A Note on the Structural Peculiarities of the Leaves of *Amentotaxus formosana* Li in Southern Taiwan

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Abstract. The relic endemic species, *Amentotaxus formosana* Li, was evaluated as having an endangered (EN) status in the *Red List of Vascular Plants of Taiwan*. Its populations have a limited geographic distribution in broadleaf forests at elevations of 800 to 1400 m in the southern Central Mountain Range of Taiwan. Genetic variations, genetic divergence, and DNA barcoding all pointed out that well-differentiated species need to be preserved, but scant evaluations have been conducted of the environmental impacts of its traits for conservation purposes. Our results are the first report on anatomical peculiarities of leaf traits of *A. formosana*, such as the leaf vascular cambium, transfusion tracheids, a thick outer cuticle layer on both sides of the epidermis, the actinocytic type of stoma complex with an arrangement of six to eight subsidiary cells, mostly two-cell distances among stomata, and no stomata being distributed in clusters. The leaf vascular cambium which is rarely found in gymnosperms produces secondary vascular tissues which are enclosed inside thick-walled bundle sheath cells with dense phenolic contents. Transfusion extensions with elongated sclerenchyma tangles provide auxiliary support from the midrib to the broad leaf blade. These peculiar transfusion extensions run from the bundle sheath or transfusion tissue in a sideways direction instead of up-and-down, perpendicular to the leaf surface, and differ from the bundle sheath extensions. It indicates important structural and functional roles for stretching out from the leaf vasculature. The occurrence of the leaf vascular cambium indicates long-lived functions in water supply and long-term photosynthate assemblages, a trade-off between a thick cuticle layer and dramatically large stomata areas of the leaf in this species for managing water loss in a foggy, humid environment accompanied by the impact of sudden drought by foehn winds in the sprouting season. All above should be considered when elucidating strategies from conservation perspectives.

Key words: leaf vascular cambium, transfusion tissue, transfusion extension, bundle sheath, stomatal complex.

INTRODUCTION

According to Tertiary fossil evidence, the *Amentotaxus* genus was widespread in the Northern Hemisphere before a range contraction that occurred during the Pleistocene and Holocene. The distributional range is currently restricted to the Himalayas, Taiwan, and Vietnam (Ferguson *et al*. 1978; Royer *et al*. 2003). *Amentotaxus formosana* H.L. Li ,

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endemic to Taiwan, is one of six relic species in this small genus (Gadek *et al*. 2000; Farjon 2001, 2010). Due to its narrow distribution and small population, the status of *A. formosana* was considered to be vulnerable (VU) in the *IUCN Red List* (Thomas 2013) and was regarded as endangered (EN) by a regional conservation assessment (Editorial Committee of the Red List of Taiwan Plants, 2017).

The divergence between *A. formosana* in Taiwan and *A. argotaenia* can be traced back 2.40 mya, a time period that approximates the coalescence of haplotypes resolved in *A. formosana*, suggesting that genetic divergence may have occurred following colonization on the island (Ge *et al*. 2014). Subsequent gene flow between populations of Taiwan and the Asian mainland during the Holocene was very restricted or is unlikely to have occurred. The vicariant event which formed the Taiwan Strait prevented gene flow between mainland and island populations. As no foreign alleles introgressed into the Taiwanese species, many ancestral polymorphisms were stochastically lost and replaced by newly mutated haplotypes, resulting in monophyly within *A. formosana* (Ge *et al*. 2014).

Low genetic variation in this particular species, *A. formosana*, but expected heterozygosity resulted from the younger tree category having a higher frequency of Pgi-la (0.125) than the older tree category (0.053) (Wang *et al*. 1996). Furthermore, limited geographic distributions of low-frequency alleles represent footprints of recent demographic expansion (Chiang *et al*. 2006, Liu *et al*. 2011). For this endangered species, ages of individuals vary from 14 to 126 years, and the average is 58 years; the diameter growth rate was reported to be 0.32 cm/year in competitive relationships among trees of the upperstory and understory (Lin *et al*. 2007). Studies on the embryology (Chen and Wang,1976) and ultrastructure of the pollen exine (Xi 1986) of certain *Amentotaxus* species were conducted for systematic significance, but few investigations have focused on long-term adaptations of vegetative growth.

