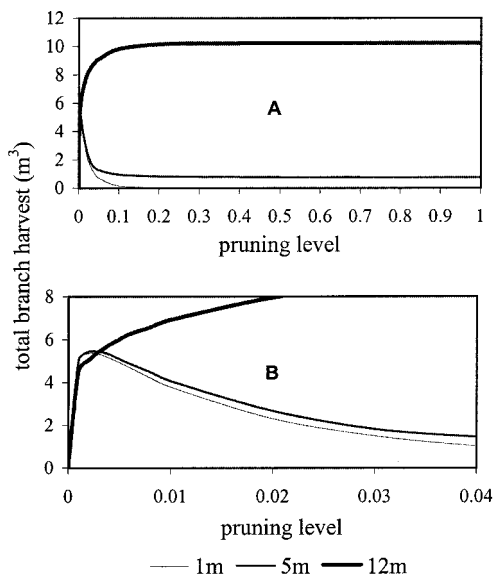


Fig. 12. Total branch harvest over a tree's lifetime as affected by tree size at which pruning starts. 1m, 5m, and 12m are the canopy heights of a tree when the pruning is started. Simulations are conducted with an evergreen tree. The maximal canopy height of this evergreen tree is 13m. Subfigure B is the zoom-in of subfigure A showing that small-sized tree obtain their maximal total branch harvest at a certain pruning level. Parameter settings: pruning interval = 1 year.

pruning level. If pruning level is above the optimal pruning level, a fully grown tree provides a larger cumulative harvest than a small-sized tree. If pruning level is below the optimal pruning level, a fully grown tree can not provide a larger cumulative harvest (Fig. 13).

Discussion

Branch harvest as affected by pruning level, pruning interval, pruning season and tree size

With respect to the total branch harvest over a tree's life time, conforming to the expectation, there exists an optimal pruning level at which the total branch harvest is maximized. This optimal level is greatly affected by pruning interval. At short pruning intervals, the relationship between total branch harvest and pruning level can be reflected by a unimodal curve, and the maximal harvest is obtained at a low pruning level. At long pruning intervals, especially when the pruning intervals are longer than the time a tree needs to reach its full size, the optimal pruning level for obtaining maximal harvest is 100 percent canopy pruning (Fig. 5).

It is expected that there exists a pruning interval at which the total branch harvest is maximized. Conforming to the expectation, the total branch harvest is maximized at

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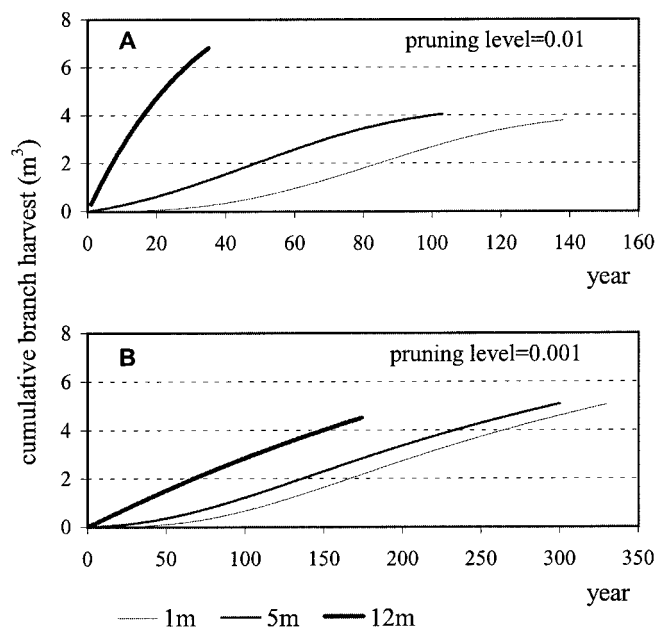


Fig. 13. Cumulative branch harvest of a tree when pruning is started at different tree size (viz. at different canopy heights: 1m, 5m, and 12m). Subfigures A and B show the cumulative branch harvests of trees at a pruning level larger (0.01) or smaller (0.001) than the optimal level at which small-sized trees obtain their maximal total branch harvest over life time (see Fig. 12). Simulations are conducted with an evergreen tree. Parameter settings: pruning interval = 1 year.

pruning intervals which are longer than the time a tree needs to reach its full size, and it is obtained at 100 percent pruning (Fig. 5).

