



# Effects of experimental defoliation on resource allocation using integrated physiological units in the andromonoecious *Camptotheca acuminata*



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## ABSTRACT

The resource allocation of individual plants is a relatively complex process. Trade-off exists between vegetative growth and reproduction, male and female characteristics in monoecious plant. *Camptotheca acuminata* Decne. (Nyssaceae) is a perennial woody plant that annually forms short shoots that contain an apex cyme consisting of four to six capitula and four to eight (usually six) alternate leaves. We regard these short shoots as integrated physiological units (IPUs). Three levels of defoliation treatments were applied to the IPUs: 100%, 50% and 0% (control). The results showed that in the primary capitula the male input (pollen production) decreased and the change of female function (pistil weight) was not statistically significant. In contrast, the secondary capitula exhibited a plastic shift toward maleness and stopped producing pistils but increased pollen production. Due to the inherent inflorescence structures and flowering time sequence of the cymes, the effects of defoliating different capitulum positions were diverse, and the secondary and tertiary capitula suffered greater effects than those in the primary position. Moreover, the effects of 100% defoliation were more significant than those of 50% defoliation. Furthermore, no new leaves were produced within the IPUs after defoliation, but the photosynthetic capacities of the remaining leaves were enhanced. The results of this study revealed that defoliation on IPUs had different impacts on the reproductive and vegetative traits, and caused a trade-off between male and female functions in *C. acuminata*. These findings indicated that defoliation on IPUs can help to explain sex allocation in the andromonoecious *C. acuminata*, and resource limitations further intensify intra-inflorescence sex allocation.

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## 1. Introduction

Plants can experience reductions in leaf biomass, some plants can produce new leaves or organs and others can enhance the photosynthetic abilities of the remaining parts to offset the loss or offset this loss by mobilizing stored resources from storage organs. These are called compensation effects (Lim and Turner, 1996; Retuerto et al., 2006; Cruz-Castillo et al., 2010; Barry and Pinkard, 2013). However, plant leaves are often unable to fully offset losses following damage through compensation, at least in the short term (Boege, 2005). Reductions in leaves decreases the amount of photosynthesis, which decrease resources available to the plants and affects reproductive performances of these plants (Steets et al., 2006; Narbona and Dirzo, 2010).

In individual plants, defoliation can affect male reproductive traits (Quesada et al., 1995), female reproductive traits or both, as well as flower-related traits. In most cases, defoliation directly affects male or

female reproductive output by affecting gamete production (Quesada et al., 1995; Mothershead and Marquis, 2000; Steets et al., 2006). The direct and indirect effects of defoliation on reproductive traits can have variable consequences for male and/or female fitness (Marquis, 1984; McCall, 2008; Penet et al., 2009). Ashman (2002) found that foliar herbivory often causes a plastic shift toward maleness not only in dioecious species, but also in species with closely related breeding systems such as monoecy and gynodioecy.

However, the studies of defoliation have mostly concentrated on monocots. In 1984, Watson and Casper defined an integrated physiological unit (IPU) as an identifiable array of morphological subunits that together function as relatively autonomous structures with respect to the assimilation, distribution and utilization of carbon. Young seedlings and many monocots may consist of a single IPU, whereas larger dicot plants become progressively more subdivided. Casper and Niesenbaum (1993) described that an IPU may include a branch with several inflorescences, they thought IPU essentially regroups flowers into units within which reallocation is possible, while exchange of nutrients between units does not occur. IPUs generally reflect the vascular architecture of the plant, in which carbon export is limited to plant parts connected to the same vascular strands (Watson and Casper, 1984). IPU is a

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semiautonomous plant sector over which assimilate is locally produced and translocated; thus an IPU may also encompass an inflorescence and all of its subtending leaves or only a portion of an inflorescence and a particular subset of the associated leaves.