Genetic variation (Wang *et al*. 1996), genetic divergence (Chiang *et al*. 2006), and DNA barcoding (Gao *et al*. 2016) all pointed out that well-differentiated species need to be preserved, but little evaluation of traits with environmental impacts for conservation purposes has been conducted. This paper aimed to explore certain microscopic leafy characteristics for further understanding of traits for conservation purposes.

MATERIALS AND METHODS

Occurrence data of *A. formosana* were collected from databases, including metadata of 118 specimens deposited in four herbaria, TAI, TAIF, HAST, and TNM, and 47 field observations with six habitats from two national biological resource inventory projects (National Vegetation Mapping in 2003~2008, and the Survey of Invasive Alien Plants in 2009~2012). Metadata of each specimen were georeferenced according to coordinates noted by the collector. Specimens with a collection locality but without coordinates were assigned by consulting archival place name databases or online maps. Finally, 96 occurrences with accurate GPS coordinates were compiled into a dataset to illustrate the geographical distributions of the target species using R 3.5.1 software.

This particular species is only distributed around the Chachayalaishan, Dawushan, and Sinsuiei to Lilongshan areas in southeastern Taiwan. Thirty leaf samples of *A. formosana* were investigated and collected. Parts of sampled leaves were processed by a clearing technique; a water bath was used to remove chlorophyll with hot alcohol for fresh material, followed by incubation in 4% NaOH in a 40 °C oven for several days until devoid of discoloration, then washing gently with distilled water, and staining with a 1% Sofranin O solution in 50% ethanol through an ethanol dehydration protocol. Other leaves were fixed in fixer with formalin: propionic acid: ethanol: glycerol: distilled water = 1:1:7:3:8 v/v, embedded in paraffin through tertiary-butanol dehydration, sectioned at a 10-μm thickness, and stained with 0.5% safranin O and 0.1% fast green through an ethanol dehydration protocol.

Micrographs of portions of the cleared leaves were taken with the Focus Stacking Automatic Microphotograph System, called TORI FOCUS, assembled and provided by the Taiwan Ocean Research Institute, National Applied Research Laboratories (Kaohsiung, Taiwan). Others were processed with a Zeiss Axioplan microscope (Zeiss, Germany) with the Axio Cam 105 color system.

RESULTS

Amentotaxus formosana is restricted to broadleaf forests in a foggy, humid environment on the western side of the upstream portion of Dawu Creek at elevations of 570~1585 m, with a mean of 1130 m, of the Hengchun Peninsula (Fig. 1). Most populations are located in a conservation area. According to historical climate data provided by the Taiwan Climate Change Projection and Information Platform Project (TCCIP) (Weng and Yang 2012), this species' habitat features an evident dry season (December to February) and an extreme wet season (May to October). The annual temperature difference ranges from 9.3 to 25.8 °C, and the mean annual precipitation was 2491 mm in the period of 1986~2005 (Fig. 2).

The linear-lanceolate, falcate leaves are spirally arranged on the shoots, but are twisted at the base and lie in two flat ranks. Leaves have a prominent midrib, and the revolute margins appear dark-greenish above and with two broad white stomatic bands beneath (Fig. 3). The stomatic bands are about twice as broad as the marginal bands and run from the blunt tip to the leaf base. Up to 32 stomata were found to lie along the transectional view of each stomatic band (Fig. 4A). However, no stomata were distributed in the midrib zone (Fig. 4).