It is hypothesized that winter pruning leads to a larger branch harvest than spring pruning. This hypothesis is partly confirmed by the simulations. For an evergreen tree, winter pruning results in a larger branch harvest than spring pruning, due to its beneficial effect on the carbon concentration (Figs. 9 and 10). For a deciduous tree, when its net canopy height growth slows down, spring pruning tends to produce more branch harvest than winter pruning (Fig. 10). However, if trees subjected to spring pruning and winter pruning have the same size, deciduous trees do not differ in height growth and branch harvest between spring and winter pruning (Fig. 9). In contrast to our expectation, difference in branch harvest between spring and winter pruning is smaller in a deciduous tree than in an evergreen tree (Figs. 9 and 10). Based on the simulations, it is clear that the respiration costs of leaves during winter determines the degree of difference in height growth and branch harvest of evergreen trees between spring and winter pruning. The

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higher the respiration costs, the larger the difference. Moreover, it is obvious that the leaf respiration in winter of evergreen trees determines the difference in maximal tree height and canopy height between evergreen and deciduous trees. The lower the leaf respiration, the smaller the difference in height.

It is hypothesized that there is an appropriate tree size at which if pruning is started, the total branch harvest is maximized. It is found in the simulations that, the bigger the tree, the larger the total harvest (Fig. 12). Therefore, in terms of obtaining the maximal total harvest, the full-sized tree is the best.

Consideration of optimal pruning

In pruning practices, what people are mostly concerned about is how to apply an optimal pruning regime so that the branch harvest of a tree can be maximized. However, how to define the optimal pruning regime is dependent on the angle from which you are looking at the issue. On the one hand, optimal pruning is a variable affected by many factors such as pruning level, pruning interval, tree size, etc. Accordingly, the optimal pruning regime can be defined on the basis of an optimal pruning level, optimal pruning interval, optimal tree size for pruning, and so on. On the other hand, optimal pruning regime can be defined either in terms of the total branch harvest over the whole lifetime of a tree, or in terms of the total branch harvest in a specific time period (cumulative branch harvest in this sense). If the definition of optimal pruning is based on the total branch harvest over the lifetime, the determination of optimal pruning level is well illustrated by Figs. 5 and 12. However, if the definition of optimal pruning is based on the cumulative branch harvest within a specific time period shorter than the lifetime of the tree, the determination of the optimal pruning level and interval is dependent on the length of the chosen specific time period. The shorter the specific time period, the more productive a high pruning level and a short pruning interval are (Fig. 8). With the increase of the length of the specific time period, the optimal pruning level and interval for obtaining a maximal cumulative branch harvest becomes lower and longer, respectively (Fig. 8).

Compensatory growth

It is shown by the simulations that, under repeated pruning, eventually, the tree height of a pruned tree is smaller than that of an unpruned tree. However, after the first few prunings, tree height growth can be enhanced (Fig. 14), and the higher the pruning level, the larger the tree height growth (Figs. 4A and 14). Thus, pruned trees apparently show compensatory growth during some time period after pruning. It has been demonstrated in field experiments that trees have compensatory growth after pruning or defoliation (Helms 1964; Cornelissen 1993). Because of the occurrence of compensatory growth, a tree can recover quickly from a single pruning (Møller 1960; Uotila and Mustonen 1994).

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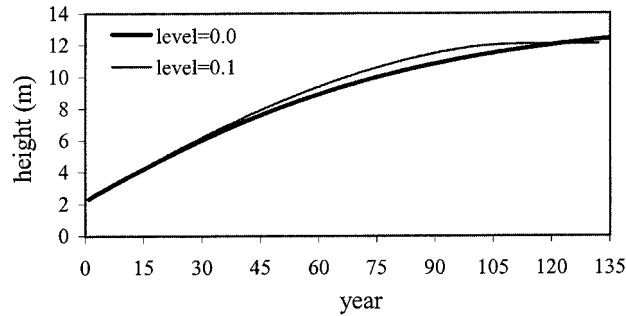


Fig. 14. Tree height of an unpruned tree (pruning level=0.0) and a pruned tree (pruning level=0.1). Simulations are conducted with an evergreen tree. Pruning interval for the pruned tree is 10 years.

Some remarks on the model

Qualitatively, model predictions are in agreement with results obtained from experimental studies. The simulations confirm that higher pruning levels lead to larger branch harvests at first few prunings, but result in smaller harvests later on (Chapter 2). The simulations also confirm that compensatory growth takes place after pruning, which have been found in our experiments (Chapter 2) and in other field studies (Helms 1964). The simulations reveal that repeated pruning reduces trees' growth and drive them to death. At longer pruning intervals, the total branch harvest over a tree's life time is maximized at a higher pruning level. These model predictions conform to our intuitions, even though no experiments have been done to test them.