*Camptotheca acuminata* Decne. belongs to the Nyssaceae family and is a perennial woody plant that is distributed along the Yangtze and Southwest provinces of China (Fang, 1983). Xu and Liu (2011) reported that the breeding system of *C. acuminata* involves out-crossing and is partly self-compatible and insect-assisted during pollination. Chen et al. (1991) observed that many types of insects, primarily bees, butterflies, flies and ants participate in the pollination activity. At the location of our study, *C. acuminata* comes into bloom at the end of June or early July. A *C. acuminata* inflorescence is generally composed of four to six capitula (Fig. 1A). Within the cymes of *C. acuminata*, the primary and secondary capitula are composed of hermaphrodite flowers in which each flower contains 10 stamens (five long stamens and five short stamens; Fig. 1B) and one pistil (Fig. 1C), while the tertiary capitula are composed of male flowers (Fig. 2A). The primary capitulum is located on the tip of the cyme, is the largest in diameter and has a higher fruiting rate. The secondary capitulum is located below the primary capitulum, is smaller in diameter and has a lower fruiting rate. The tertiary capitulum is located at the base of the cyme, is the smallest in diameter and is generally unfruitful. The primary capitula begin to blossom earliest, approximately one week before the secondary and tertiary capitula (Xu and Liu, 2011). *C. acuminata* is dichogamous, and the male and female functions occur in the same capitulum at different times (Wang et al., 2009). Usually all of the flowers of the same capitulum in the same level capitula bloom synchronously and exhibit protandry.

Xu and Liu (2011) removed the primary and/or secondary capitula to increase the available resources to research the sex allocation issues and initially confirmed that a strong correlation between resource allocation and sex allocation exists in the *C. acuminata*. Natural selection cannot cause an unlimited increase in some components of fitness without simultaneously causing a decrease in others, as long as these components share the same limited resource pool (Bona et al., 2015). If the male and female functions share the same limited resource budget when they are tied in the same unit, a larger resource allocation to, for example, the female function, will result in a smaller allocation to the male function and vice versa. In other words, sexual functions are linked by an intrinsic trade-off with strong effects on sexual selection in hermaphrodites (Anthes et al., 2010). The annually formed short shoots of *C. acuminata* contain an apex cyme and four to eight (usually six) alternate leaves and are photosynthetically independent units, which accord with condition of IPU. These new shoots were called IPU (Fig. 2B).

Male and female reproductive functions of *C. acuminata* share a common limited resource pool on an IPU. Artificial defoliation reduced the amount of the available resources and caused a new trade-off between male and female reproductive functions. In this paper, we researched resource and sex allocation within IPU through different levels of experimental defoliation to reduce the amount of the available resources. The aims of this study were to the following: (1) to determine whether defoliation affects the photosynthetic rate. (2) to determine whether defoliation affects reproductive traits and reproductive success and (3) to determine whether defoliation causes a trade-off between the male and female functions and further provides an experimental basis for resource allocation and gender evolution theory in the andromonoecious *C. acuminata*.

## 2. Materials and methods

### 2.1. Plant materials and study site

Seeds of *C. acuminata* were collected and dipped in water 24 h at 40 °C then embedded in wet sand at 27 °C in November, 2003. The seedlings at the 4-leaf stage were transplanted into flowerpots (Wang and Liu, 2005). Then, in March of 2004, uniform plants were transplanted to the botanical gardens of Northwest University (34°14'N, 108°55'E, 418 m H). The *C. acuminata* plants were grown under natural conditions in which the annual average temperature was 13.0–13.7 °C, the annual rainfall was 500–750 mm, and there were 1983–2267 h of light annually. By 2006, a small number of the *C. acuminata* plants began to blossom for the first time. In 2007, a much large number of *C. acuminata* fruited. The first flowering typically involved only one capitulum in the new shoots, and after two or three years, the secondary and tertiary capitula were gradually produced. When the number of capitula within a cyme became fixed, the state of reproductive physiology began to stabilize. Four to six capitula were most common, and this arrangement formed the main functional inflorescence. We artificially divided the functional inflorescences into three levels according to the capitulum locations (Fig. 2A).

### 2.2. Defoliation experiment

In early June 2012, the flowering dynamics of *C. acuminata* were preliminarily observed and recorded. And then 30 individual *C. acuminata* plants of similar size (6 m in height) with steady reproductive and physiological traits were marked with PVP plastic hanging cards. A total of 450 IPU were selected among the 30 plants, including 15 IPU per individual tree that included five-100%-defoliation, five-50%-defoliation,



Fig. 1. The cyme, stamens and pistil of *C. acuminata*. A. A cyme is composed of five capitula. Bar = 8 mm; B. Ten stamens contained in a floret of capitulum. Bar = 2 mm; C. The floret pistil in the capitulum after the stamens fell off. Bar = 2 mm.

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