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
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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
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.
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 ºC. The average temperature of the coldest month (January) and the hottest month (July) are 7.5 ºC and 28.6 ºC, 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 branch dry weight were again 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
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).
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).
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
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).
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
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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