In the simulations, the optimal pruning levels for obtaining maximal total branch harvest over a tree's life time are very small (Figs. 5 and 6), especially at short pruning intervals (e.g. one year). Additionally, although model simulations show some differences in height growth and branch harvest between spring and winter pruning, the differences are small. It seems that these model predictions do not well conform to the real world. These dissimilarities between the model predictions and the real world might be due to the simplicity of the model. In the model, tree growth is affected by the carbon concentration and the shoot root ratio of the tree. Many factors which might influence the growth of a real pruned tree are not incorporated in the model, such as the removal of less productive deep shaded leaves in the lower crown by pruning (Witowski 1997), the enhanced water and nutrient status of shoots after pruning (Margolis et al. 1988; Nuorteva and Kurkela 1993), the enhanced stomatal conductance of leaves after pruning (Pinkard et al. 1998), the death of redundant root after pruning (Comas et al. 2000), etc. All these aspects may benefit the carbon production and reduce the carbon consumption in a real tree, which makes a real

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tree more robust to stand pruning treatment. In further modelling studies on pruning, these factors should be included.

Suggestions for pruning practice

Based on the model predictions, it is apparent that the establishment of an optimal pruning regime is dependent on the time scale of pruning practice. If long-term pruning is applied, a longer pruning interval is better than a shorter one. Because on the one hand, the total branch harvest is larger especially when the pruning intervals are near or longer than the time a tree needs to reach its full size; on the other hand, it is much easier to select a pruning level to obtain maximal total branch harvest due to the lower sensitivity of the total branch harvest to pruning level. Furthermore, under long-term pruning regime, starting pruning to a large-sized tree is better than to a small-sized tree. However, if the intention of pruning is to get branch harvest as much as possible within a short time period, choosing a high pruning level and short pruning interval can be a choice. The longer this time period, the lower and longer the chosen pruning level and pruning interval should be.

Acknowledgements

We thank Prof. dr. Marinus J. A. Werger for his helpful comments on the earlier version of the manuscript.

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8

Summary and general discussion

Pruning of trees, in which some branches are removed from the lower crown of a tree, has been extensively used in China in silvicultural management to improve timber quality through minimizing knotty cores, provide easy access into a stand for inspection, and reduce the risk of crown fire by diminishing the chance of ground fires burning up into the crown (Shepherd 1961; Evans 1992). It is also used to obtain branches and/or leaves as fuel, fodder and forage, and industrial raw materials (FAO 1985a, b; Anonymous 1992; Evans 1992). This study, carried out in subtropical China, intends to explore the impacts of pruning on tree growth and the harvest of plant material. To this end, both experimental and modelling approaches are applied.

Pruning effects

With field experiments and a simulation model, the effects of pruning on biomass production, biomass allocation, leaf efficiency, shoot and leaf emergence, and the harvest of plant material of trees have been studied. The main results are summarized in the following paragraphs.

Biomass production and height growth

Because of the removal of productive leaves, it is likely that the growth of trees is affected by pruning. Field experiments revealed that the biomass production of trees decreased after pruning. The reduction in biomass production was correlated with pruning intensity. Moreover, the reduction in biomass production was aggravated by repeated pruning (Chapter 2). No significant effect of pruning on height growth was found (implicitly shown in Chapter 4), which is in agreement with some other pruning studies. These studies have revealed that pruning has a much greater effect on diameter growth than on height growth. If pruning intensity is not too high, height growth may not be affected at all (Møller 1960; Shepherd 1961; Pinkard and Beadle 1998). The simulation results of the model developed in Chapter 7 are consistent with the experimental results, but the model predicts that after many pruning events, height growth of a tree will slow down.

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Biomass allocation and leaf efficiency

Tree growth is dependent on the carbohydrates produced by leaves. Because of the leaf removal, the carbohydrate production of a tree after pruning may be diminished. Therefore, the pattern of allocation of biomass to the production of new leaves seems crucial to the future growth of a pruned tree. It was found in the field experiments that, after pruning, proportionately more biomass was allocated to new leaves. This enhanced allocation to leaf production tended to increase with pruning intensity (Chapter 3).