Dominant sclerenchymatous transfusion extensions from the midrib toward the leaf margin comprise the strong beam architecture as an auxiliary supporting structure from the midrib
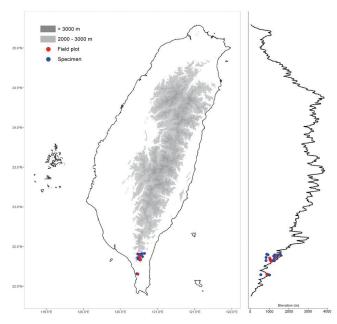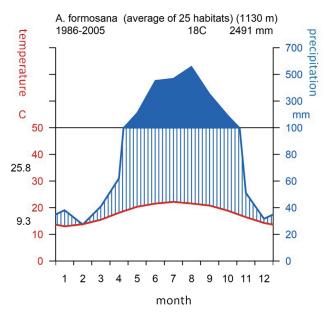

Fig. 2. Climatic diagram calculated by historical climate data (1986~2005) from the distributional range of *Amentotaxus formosana*..
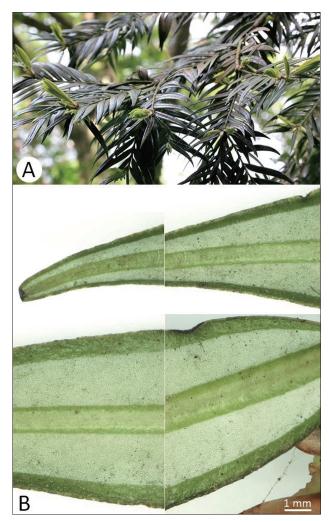

Fig. 3. Habitat and leaf abaxial surface of *Amentotaxus formosana*. A. Dark-greenish leaves with a prominent midrib and sprouting buds with light-green immature leaves. B. There are two broad, white stomatic bands beneath, about twice as broad as the marginal bands.

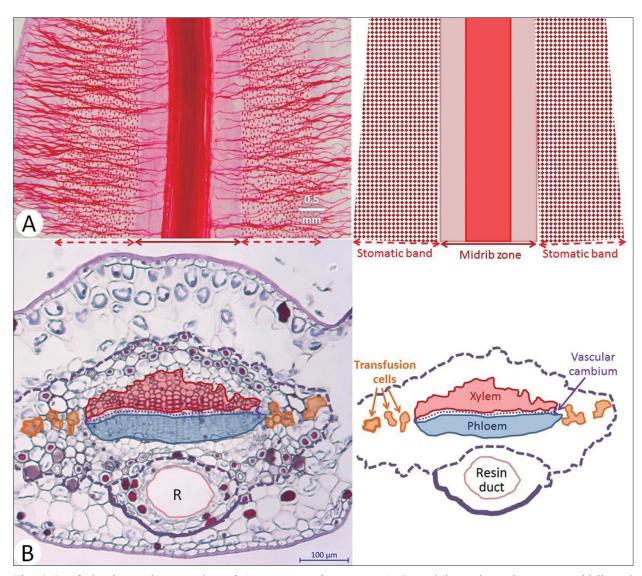Fig. 1. Distribution of *Amentotaxus formosana* in Taiwan.

Fig. 4. Leaf clearing and transection of *Amentotaxus formosana*. A. Remaining sclerenchymatous midrib and transfusion extensions after clearing. B. Transection of the midrib shows the distribution of the sclerenchyma (dashed-line) on the bundle sheath surrounding the vascular bundle, transfusion cells including tracheids with thick secondary walls, and the resin duct (R) beside the bundle sheath excluded/included (solid-line) in the bundle.

to the broad leaf blade (Fig. 4A). They radiate toward the leaf margin but differ from usual leaf bundle sheath extensions by expansion of both the adaxial and abaxial surfaces along the vein. One end of the elongated sclerenchymatous cells in the transfusion extensions invades in or reaches the leaf vasculature. These sclereids have spinous, curved, or bent ends which might be entangled in adjacent tissues to fix the architecture (Fig. 5A, B, F). In addition, these transfusion extensions are not only involved in bidirectional radial support between the leaf vein and mesophyll but also protrude into the palisade mesophyll (Fig. 5A, F) like the mezzanine floor of a penthouse. Lengths of the elongate sclereids in the transfusion extensions are equal to or less than the width between the midrib and leaf margin.

