

---

# Insight into the Relationship Between Plant Photosynthetic Production Allocation and Ontogeny from Population Dynamics

Renfei Chen<sup>1,\*</sup>, Suping Xiao<sup>2</sup>, Yongji Wang<sup>1</sup>, Qindi Zhang<sup>1</sup>

<sup>1</sup>School of Life Science, Shanxi Normal University, Taiyuan, China

<sup>2</sup>School of Mathematics and Computer Science, Shanxi Normal University, Taiyuan, China

## Email address:

chenrf@sxnu.edu.cn (Renfei Chen)

\*Corresponding author

## To cite this article:

Renfei Chen, Suping Xiao, Yongji Wang, Qindi Zhang. Insight into the Relationship Between Plant Photosynthetic Production Allocation and Ontogeny from Population Dynamics. *Ecology and Evolutionary Biology*. Vol. 7, No. 2, 2022, pp. 23-29. doi: 10.11648/j.eeb.20220702.13

**Received:** April 1, 2022; **Accepted:** April 18, 2022; **Published:** April 25, 2022

---

**Abstract:** Plant biomass allocation is a central issue in ecology. Plant ontogeny, as biotic influencing factors, spurs allocation shift among plant different organs. The difficulty is separating the obscure and mixed effect of ontogeny and environmental stress on biomass allocation because of lacking specific information during plant whole life history. In combination with theory in population dynamics and metabolic theory of ecology, we developed a theoretical framework in biomass allocation to investigate the quantitative relationship of leaf biomass fraction vs. plant age, leaf primary productivity fraction vs. plant age. These models fit well with the analysis results from empirical forest dataset. The results show that plant photosynthetic efficiency in accumulation decrease with plant ontogeny, but the annual growth photosynthetic efficiency has no regression relationship with plant age. In addition, plant taxon plays an important role in the relationship of leaf biomass fraction and plant age, and evergreen plants have a higher leaf biomass fraction than deciduous ones. The research here will provide a foundation for further understanding the effect of both plant “true plasticity” and “apparent plasticity” on plant biomass allocation patterns, respectively.

**Keywords:** Biomass Allocation, Plant Ontogeny, True Plasticity, Apparent Plasticity, NPP

---

## 1. Introduction

Plant biomass partitioning pattern plays an important role in ecological research [1-3]. A clear understanding in the relationship between plant above- and belowground biomass can provide significant directions to global carbon sink estimation caused by the fact that plant root system (difficult to measure directly) is often estimated through plant aboveground biomass indirectly [4]. The plasticity of allocating energy to different plant organ parts strongly affect the decision farmers make to harvest maximum agricultural products they want [5], and the allocation patterns between plant photosynthetic and non-photosynthetic organs have strong links to improve ecosystem net primary productivity (NPP) [6, 7]. Therefore, large number of investigations try to find how biotic and abiotic factors influence plant biomass allocation patterns both theoretically and empirically [1, 3, 8-12].

One of the most important theories in biomass allocation is

isometric and allometric theory derived from metabolic theory of ecology, which believes that there is an isometric relationship between plant above- and belowground biomass, while leaf biomass scales as 3/4 power of plant total biomass [1, 13-15]. These allocation patterns, derived through mathematical approaches, turns out to be general and is demonstrated by large quantity of empirical data worldwide along different precipitation and temperature gradients [1, 2], which suggests that the scaling exponents used in allometric approach is highly insensitive to environmental factors.

Another important theory is optimal allocation theory which believes that plants allocate more biomass to the parts that is subjected to more environmental stress [16, 17]. For example, more photosynthetic product will be allocated to plant belowground part when plant is subjected to water stress, which explains the phenomenon that shrubs living in deserts have very developed root systems, while plants living in dark have smaller root shoot ratio because of lacking light [3, 18,

19]. In comparison with isometric theory, optimal allocation theory indicates that plant biomass allocation pattern is strongly influenced by environmental factors such as precipitation and temperature [3, 11]. This contradictory paradox partly owes to the fact that the index of root shoot ratio mathematically is much more sensitive to variables than scaling exponents.

However, one of the problems is that plant plasticity among different organs predicted by optimal allocation theory is much easy to be obscured by the phenomenon of ontogenetic drift [3, 11]. Defined by Evans (1972), ontogenetic drift is applied into plasticity of biomass allocation to describe the phenomenon that plant biomass allocation pattern changes with plant ontogeny [20]. For example, previous research indicates that root shoot ratio for trees is much higher initially when plant is seedlings for establishment, and then it becomes smaller with plant ontogeny [21-23]. To distinguish the "apparent" and "true" plasticity in biomass allocation, empirical data analyses indicate that optimal allocation theory can only partly tested by the plasticity of biomass allocation patterns [11]. Some researches even found that plant ontogeny plays a much more important role in biomass allocation pattern than environmental factors such as resource availability emphasized by optimal allocation theory [17]. Therefore, it cannot be ignored to investigate how plant age regulates plant photosynthetic allocation pattern.