Pruning reduced the leaf mass ratio of a tree (Chapter 3). This implies that, for a unit area of remaining leaves in a pruned tree, more carbohydrates will be used for maintenance respiration. Consequently, the biomass produced per unit leaf area (viz. leaf efficiency) is expected to be lower after pruning. In contrast to this expectation, it was found in the field experiment that the leaf efficiency of a tree after pruning was not reduced, but increased (Chapter 5). This means that trees can achieve a more efficient growth after pruning treatment, which could be due to the enhanced photosynthetic production (Pinkard et al. 1998).

Branch and leaf emergence

The emergence of branches and leaves in different positions in the crown after pruning was investigated in the field experiments. It was found that the number and density of newly produced leaves on a branch in any part of the crown were not affected by pruning. The branch production in the crown of a tree after pruning was not influenced either. However, the branch production on the pruned stem part beneath the crown was strengthened. The number and density of new branches sprouted on this stem part increased with pruning intensity (Chapter 4).

Harvest of plant material

In the field experiments, trees were annually pruned during three consecutive years at fixed pruning intensities. It is obvious that a higher pruning intensity resulted in a larger amount of plant material harvested at the first pruning. However, it did not necessarily lead to a larger harvest at the third pruning (Chapter 2). The reason is that the growth of heavily pruned trees was greatly impaired.

In order to analyse the consequences of a large variation of pruning intensities and pruning frequencies, a simulation model was constructed. Based on this model, harvesting branches from trees of different size, which are subjected to different pruning intensities and different pruning intervals, was simulated (Chapter 7). The simulations showed that higher pruning intensities can result in a larger harvest of branches at the first few prunings, but lead to a smaller harvest later on. This corresponds to the results found in the field experiments reported above. The simulations also showed that, with repeated pruning, the total branch harvest over the whole lifetime of a tree is affected by pruning intensity, time

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interval between successive prunings, and the size of the tree at the first pruning. If the pruning interval is longer than the time period a tree needs to reach its full size, a higher pruning intensity consistently results in a larger total branch harvest. As soon as a tree has reached its full size, its growth is not much affected by pruning, whether the pruning intensity is high or low. Therefore, for a full-sized tree, a higher pruning intensity always means a larger total branch harvest. However, if the pruning interval is shorter than the time needed to reach full tree size, the relationship between total branch harvest and pruning intensity is unimodal. The shape of the unimodal curve is affected by the length of the pruning interval: the shorter the pruning interval, the steeper the curve. This implies that, if a tree is pruned at short intervals (e.g. one year), the total branch harvest will strongly depend on pruning intensity. In that case, slight changes in pruning intensity may lead to a total branch harvest which strongly deviates from the maximal one.

Comparisons of pruning to defoliation and coppicing

Pruning versus defoliation

Both pruning and defoliation lead to the loss of leaf area. However, the difference between pruning and defoliation is that pruning removes meristems (buds), but defoliation does not. It has been well demonstrated that the growth of a plant is not only dependent on the nutrients and carbohydrates in the plant, but is also constrained by the availability of meristems (Geber 1990). Provided that the supply of nutrients and energy is sufficient, a defoliated plant can grow better than a pruned one. Moreover, due to the same reason, the difference in growth between heavily defoliated plants and lightly defoliated ones may be smaller than that between heavily pruned plants and lightly pruned ones. In the field study, *Koelreuteria bipinnata* Fr. was different from the other species in that it had few branches when it was pruned during the first two years. For *Koelreuteria bipinnata*, pruning of the lower crown was in effect a sort of defoliation rather than pruning. Field study showed that the growth of *Koelreuteria bipinnata* was not affected after pruning in the first two years, and no difference in growth could be detected between pruning intensities (Chapter 2). This lack of effect on the growth of *Koelreuteria bipinnata* after pruning (defoliation actually) could be attributed to the nil effect of the treatment to the meristems on the tree.

Pruning versus coppicing

In this study, pruning was implemented by removing branches from the lower crown of a tree. Because of this way of branch removal, the meristems of the remaining crown of a tree are not affected by the pruning. Thus, the production of new branches and leaves in the crown remaining after pruning may stay unaltered (Chapter 4). In contrast, coppicing removes all branches from a tree, only leaving a bare stem stump. The growth of branches and the establishment of a crown on a coppiced tree have to start from scratch. In addition,

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because the apical meristem stays unaffected in a pruned tree, it still can realize an unhampered height growth. If a tree is pruned repeatedly, its leaf area ratio (leaf area/ total plant mass) will be reduced stepwise. This will consistently increase the respiration costs relative to the photosynthetic production and decrease the biomass production of the tree and eventually drive it to death (Chapter 7). However, because of the removal of the apical meristem, the stump of a coppiced tree can not grow in height any more. The increase in respiration costs in a coppiced tree is much less than that in a pruned tree. As a consequence, the maintenance costs of a coppiced tree can more easily be met by its assimilate production. This would suggest that a repeatedly coppiced tree is able to live for quite a longer time than a pruned tree.