The vascular structure in the midrib includes primary and secondary tissues. Vascular cambium is rarely found in other gymnosperm leaves that produce thick-walled secondary xylem and aligned secondary phloem, and the primary xylem and primary phloem are exterior to the secondary xylem and secondary phloem (Fig. 4B). The extrusion of the protophloem which forms a dense line at the near side of resin ducts is conspicuously large and includes a ring of secretory cells surrounding the resin canal (Fig. 4B, labeled R). A bundle sheath, mingled with sclerenchyma and parenchyma cells, forms an intermittent boundary surrounding the vasculature (Fig. 4B, dashed line). It is broken through by transfusion tissues on both wing-sides of the vascular bundle. Transfusion tissue between

the bundle sheath and axial vascular elements includes the labeled transfusion tracheids located at both ends, toward the mesophylls, in an oblong transectional view of the vascular bundle (Fig. 4B). The intermittently distributed sclerenchyma of the bundle sheath has a very thick wall and contains dense phenolic contents aligned in a paraveinal direction (Figs. 4B, 5E). These bundle sheath cells are fibers with less lignification than the secondary xylem.

The epidermal cuticle is thickened the most at the outer peripheral walls, and the thickness declines toward the inside wall of the epidermis.

Each stoma complex contains two guard cells, a substomatal chamber, and six to eight subsidiary cells arranged in an actinocytic type (Fig. 5D). The guard cells are sometimes submerged below the epidermal layer at a similar level of the epidermis without emerging above the dermal surface (Fig. 5B, C). Furthermore, the stomata in stomatic bands are almost uniformly distributed at a distance of one to three epidermal cells, and most are separated by a two-cell distance (Fig. 5B-D). No pairs of guard cells were in contact with each other, and no stomata were found in a cluster.
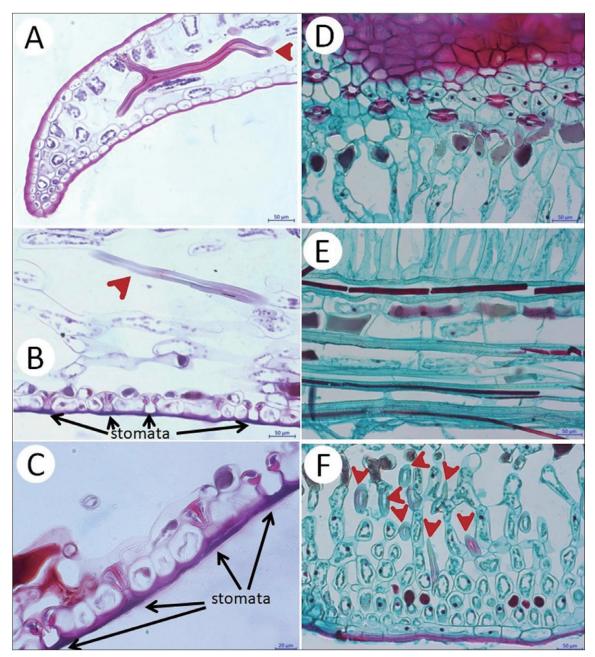

Fig. 5. Transections (A, B, C) and paradermal sections (D, E, F) of the leaf margin and blade showing transfusion extensions (red arrowheads) and stomata (black arrow). Sectional view of stomata (B, C) and top view of stomata and subsidiary cells (D).

DISCUSSION

All *Amentotaxus* species are currently listed as either nationally or globally threatened (Wang and Xie 2004; IUCN 2013, 2016, 2021) on the global *IUCN Red List*, including *A. formosana* with a vulnerable status (http://www.iucnredlist.org/search). Results of DNA barcoding indicated that a species complex of *A. formosana*, *A. argotaenia*, and *A. yunnanensis* could be well differentiated at a high level of universality by a polymerase chain reaction (PCR) and sequencing (Liu *et al.* 2011, Gao *et al.* 2016). This suggests that *A. formosana* is a distinct species corresponding to different individual lineages, rather than a species complex. Morphological characters, such as the width of the stomatal band, the color of the stomatal band, and the leaf shape and size, need to be recognized to indicate environmental suitability and conservation.