Most researchers who study age-dependent biomass allocation pattern pay much attention to leaf traits such as leaf dry biomass per unit leaf area, fraction of total plant dry biomass in leaves and leaf area ratio because the photosynthetic organ leaf has strong links to plant potential for light harvesting and, accordingly, species status in vegetation community [24, 25]. Empirical data from both herbaceous and woody plants demonstrates that plant leaf biomass fraction declines with plant ontogeny [25-27]. Much biological mechanisms have been proposed to explain this phenomenon. For example, woody plants accumulated much biomass in stem so that to resist gravity and support the whole plant establishment [28]. However, large gap still exists in our understanding of photosynthetic product allocating to plant leaf in response to ontogeny because much attention has been paid to the general variation trend, while the specific dynamics as well as the intrinsic mechanism is still not clear.

The main goal in this study is to investigate the ecological dynamics of leaf biomass allocation traits (leaf biomass fraction and leaf net primary productivity fraction) with plant age based on the classical theory in population dynamics. We use the mathematical models to theoretically predict the variation dynamics, and then global forest data set is used to empirically demonstrate the prediction from both individual and community level, respectively. Further, global forest data set is separated into different subsets to study the different leaf photosynthetic product allocation patterns in response to plant age between natural and planted forests as well as among different plant families. Specifically, we make a comparison between evergreen gymnosperm and deciduous angiosperm for the relationship of leaf biomass fraction vs. plant age.

## 2. Materials and Methods

### 2.1. Theoretical Model

Metabolic theory of ecology indicates that plant leaf biomass scales as 3/4 power of plant total biomass [13-15, 29]. Therefore, leaf biomass fraction (LMF, i.e. the quotient of leaf biomass and total biomass) scales as -1/4 power of plant total biomass. That is:

$$\frac{M_L}{M_T} \propto M_T^{-1/4} \quad (1)$$

Where  $M_L$  and  $M_T$  represent plant leaf biomass and plant total biomass respectively. The logistic equation model has been widely used to describe population dynamics for both plants and animals as well as to describe individual plant growth process [30, 31]. This derives from the fact that environment or plant biophysical traits impose limitations to population or individual plant growth so that plants cannot have a constant growth rate. It contains much ecological implications although the model is simply [32, 33]. Here, we use the integral form of logistic equation model:

$$m_t = \frac{M_{mat}}{1 + e^{a-gt}} \quad (2)$$

Where  $t$ ,  $m_t$ ,  $M_{mat}$  and  $g$  represent plant growth time (i.e. plant age), individual plant total biomass at time  $t$ , plant maximum total biomass and plant intrinsic growth rate respectively, while  $a$  represents normal constant. Assuming studying equation (1) and (2) at the same plant growth time, the variables of  $M_T$  and  $m_t$  are the same. Thus, the relationship between plant leaf biomass fraction and plant growth time can be expressed as the following:

$$\frac{M_L}{M_T} = \alpha(1 + e^{a-gt})^{1/4} \quad (3)$$

Where  $\alpha$  is another normal constant. According to equation (3), plant leaf biomass fraction decreases with plant ontogeny, which indicate that plant photosynthetic capacity or efficiency become weak during plant whole life history although the amount of net primary productivity (NPP) increase before plants come to mature. However, this does not mean that plant leaf NPP fraction (LPF, i.e. the quotient of leaf NPP and plant total NPP) has the same or similar variation tendency. In order to investigate this point, we study the relationship between plant leaf productivity ( $P_L$ ) and plant total productivity ( $P_T$ ). Assuming that  $P_L \propto P_T^\beta$ , then  $LPF \propto P_T^{\beta-1}$ . Thus, leaf NPP fraction will be independent of plant total NPP on condition that the scaling exponent  $\beta$  equals 1, and it will not be subject to plant ontogeny.

### 2.2. Empirical Test

To evaluate the theoretical framework proposed, we collected the directly measured forest data from both individual and community level. Assuming that there is a consistent data analysis result between individual and community level, the hypothesis which is appropriate to

individual plant may also be applied to plants in community level. This assumption is based on the truth that both LMF and LPF are fractions which canceled the effect of plant density between denominator and numerator. Moreover, the conclusions derived from empirical data may be affected by environmental and other biotic factors. Therefore, we analyzed the natural and planted forest data separately to observe the effect of artificial treatment on the relationship between biomass allocation pattern and plant ontogeny, and the effect from biophysical traits were reviewed based on the comparisons among several main families contained in the dataset. Leaf biomass fraction which represents the accumulation of photosynthetic carbohydrate may response differently to plant age in comparison with leaf NPP fraction which represents the new obtained assimilation production each year, and the scaling relationship between leaf net primary productivity and total net primary productivity was inspected before studying the relationship between leaf NPP fraction and plant age.