Model evaluation

The field experiment focused on the effects of a restricted number of prunings with different pruning intensities on small trees. No study was conducted on pruning interval and tree size. For the experimental study on pruning intensity, only three typical intensity levels were selected. To deepen the understanding of pruning effect and extrapolate the experimental results obtained from the field study, a simulation model was constructed.

Qualitatively, the results of the simulations based on the model are in agreement with the experimental results. According to both field study and modelling, pruning reduces tree growth eventually (Chapters 2 and 7). Higher pruning intensities result in a larger branch harvest at the first pruning, but lead to a smaller harvest later on (Chapters 2 and 7). In the experiment, it was found that the leaf efficiency after pruning was enhanced (Chapter 5). Considering the increased respiration loads per unit leaf area (due to the reduced leaf area ratio), one may speculate that, after pruning, the photosynthetic rates of leaves increase (Pinkard et al. 1998). Similarly, in the model, it is presumed that the leaf photosynthetic rate is adjusted by the carbon concentration of the tree through negative feed back (Jeannette et al. 1995; Layne and Flore 1995; Myers et al. 1999). Photosynthetic rate is reduced or enhanced by a high or low carbon concentration, respectively. The model shows that the total branch harvest from a tree is influenced by pruning intensity, pruning interval, and tree size. When a tree is still in its fast growing stage, the total branch harvest over the lifetime of the tree is maximized at a certain level of pruning intensity. Moreover, any pruning interval may lead to about the same maximal total branch harvest. The total branch harvest is much less sensitive to pruning intensity if the pruning interval is longer. In addition, the model simulations show that, if a tree is in its fast growing stage, the bigger the tree is, the more total branch harvest can be obtained. Taking the effect of both pruning interval and tree size into account, if one is interested in the total branch harvest over the lifetime of a tree, pruning a big tree with a long pruning interval would be the choice.

Although the effects of shoot: root ratio on growth and the negative feed back of the carbon concentration on photosynthetic rate are considered in the model, some other factors which may influence the growth of a real-world pruned tree are not included, such

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as the removal of less productive deeply shaded leaves in the lower crown (Witowski 1997), the enhanced water and nutrient status (Margolis et al. 1988; Nuorteva and Kurkela 1993), the enhanced stomatal conductance (Pinkard et al. 1998), and the death of redundant roots (Comas 2000). As a consequence, the carbohydrate production should be comparatively less and the respiration cost should be higher in the model tree than in a real tree after pruning. This could be the reason why simulations reveal that the optimal pruning intensity at which the maximal total branch harvest is obtained is so low. It also explains why model trees seem to die earlier after repeated pruning than trees in the real world do.

Practical implications for pruning

In practice, pruning is usually applied to young trees, especially when the pruning is conducted in special plantations to get plant materials for industrial use. In this study, the model simulations showed that, for a young tree, if the pruning interval is one year, the maximal total harvest over the lifetime of the tree is obtained at a very low pruning intensity. In the field study lasting for three years, in which pruning was done annually, 70% crown (height) pruning gave the largest harvest at the first pruning, but it was too heavy to realize a large harvest at the third pruning. On the contrary, pruning intensities of 20% or 50% achieved a higher harvest at the third pruning. Some researchers have found that tree growth may be significantly affected by pruning intensities higher than 35% crown pruning (Møller 1960; Shepherd 1961; Pinkard and Beadle 1998). Based on our field study and simulations, and considering the experimental results of other researchers, we suggest that, for long term pruning practice on an annual basis, an optimal pruning intensity for a young tree should be 20% at most.

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Samenvatting

Het snoeien van bomen, waarbij er takken van het onderste deel van de boomkroon worden verwijderd, is in de bosbouw in China erg veel toegepast. Het wordt gedaan om de kwaliteit van timmerhout te verbeteren door het aantal knoesten te beperken, maar ook om gemakkelijker voor inspectie in dichte bosaanplantingen te kunnen rondlopen en om het gevaar van brand in het kronendak te verminderen door de kans op brand op de bosbodem te minimaliseren. Ook om takken en bladeren te oogsten en als brandstof of veevoer, of als grondstof voor het verkrijgen van sommige chemische producten te gebruiken, wordt er veel gesnoeid. In deze dissertatie wordt het effect van snoeien op de groei van de boom, met behulp van experimentele ingrepen en een modelmatige analyse, onderzocht.