Our results are the first report on anatomical peculiarities of the leaf traits of *A. formosana*, such as the leaf vascular cambium, transfusion tracheids, thick outer cuticle layer on both sides of the epidermis, the actinocytic type of stoma complex with an arrangement of six to eight subsidiary cells, most distances among stomata being two-celled, and no stomata distributed in clusters. The epidermal traits indicate that the thick outer cuticle layer throughout almost the entire outer surface of the leaves prevents water loss in the mature stage. This suggests that the thick cuticular layer and dramatically large stomata areas of the leaf in this species manage water loss from an environment which is almost the most humid site in Taiwan. However, the impact of drought in the sprouting season could cause mass wilting of immature leaves without the well-developed thick cuticle and stomata. The foehn wind, a dry warm downwind-side, downhill wind like the chinook, can result in all sprouting buds and immature leaves wilting at once, as was observed in 2012. This resulted in a failure of reproductive development and also bad reproduction in subsequent years depending on the level of damage.

The vascular cambium is rarely found in leaves of gymnosperms, but *A. formosana* produces secondary vascular tissues which are enclosed inside thick-walled bundle sheath cells with dense phenolic contents. Needle leaves of *Pinus longaeva* remain alive on branches for more than 30 years and produce secondary phloem, but no secondary xylem. In needles of 10 other coniferous taxa, no secondary xylem is produced, but secondary phloem production occurs throughout the post-elongation lifespan of the needles regardless of the maximum needle longevity (Ewers 1982). The whole-leaf vascular volume does not significantly change with height in most trees (Oldham *et al.* 2010), but this might not be true in *A. formosana* due to the occurrence of the leaf vascular cambium which produces sustainable secondary xylem and phloem. It depends on when cambium activity is initiated and ceases, and how much secondary tissues are produced to display long-lived functions for an evergreen leaf in terms of water supply and long-term photosynthate assemblages. This is a trade-off for optimum growth and survival in limited and critical environments such as the Amentotaxus conservation area where it is almost always humid throughout the year, an important perspective for conservation.

The transfusion extensions with elongate sclerenchyma tangles provide auxiliary strength from the midrib to the broad leaf blade. These peculiar transfusion extensions extend from the bundle sheath or transfusion tissue in a sideways direction instead of up-and-down, perpendicular to leaf surface, and this differs from the bundle sheath extensions. This indicates that those transfusion extensions play important structural and functional roles by stretching out from the leaf vasculature.

The post-xylem pathway in pines begins in the transfusion tracheids and has to enter the bundle sheath via the inner tangential wall, since the radial walls are sealed by the suberized Casparian strips in the Pinaceae (Liesche *et al.* 2011). In *Cryptomeria japonica*, the transfusion tissue in leaves may have functions of water storage and supply, which could compensate for hydraulic constraints with increasing height (Azuma *et al.* 2015). Transfusion tracheids become deformed with height in *Sequoia sempervirens*, suggesting they may collapse under water stress and act as a hydraulic buffer that improves the leaf water status and reduces the likelihood of xylem dysfunction (Oldham *et al.* 2010). Obvious transfusion tracheids in the cross-sectional area of transfusion tissues act as in other gymnosperms for water storage and supply and for radial efficiency toward the leaf margin.

Thick-walled bundle sheath cells with dense phenolic contents and the transfusion extensions

with elongate sclerenchyma in *A. formosana* are other peculiarities in a gymnosperm leaf. Other than the leaf bundle sheath with Casparian strips in the Pinaceae, the thickened and lignified walls of bundle sheath cells in leaves of *Cycas revoluta* and *Gingko biloba* are attributed to the hydraulic isolation of vascular and photosynthetic tissues (Zwieniecki *et al*. 2007). A combination of parenchyma and thick-walled, fiber-like cells in an intermittent distribution surrounding transfusion tissues differs from conspicuous differentiated bundle sheaths with a uniform type of cells. This implies that an incomplete apoplasmic barrier for the transpiration stream results in inefficient drought resistance, but the intermittently distributed thick-walled bundle sheath allows both apoplasmic and symplastic hydraulic pathways for managing water resources.

