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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.

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 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, 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 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.