In hoofdstuk 2 wordt het effect van jaarlijks snoeien op de productie van bovengrondse biomassa en de grootte van de oogst van takken en bladeren in vijf Chinese boomsoorten onderzocht. De snoeibehandelingen werden drie jaar lang voortgezet. Ze bestonden uit vier snoei-intensiteiten (0%, 20%, 50 % en 70%) en twee snoeiseizoenen (in de lente en de herfst). De biomassaproductie van de bomen nam evenredig met de snoei-intensiteit af. Jaarlijks herhaald snoeien versterkte deze afname in biomassaproductie. Hogere snoei-intensiteiten leidden tijdens het eerste jaar tot grotere oogsten, maar niet noodzakelijk tijdens de daaropvolgende jaren. Bomen die in de herfst werden gesnoeid hadden een hogere biomassaproductie en leverden een grotere oogst dan bomen die in de lente werden gesnoeid. Dat kwam, omdat bomen die in de herfst gesnoeid werden, iets groter waren. Er was geen effect van de interactie van snoeiseizoen en snoei-intensiteit op de biomassaproductie en de grootte van de oogst. De resultaten lieten zien, dat voor de vijf subtropische soorten die onderzocht werden, een jaarlijkse snoeibehandeling de boom niet voldoende tijd liet om er geheel van te herstellen. Dat betekent, dat het uitgesloten is om jaar in, jaar uit een grote oogst te behalen.

In hoofdstuk 3 worden de patronen van biomassa-allocatie en de dynamiek in bladgroei bij vier soorten bestudeerd. Gesnoeide bomen alloceerden verhoudingsgewijs een groter deel van hun bovengrondse biomassa naar hun bladeren dan naar hun houtige delen en dit was onafhankelijk van de boomsoort en van het snoeiseizoen. Dit allocatiepatroon was sterker naarmate de snoei-intensiteit toenam. Het snoeien verminderde in eerste instantie de hoeveelheid bladmassa per eenheid van totale bovengrondse biomassa (LMR). Maar doordat de boom na het snoeien verhoudingsgewijs meer biomassa naar de bladeren alloceerde, bereikten de gesnoeide bomen binnen een jaar een evenhoge LMR als de niet-gesnoeide bomen. Dit onverwachte patroon in de allocatie van biomassa kan wellicht aan het hergebruik van de open vaten in de stam worden toegeschreven, die voor de snoei met de verwijderde takken en bladeren verbonden waren. Een versterkte allocatie van biomassa naar nieuwe bladeren na het snoeien moet voor de boom van voordeel zijn om de negatieve gevolgen van het snoeien te overkomen en van de schade te herstellen.

Het doel van hoofdstuk 4 is om te onderzoeken of de vorming van nieuwe bladeren en de produktie van scheuten van belang zijn voor het veranderde patroon van biomassa-allocatie van de boom na het snoeien. Dit onderzoek werd aan twee soorten *Ficus* uitgevoerd. Het snoeien, ongeacht de snoei-intensiteit of het snoeiseizoen, had geen effect op de bladdichtheid op de nieuwe scheuten (aantal bladeren per eenheid taklengte). Het snoeien had bij beide soorten geen effect op de produktie van scheuten aan de zijtakken in de kroon en de positie van de zijtak in de kroon was ook niet van belang. Maar de positie waar na snoeien nieuwe scheuten aan de hoofdstam werden geproduceerd was niet willekeurig. Snoeien, of dat nu in de lente of in de herfst plaats had, had geen effect op het aantal en de dichtheid van de nieuwe scheuten in het bovenste, net uitgroeiende deel van de kroon en in het deel van de kroon dat na het snoeien nog takken droeg, maar beïnvloedde wel de produktie van nieuwe scheuten langs het kale deel van de stam onder de kroon. Die produktie nam toe met de snoei-intensiteit. Na snoeien in de herfst groeiden er op het kale deel van de stam meer scheuten uit dan na snoeien in de lente. Het lijkt erop, dat van alle variabelen die zijn onderzocht, slechts de toegenomen produktie van nieuwe scheuten op het kale stamdeel de toegenomen allocatie van biomassa naar de bladeren verklaren.