The peculiar elongated sclereids of the transfusion extensions in *A. formosana* leaves across the blade of a gymnosperm broad leaf possibly function in both support and radial/sideways transport. These sclereids that stretch out from leaf vasculature indicate a close relationship in structure and function. Because they extend from the bundle sheath or transfusion tissue in a sideways direction instead of up-and-down, perpendicular to leaf surface, and differ from the bundle sheath extension, we called this structural peculiarity "transfusion extension". From the bundle sheath onwards it is not known to what extent the transpiration stream follows an apoplasmic, symplasmic, or transcellular route towards the sub-stomatal chambers. As an apoplasmic barrier for the transpiration stream, the bundle sheath might play an important role in drought resistance (Soar 1922) and frost tolerance (Kaku 1971; Roden *et al*. 2009). The occurrence of these peculiar transfusion extensions for supporting tissue and the xeromorphic tendency implies the existence of strong local adaptation.

In conclusion, this peculiar transfusion extension extends from the bundle sheath or transfusion tissue in a sideways direction instead of up-and-down, perpendicular to leaf surface, and differs from the bundle sheath extension, indicating important structural and functional roles for stretching out from the leaf vasculature. The occurrence of the leaf vascular cambium which produces sustainable secondary xylem and phloem indicates long-lived functions of water supply and long-term photosynthate assemblages in an evergreen leaf. A trade-off between a thick cuticle layer and dramatically large stomatal areas of the leaf in this species allows management of water loss from an intensive environment which is almost the most humid site in Taiwan. However, the impact of drought by foehn winds in the sprouting season can cause mass wilting of immature leaves without the well-developed thick cuticle and stomata. We must determine how to manage structural advantages and disadvantages to adapt to environmental impacts, which brings to mind elucidation of strategies and perspectives for conservation.

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南臺灣的臺灣穗花杉的構造特點簡記

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　　臺灣穗花杉（*Amentotaxus formosana* Li）為臺灣維管束植物紅皮書評估為瀕危（endangered, EN）的特有物種，地理分布侷限臺灣中央山脈南部海拔800至1400公尺的闊葉林內。遺傳變異、遺傳差異和DNA條碼都指出此分化完全的物種需要保護，但很少對保護區環境壓縮的特性進行評估。我們的研究結果是關於臺灣穗花杉葉性狀解剖學特徵的首次報導：葉維管束形成層，轉輸管胞組織，表皮上下側的外角質層較厚，氣孔複合體（或稱氣孔器）具有 6 至 8 個副細胞的放射型排列，大多數氣孔之間是2個表皮細胞間距，以及氣孔無成簇分佈的現象。極少在裸子植物中可發現，葉具有維管束形成層且產生次生維管束組織，此被具有高濃含量酚類的厚壁束鞘細胞所圍住。轉輸組織延伸具有細長的厚壁組織纏結，作為從中脈到寬的葉身的支撐輔助力量。這種特殊的轉輸組織延伸從束鞘或轉輸組織，以側向、而不是上下垂直於葉面的方向延伸，與束鞘延伸組織不同，顯示從葉脈維管束系統伸展出在結構和功能中扮演重要的作用。葉片維管形成層的出現在供水和長期光合作用合成中具有長壽命、長效功能，在該物種厚厚的角質層和葉片大面積的氣孔帶之間進行權衡，藉以管理欠缺敏感環境中的水分流失，以及發芽季節時焚風的影響，以上結果可能會激發保育策略的新觀點。

關鍵詞：葉維管束形成層、轉輸組織、轉輸組織延伸、維管束鞘、氣孔器