### 2.3. Data Collection

Two forest data sets were used to examine the theoretical framework predictions. The two data sets are (1) the forest biomass and primary production compendium for Eurasian species compiled by Usoltsev (2001) [34], and (2) the biomass and allometry database for individual woody plants [35]. We used the first data set [34] to study the relationship of leaf biomass fraction vs. plant age at community level as well as to study the relationships of leaf NPP fraction vs. plant age and leaf NPP vs. total NPP. We used the second data set [35] to study the relationship of leaf biomass fraction vs. plant age at individual level.

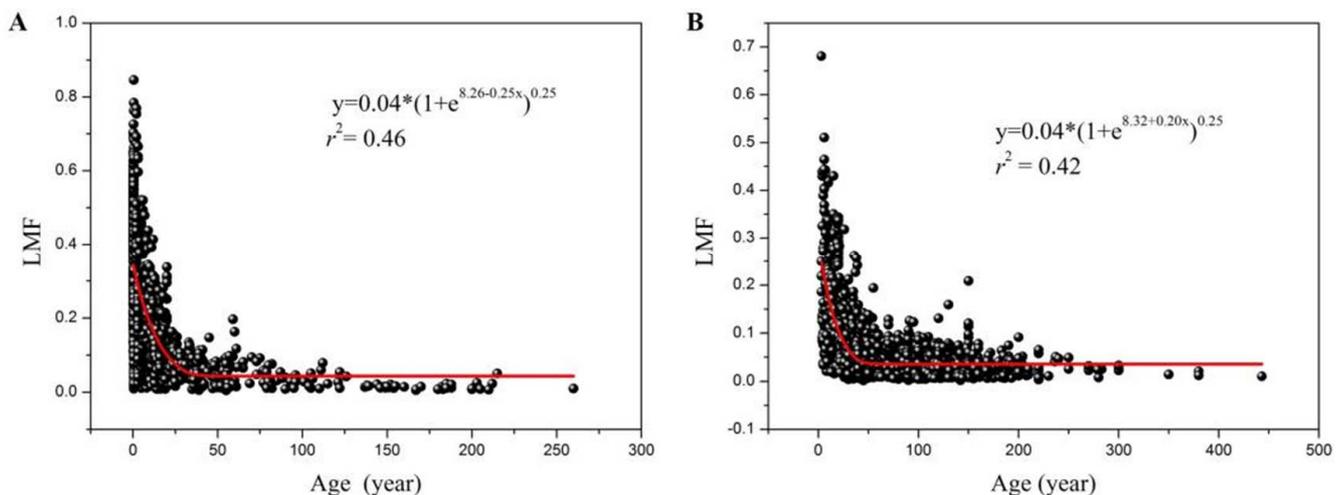
The following several criterions were used to cull the two compilations: i) the data reported for each forest individual or community must contain all the variables we need to test our theoretical frameworks. In other words, they must contain photosynthetic functional traits (leaf and total biomass or leaf and total NPP) and plant age. ii) All the variables we selected must be directly measured rather than estimated from other variables. This can make sure our models are tested reasonably. iii) For the analysis among different plant families, the minimum sample size is 30 for each family selected so that it is suitable to do regression analysis.

### 2.4. Statistical Analysis

We used non-linear regression method to study the relationships of leaf biomass fraction vs. plant age, leaf NPP fraction vs. plant age with software Origin Pro 8. RMA regression method is a widely used approach to study the allometric and isometric scaling relationships [10, 31, 36-42], and we use RMA method to calculate the scaling relationship between plant leaf productivity and plant total productivity.

## 3. Results

The analysis results indicate that the regression relationship between leaf biomass fraction and plant age can be tested by the theoretical models we developed from both individual and community level (Figure 1). The nonlinear regression analysis shows that the regression equation used for the relationship between leaf biomass fraction and plant age at individual level ( $r^2=0.46$ ) is much similar to that at community level ( $r^2=0.42$ ) (Figure 1).