De gevolgen van snoeien op de bladefficiëntie bij de twee soorten *Ficus* wordt in hoofdstuk 5 onderzocht. Bij beide soorten nam de bladefficiëntie na snoeien toe. Het snoeiseizoen had wel effect op de bladefficiëntie: bomen die in de herfst gesnoeid waren hadden een grotere bladefficiëntie dan bomen die in de lente gesnoeid waren en het leek erop, dat zwaar gesnoeide bomen een wat grotere bladefficiëntie hadden dan licht gesnoeide bomen. De toename in bladefficiëntie in bomen die in de herfst gesnoeid waren was groter in *Ficus virens* dan in *Ficus microcarpa*. De toename van de bladefficiëntie van een gesnoeide boom compenseert voor de geringere hoeveelheid assimilaten, die door het wegsnoeien van de bladeren wordt veroorzaakt, en verlicht dus de schade die het snoeien teweeg brengt.

In hoofdstuk 6 wordt een model voor boomgroei gepresenteerd en in hoofdstuk 7 wordt dat model gebruikt om de effecten van snoeien op de takkenoogst te simuleren. De simulaties laten zien, dat:

(1) een niet-gesnoeide boom snel in hoogte groeit wanneer hij jong is, maar dat hij daar later geleidelijk aan mee stopt en een stationair stadium ('steady state') bereikt. Bij de gebruikte parameter-instelling blijft een altijdgroene boom uiteindelijk lager dan een bladwisselende boom. Dat komt door de onderhoudsrespiratie van de bladeren tijdens de winter.

(2) herhaald snoeien de maximaal haalbare hoogte van de boom doet afnemen en tot de dood van de boom leidt. Een hogere snoei-intensiteit en een korter snoei-interval leidt ook tot een lagere boom en tot een vroegere dood. Zwaar snoeien levert de eerste paar keer natuurlijk een grotere takkenoogst op dan licht snoeien, maar leidt daarna al gauw tot een geringe takkenoogst.

(3) bij een kort snoei-interval de totale takkenoogst, die van een jonge boom gedurende zijn gehele levensduur verkregen wordt, unimodaal samenhangt met de snoei-intensiteit. De totale takkenoogst is maximaal bij een specifieke snoei-intensiteit. Deze intensiteit

komt bij een langer snoei-interval hoger te liggen. Als het snoei-interval erg lang wordt, is de boom al ongeveer tot zijn maximale omvang uitgroeid voordat hij voor het eerst wordt gesnoeid en dan wordt de totale takkenoogst groter naarmate de snoei-intensiteit hoger ligt, want de boom gaat dan al dood voordat er een tweede keer gesnoeid kan worden.

(4) snoeien in de herfst bij een altijdgroene boom een grotere takkenoogst oplevert dan snoeien in de lente. Dat komt door de verminderde onderhouds-ademhaling van de gesnoeide altijdgroene boom gedurende de winter. Bladwisselende bomen hebben dat voordeel niet.

(5) de boomgrootte waarop het snoeien begint gevolgen heeft voor de totale takkenoogst over de gehele levensduur van de boom. Als het snoeien al in kleine bomen begint kan de totale takkenoogst maximaal zijn als er een bepaalde snoei-intensiteit wordt toegepast. Begint het snoeien pas als de boom al bijna zijn uiteindelijke grootte heeft bereikt, dan is de totale takkenoogst groter naarmate de snoei-intensiteit toeneemt.

(6) een hogere snoei-intensiteit en/of een korter snoei-interval voor de eerste paar snoeibeurten een grotere cumulatieve takkenoogst opleveren, maar later niet meer. Een grotere boom levert in vergelijking met een kleinere boom een grotere cumulatieve takkenoogst op voordat hij dood gaat.

Samenvattend kunnen we zeggen, dat de gevolgen van snoeien op de groei van bomen van veel factoren afhangen, waarvan snoeiseizoen, snoei-intensiteit snoei-interval, boomsoort en de grootte van de boom belangrijk zijn. Zwaar en vaak snoeien heeft altijd een verminderde groei tot gevolg. Dit negatieve effect wordt door een verhoogde allocatie van biomassa naar de bladeren en een verhoogde produktiviteit van de bladeren van de gesnoeide boom een beetje verminderd.

Acknowledgements

On the occasion of the finalization of this thesis, I would like to express my sincere gratitude to the people who provided me with their help during the past five years. Without their help, this thesis would never have come into being.

First, I would like to thank my Dutch promotor Prof. dr. Marinus J. A. Werger. He helped me to set up the research plan, taught me how to approach scientific issues from various perspectives, and how to write a concise scientific paper. He also expanded my knowledge of the Dutch culture. I would especially like to thank Prof. Werger and his wife Elke Werger for their hospitality during my stay in Utrecht. I am also very grateful to my Chinese promotor Prof. dr. Zhangcheng Zhong for continually stimulating me during my study and for giving me support during my field work. I would like to express my heartfelt gratitude to Prof. Zhong and his wife Ruizhi Li for their concern for my personal well-being.

I am very indebted to Heinjo During and Feike Schieving for their assistance in my work. They were always enthusiastic when discussing my ideas and results and patient when answering my questions. Talking with them was very pleasant, because of their wisdom, cordiality, and kindness. I want to thank my two roommates Mark van Nieuwstadt and Marielos Peña-Claros for their support in all possible ways during my stay in Utrecht. I am grateful to Lourens Poorter, Josef Stuefer and Heidrun Huber for their discussions about my work, their help with statistical problems, and their general encouragement. Many people at the Department of Plant Ecology in Utrecht University helped to make my time in Utrecht unforgettable, they are Bert van Ulf, Betty Verduyn, Eric Arets, Frank Millenaar, Frank Sterck, Gerrit Heil, Hans ter Steege, Hendrik Poorter, Ilona Blinova, Jacaranda van Rheenen, Jan van Rheenen, Jo Willems, Makihiko Ikegami, Marja van Staalduinen, Marjet Elemans, Merel Soons, Pieter Zuidema, René Verburg, Roderick Zagt, Roel Brienen, Sander van Hal, Shirrinka Goubitz, Simmone Rose, Tessa Pronk, Toon Rijkers, and Wim Dijkman. I would like to thank Dew Makhan and his family for their generous hospitality.

Many Chinese friends made my stay in Utrecht easy, they are Dong Ming, Guo Ke, Guo Yuanfang, He Ping, He Taiping, Li Guangfen, Li Jiaping, Li Rui, Lu Shanyun, Shi Ying, Sun Pengyue, Sun Xiaotian, Tian Yixin, Wang Chengfang, Wang Deshou, Wu Aiju, Xia Xinghua, Yuan Zhaorui, Zhang Kecheng, etc.

I am grateful to Prof. Li Xuguang, Prof. Liu Yucheng, Tao Jianping, and Wei Hong at the Plant Ecology Research Group in Southwest China Normal University for their help during my work. My labour in the field was alleviated and the field work was made more pleasant by the dedicated assistance of many students from the Faculty of Life Sciences, Southwest China Normal University. I can not forget the days working with them in the field when the temperature was higher than 40 °C and the relative humidity larger than 85 percent. I also bear vivid memories of the days we walked back 10 km to the campus because we missed the last bus. These students are: Bai Xue, Chen Guangsheng, Dan Xueming, Deng Chaozhi, Guo Jianhua, Guo Peijun, He Jisheng, Huang Zhengwei, Jiang Min, Jiao Baowei, Li Chunhua, Li Cuilan, Li Huiqin, Li Jun, Li Li, Liu Guangli, Liu Lunhua, Liu Qinghua, Lu junqiang, Luo Yiping, Luo Zhaoqing, Ma Jijun, Mo Banghui, Peng Shuming, Qi Daihua, Qi Zemin, Quan Hong, Shi Shengyou, Tu Weiguo, Wang Kan, Wang Ye, Wang Zhouping, Wu Tianli, Xuan Yu, Yan Zhiquan, Yang Bing, Yang Jinxiu, Yang Juan, Yin Changping, Zeng Jinzhou, Zhang Meng, Zhang Mingsheng, Zhao Qunfen, and Zou Xiuping.

I would like to thank many members of the administrative staff in both the Netherlands and China who helped me in a multitude of practical ways. They are Bertus Ebbenhorst, Helene Eijkelenboom, Henny Blom, Leonard Bik, Margriet Dekker, Petra van den Beemt, René Kwant, and Theo Mastwijk at the Department of Plant Ecology, Utrecht University; and An Chunyuan, Tan Yao, Yang Hua, Zhang Yong, Zhang Yaoguang, Gao Feng, Huang Lin, Wang Zhijian, Wu Yingfen and Pan Mei at Southwest China Normal University.

I thank the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) and Science and Technology Commission of Chongqing Municipality, China for their financial support for the research.

I am very grateful to my parents and brothers and to my parents-in-law for their continuous support. Most of all, I want to express my special thanks to my wife for her consideration, understanding, patience, and love.

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