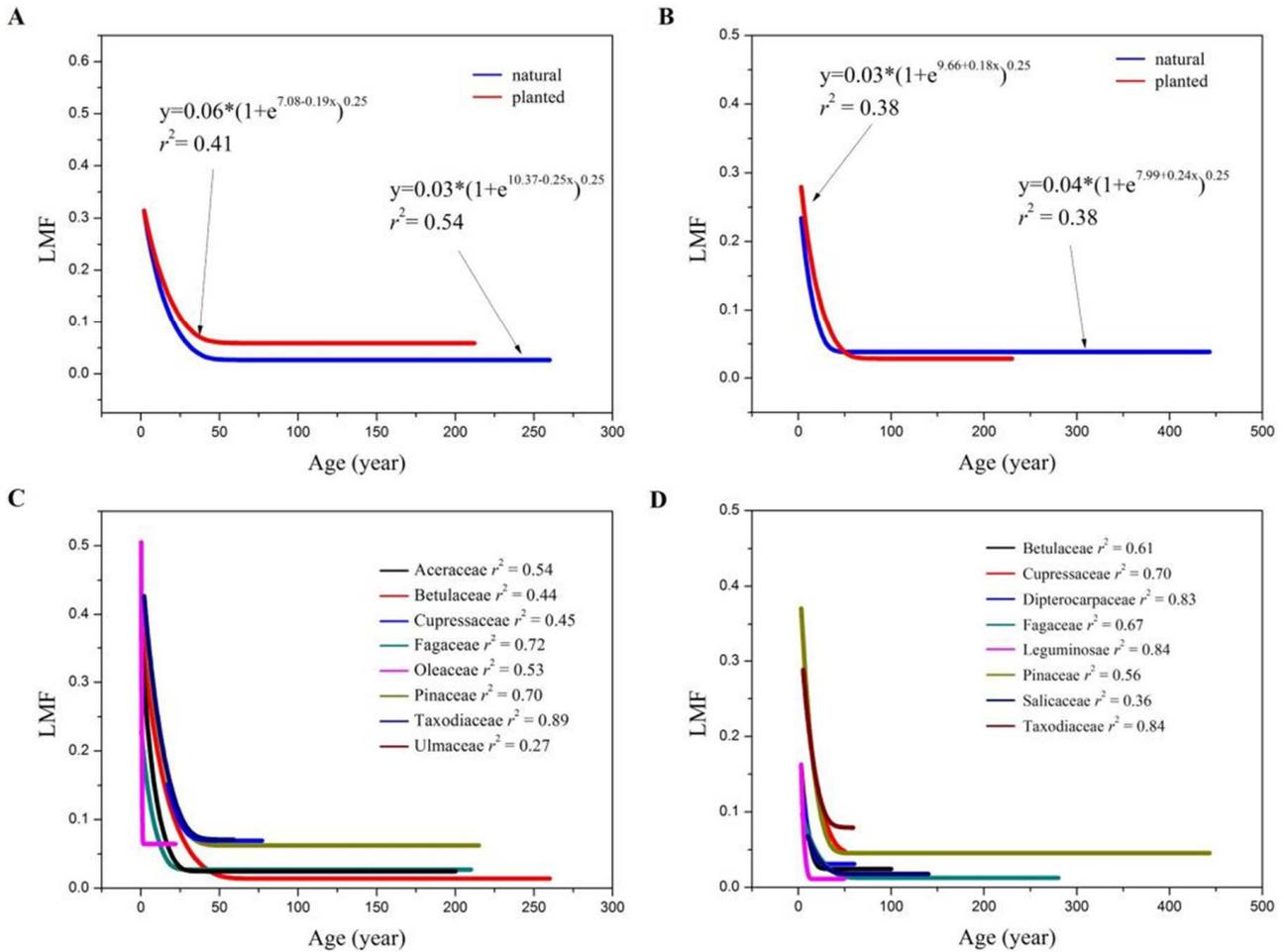
**Figure 1.** Non-linear regression relationship between leaf biomass fraction and plant age in (A) individual level and (B) community level with empirical forest dataset. All datasets used here are obtained through directly measured method without deriving from allometric relationships.

The leaf biomass fraction is higher for planted forests than for natural forests in individual level through the whole life history, while planted forests in community level have a faster decreasing speed with plant ontogeny which makes the leaf biomass fraction higher at the beginning and lower in the end

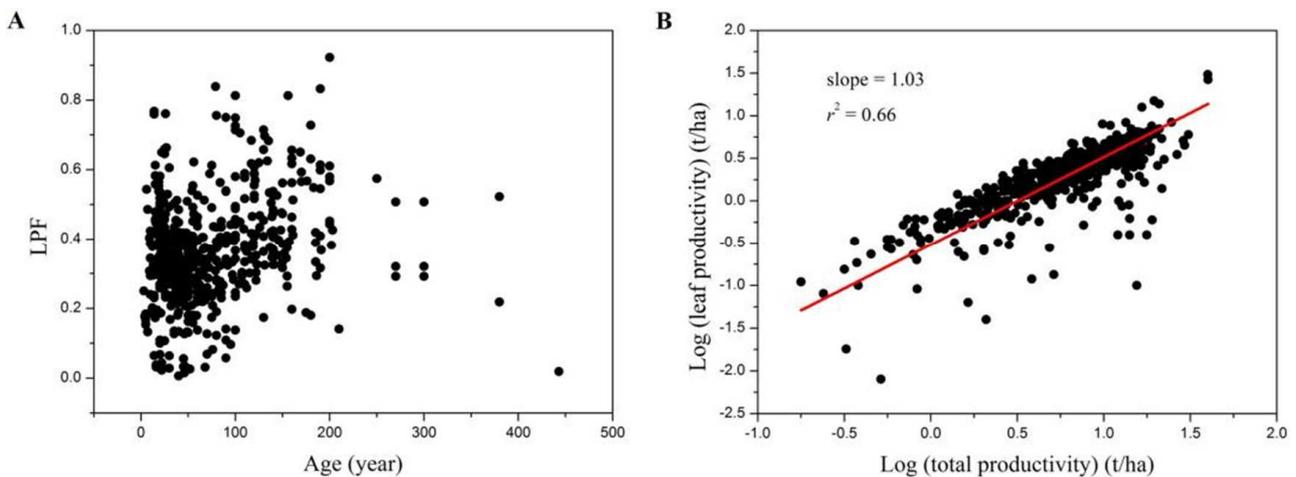
for planted forests than for natural forests (Figure 2, A and B). The regression  $r^2$  is higher for most of the families than that for the pooled data analysis results both in individual and community level (Figure 2, C and D), which suggest that plant taxon plays a role in the interested relationships.

Although there is a strong relationship between leaf biomass fraction and plant age, data analysis results show that there is no relationship between leaf NPP fraction and plant age (Figure 3, A). In addition, the log-log transformed regression analysis shows that the scaling exponent between leaf productivity and

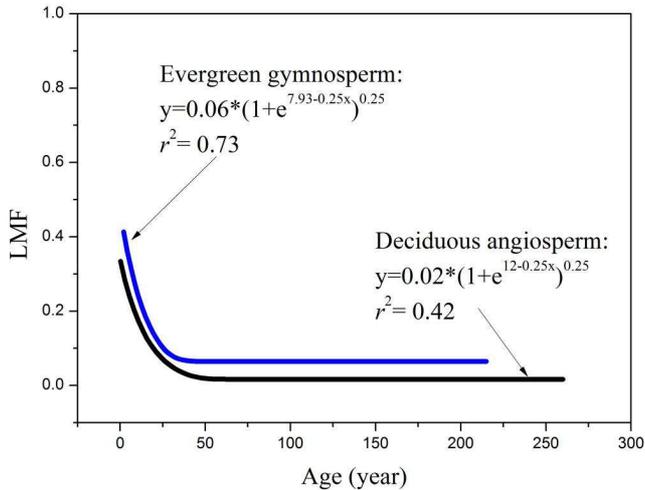
total productivity approximates to 1 ( $r^2=0.66$ ) (Figure 3B). The comparison between evergreen gymnosperm and deciduous angiosperm shows that leaf biomass fraction is higher for evergreen gymnosperm than that for deciduous angiosperm throughout all age stages (Figure 4).



**Figure 2.** The effect of different taxa on the relationship of leaf biomass fraction and plant age. (A) Comparisons between natural and planted forest in individual level, (B) comparisons between natural and planted forest in community level, (C) comparisons among different plant families in forest individual level, (D) comparisons among different plant families in forest community level.



**Figure 3.** Effects of plant age on leaf net primary productivity fraction (LPF) and mechanism in it. (A) Regression result shows that there is no relationship between LPF and plant age. (B) Scaling relationship between plant leaf and total primary productivity. The scaling exponent approximates to 1, which predict the weak relationship between LPF and plant age based on the theoretical or hypothesis proposed in the main text.



**Figure 4.** Comparison between evergreen gymnosperm and deciduous angiosperm for the relationship between leaf biomass fraction and plant age.

## 4. Discussion

This study focus on the effects of influencing factors on plant biomass allocation, which is a classic issue [5, 6, 19, 23, 27]. The relationship in Eq. (3) is well-supported by the available data. Our investigation about the relationship between leaf biomass fraction and plant age from both empirical and theoretical perspectives provides a method to study how plant photosynthetic product allocation varies with plant ontogeny through “apparent plasticity” rather than “true plasticity”. Apparent plasticity suggests that plant biomass allocation is subject to biotic influence such as plant ontogeny, while true plasticity indicates that environmental factors such as precipitation and temperature play an important role in plant biomass allocation pattern [11]. However, in most cases, the intrinsic truth in biomass allocation are confused by optimality or ontogeny because optimal allocation theory indicate that plant allocate more biomass to the parts that are subject to more environmental stress, which usually have a similar trend in comparison with the variation of biomass allocation in response to plant ontogeny [11, 23]. The quantitative relationship between leaf biomass fraction and plant age provide a theoretical method to separate the two effects (ontogeny and optimality) on biomass allocation. With the mathematical model we developed, an age-dependent leaf biomass fraction (i.e. leaf biomass fraction weighed by plant age) can be calculated to study the net effect of environmental stress on plant leaf biomass fraction.

Contrary to the relationship between leaf biomass fraction and plant age, data analysis results indicate that there is no regression relationship between leaf NPP fraction and plant age. This amazing fact is possibly explained by the following two points: i) this demonstrate the hypothesis proposed in our theoretical framework as it turns out to approximate to 1 for the scaling relationship between leaf and total net primary productivity based on the investigation of empirical forest data analysis (Figure 3, B). Therefore, the quotient between leaf and total net primary productivity is a constant

and does not vary with plant total net primary productivity. Further, according to our theoretical models, leaf NPP fraction does not vary with plant age. ii) Primary productivity is measured by the new obtained part of plant, which means that both leaf and total primary productivity just include the alive and activated plant organs, while plant total biomass contain large amount of non-active tissues for studying the allometric relationship of leaf vs. total biomass derived from metabolic theory of ecology [13-15, 28]. The difference between leaf biomass fraction and leaf NPP fraction in response to plant age suggests that plant leaf and total biomass cannot be regarded as the simple sum or the accumulation of annual new obtained photosynthetic product although leaf primary productivity varies proportionally with plant total primary productivity.

The differences between plantation managed and field wild forests in terms of the relationship between leaf photosynthetic production allocation and plant ontogeny indicate that planted treatment affects the variation of leaf biomass fraction with plant age. Plants acquire relatively more water or nutrients under human managed condition, which result in less photosynthetic production allocated to plant root based on optimal allocation theory [3, 11, 23]. Therefore, the higher leaf biomass fraction suggests that more photosynthetic production is allocated to leaf for planted forests than for natural ones. However, this rule cannot apply to vegetation in community level (Figure 2, B), which suggests that community structure and interactions can change the effect of plant ontogeny on plant biomass allocation pattern although the effect of density is canceled between denominator and numerator for leaf biomass and productivity fractions. In addition, plantation managed forests have faster decreasing speed of leaf biomass fraction with plant age, and it suggests that more and more photosynthetic production is allocated to plant non-photosynthetic organ parts such as plant stem which is one of the main intentions for plantation management and application. The different variation curves for different plant families attribute to plant traits in tree physiology. For instance, *Taxodiaceae* has a much higher leaf biomass fraction than *Betulaceae*. This derives from the fact that most *Taxodiaceae* plants are evergreen while *Betulaceae* belongs to deciduous angiosperm, and leaf biomass fraction is much higher for evergreen than for deciduous (Figure 4). Evergreen plants can have leaves all the time during plant ontogeny and development because not all leaves dropping down each year, and new leaves will generate next year. This leads to the accumulation of leaf amount for evergreen plants year after year, while deciduous plants have no leaves left after growing season every year and their survival depends on the leaves new generated in the current year [2]. As a result, consistent with previous research [12, 19, 27, 43], evergreen plants have a higher leaf biomass fraction than deciduous plants (Figure 4).

With the relationship between leaf biomass fraction and plant age, we make a bridge to integrate plant individual biomass allocation pattern into population dynamic, which lay

a foundation for further understanding the role plant biomass partitioning played in the process of population self-regulation. Moreover, the famous logistic equation is the basis for many important ecological theories such as metapopulation, which suggest the possibility to apply biomass allocation theory into metapopulation theory [44-46]. Previous research indicates that the persistence of a metapopulation comes true on condition that per-patch colonization rate is greater than the inverse of mean patch age [47]. Assuming each patch in a metapopulation is a population or community, and the succession or mean patch age is regarded as the process of plant ontogeny, the theoretical framework developed here will make the future extension work clear: under certain specific plant photosynthetic efficiency, what per-patch colonization rate should be required in order to make a metapopulation persistence.

The logistic equation we used here is the simplest one, and it does not contain many other influencing factors such as time lag which will make the dynamics a little complex. Base on the simplest logistic equation, there will be an equilibrium at the end of plant ontogeny and leaf biomass fraction turn out to be a stable value. However, things will change when time lag is considered especially under the circumstances that the product of population growth rate and time lag is greater than 0.35 according to the theory in population dynamics [32, 48, 49]. If population time lag is so long that Hopf's bifurcation occur [50, 51], a stable system will be unstable [49, 52], and plant leaf biomass fraction will vary. More empirical data analyses are worthy to demonstrate this prediction. The theoretical predictions make a caution that more attention should be paid to population dynamics when evaluating forest belowground carbon storage.

## 5. Conclusion

How plant photosynthetic production allocated to plant leaf organ parts plays an important role in both theoretical predictions and empirical test of ecological systems. Our results suggest that plant leaf biomass fractions decrease during plant ontogeny from both community level and individual level. Moreover, this relationship is regulated by plant taxon, and evergreen plants have a higher leaf biomass fraction than deciduous ones. However, plant ontogeny has no effect on the annual growth photosynthetic efficiency. Our work provides theoretical foundation in studying the effect of both plant "true plasticity" and "apparent plasticity" on the allocation patterns among different plant organ parts, respectively.

## Ethics

There is no any ethic problem about this paper.

## Data, Code and Materials

The dataset we used can be found in the references we referred in the section of *materials and methods*.

## Conflict of Interest Statement

All the authors do not have any possible conflicts of interest.

## Acknowledgements

This work is supported by National Natural Science Foundation of China (grant 32101235) and Basic Research Program of Shanxi Province (20210302124141).

## References

- [1] Enquist, B. J. & Niklas, K. J. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295, 1517-1520 (2002).
- [2] Niklas, K. J. & Enquist, B. J. On the vegetative biomass partitioning of seed plant leaves, stems, and roots. *The American Naturalist* 159, 482-497 (2002).
- [3] McCarthy, M. & Enquist, B. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Funct. Ecol.* 21, 713-720 (2007).
- [4] Mokany, K., Raison, R. J. & Prokushkin, A. S. Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biol.* 12, 84-96, doi: 10.1111/j.1365-2486.2005.001043.x (2006).
- [5] Weiner, J. Allocation, plasticity and allometry in plants. *Perspect. Plant Ecol. Evol. Syst.* 6, 207-215 (2004).
- [6] Poorter, H. & Sack, L. Pitfalls and possibilities in the analysis of biomass allocation patterns in plants. *Frontiers in plant science* 3, 259 (2012).
- [7] Monsi, M. & Saeki, T. On the factor light in plant communities and its importance for matter production. 1953. *Ann. Bot.* 95, 549-567, doi: 10.1093/aob/mci052 (2005).
- [8] Reich, P. B., Rich, R. L., Lu, X., Wang, Y. P. & Oleksyn, J. Biogeographic variation in evergreen conifer needle longevity and impacts on boreal forest carbon cycle projections. *Proc. Natl. Acad. Sci. USA* 111, 13703-13708 (2014).
- [9] Luo, Y., Wang, X., Zhang, X., Booth, T. H. & Lu, F. Root: shoot ratios across China's forests: Forest type and climatic effects. *For. Ecol. Manage.* 269, 19-25 (2012).
- [10] Niklas, K. J. Plant allometry: is there a grand unifying theory? *Biological reviews* 79, 871-889 (2004).
- [11] McConnaughay, K. & Coleman, J. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* 80, 2581-2593 (1999).
- [12] Reich, P. B. *et al.* Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proc. Natl. Acad. Sci. USA* 111, 13721-13726 (2014).
- [13] West, G. B., Brown, J. H. & Enquist, B. J. A general model for the origin of allometric scaling laws in biology. *Science* 276, 122-126 (1997).
- [14] West, G. B., Brown, J. H. & Enquist, B. J. The fourth dimension of life: fractal geometry and allometric scaling of organisms. *science* 284, 1677-1679 (1999).

- [15] West, G. B., Brown, J. H. & Enquist, B. J. A general model for the structure and allometry of plant vascular systems. *Nature* 400, 664-667 (1999).
- [16] Brouwer, R. Some aspects of the equilibrium between overground and underground plant parts. *Jaarboek van het Instituut voor Biologisch en Scheikundig onderzoek aan Landbouwgewassen 1963*, 31-39 (1963).
- [17] Noulékoun, F., Khamzina, A., Naab, J. B. & Lamers, J. P. Biomass allocation in five semi-arid afforestation species is driven mainly by ontogeny rather than resource availability. *Annals of Forest Science* 74, 78 (2017).
- [18] Thornley, J. A balanced quantitative model for root: shoot ratios in vegetative plants. *Ann. Bot.* 36, 431-441 (1972).
- [19] Poorter, H. *et al.* Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193, 30-50 (2012).
- [20] Evans, G. C. *The quantitative analysis of plant growth*. Vol. 1 (University of California Press, 1972).
- [21] Ledig, F. T., Bormann, F. H. & Wenger, K. F. The distribution of dry matter growth between shoot and roots in loblolly pine. *Botanical Gazette* 131, 349-359 (1970).
- [22] Bazzaz, F., Garbutt, K., Reekie, E. & Williams, W. Using growth analysis to interpret competition between a C 3 and a C 4 annual under ambient and elevated CO<sub>2</sub>. *Oecologia* 79, 223-235 (1989).
- [23] Gedroc, J. Plasticity in root/shoot partitioning: optimal, ontogenetic, or both. *Funct. Ecol.* 10, 44-50 (1996).
- [24] Poorter, H. & Nagel, O. The role of biomass allocation in the growth response of plants to different levels of light, CO<sub>2</sub>, nutrients and water: a quantitative review. *Funct. Plant Biol.* 27, 1191-1191 (2000).
- [25] Niinemets, U. Key plant structural and allocation traits depend on relative age in the perennial herb *Pimpinella saxifraga*. *Ann. Bot.* 96, 323-330 (2005).
- [26] Chaudhary, N., Narayan, R. & Sharma, D. Differential biomass allocation to plant organs and their allelopathic impact on the growth of crop plants: A case study on the invasibility of *Ageratum conyzoides* in Indian dry tropics. *Indian J. Agric. Sci.* 85, 1405 (2015).
- [27] Poorter, H. *et al.* How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytol.* 208, 736-749, doi: 10.1111/nph.13571 (2015).
- [28] Mori, S. *et al.* Mixed-power scaling of whole-plant respiration from seedlings to giant trees. *Proc Natl Acad Sci U S A* 107, 1447-1451, doi: 10.1073/pnas.0902554107 (2010).
- [29] Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecology* 85, 1771-1789 (2004).
- [30] Reed, L. J. & Pearl, R. On the Summation of Logistic Curves. *Journal of the Royal Statistical Society* (1927).
- [31] Deng, J. *et al.* Models and tests of optimal density and maximal yield for crop plants. *Proc. Natl. Acad. Sci. USA* 109, 15823-15828 (2012).
- [32] May, R. M. theoretical ecology. *Blackwell, Oxford, England* (1974).
- [33] Hastings, A. population ecology: concepts and models. *Springer* (1997).
- [34] Usoltsev, V. Forest biomass of northern Eurasia. *Russian Academy of Sciences, Ural Branch, Botanical Garden and Ministry of Education of Russian Federation, Ural State Forest Engineering University, Yekaterienburg*(in Russian) (2001).
- [35] Falster, D. S. *et al.* BAAD: a Biomass And Allometry Database for woody plants. *Ecology* 96, 1445-1445 (2015).
- [36] Deng, J. M. *et al.* Plant mass–density relationship along a moisture gradient in north-west China. *J. Ecol.* 94, 953-958 (2006).
- [37] Deng, J. M. *et al.* Trade-offs between the metabolic rate and population density of plants. *PLoS One* 3, e1799, doi: 10.1371/journal.pone.0001799 (2008).
- [38] Robinson, D., Davidson, H., Trinder, C. & Brooker, R. Root–shoot growth responses during interspecific competition quantified using allometric modelling. *Ann. Bot.* 106, 921-926 (2010).
- [39] Chen, G., Yang, Y. & Robinson, D. Allocation of gross primary production in forest ecosystems: allometric constraints and environmental responses. *New Phytol.* 200, 1176-1186 (2013).
- [40] Niklas, K. J. & Hammond, S. T. Biophysical effects on plant competition and coexistence. *Funct. Ecol.* 27, 854-864 (2013).
- [41] Chen, G., Yang, Y. & Robinson, D. Allometric constraints on, and trade-offs in, belowground carbon allocation and their control of soil respiration across global forest ecosystems. *Global Change Biol.* 20, 1674-1684 (2014).
- [42] Deng, J. *et al.* Insights into plant size-density relationships from models and agricultural crops. *Proc. Natl. Acad. Sci. USA* 109, 8600-8605 (2012).
- [43] McCarthy, M. C., Enquist, B. J. & Kerkhoff, A. J. Organ partitioning and distribution across the seed plants: assessing the relative importance of phylogeny and function. *Int. J. Plant Sci.* 168, 751-761 (2007).
- [44] Hanski, I., Gilpin, M. E. & McCauley, D. E. *Metapopulation biology*. Vol. 454 (Elsevier, 1997).
- [45] Hanski, I. & Ovaskainen, O. Metapopulation theory for fragmented landscapes. *Theor. Popul. Biol.* 64, 119-127 (2003).
- [46] Opdam, P. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape Ecol.* 5, 93-106 (1991).
- [47] Hastings, A. Metapopulation Persistence with Age-Dependent Disturbance or Succession. *SCIENCE* (2003).
- [48] May, R. M. Deterministic models with chaotic dynamics. *Nature* 256, 165 (1975).
- [49] May, R. M. *Stability and complexity in model ecosystems*. Vol. 6 (Princeton university press, 2001).
- [50] Hassard, B. D., Hassard, D., Kazarinoff, N. D., Wan, Y.-H. & Wan, Y. W. *Theory and applications of Hopf bifurcation*. Vol. 41 (CUP Archive, 1981).
- [51] Marsden, J. E. & McCracken, M. *The Hopf bifurcation and its applications*. Vol. 19 (Springer Science & Business Media, 2012).
- [52] May, R. M. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269, 471 (1977).