Ecological Informatics 19 (2014) 47–52

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

# Leaf reddening of sweet gum in water imbalance☆

Fei Wang [a,]*, Haruhiko Yamamoto [b], Xiaoming Li [c], Jiquan Zhang [d]

[a] *Shandong Forestry Research Academy, Jinan 250014, China*
[b] *Agricultural Faculty, Yamaguchi University, Japan*
[c] *Shandong University, Jinan, China*
[d] *Northeast Normal University of China, Changchun, Jilin, China*

ARTICLE INFO

*Article history:*
Received 30 April 2013
Accepted 15 December 2013
Available online 19 December 2013

*Keywords:*
Sweet gum
Leaf reddening
Water imbalance
Transpiration-cooling failure
Leaf temperature
Petiole snapping strength

ABSTRACT

The ornamental value of many trees is often based on their special colour, shape and structures. Its autumn leaf colour makes sweet gum (*Liquidambar styraciflua* L.) a favourable ornamental tree species for landscape beautification and urban greening. In addition to specific genetic control, to some extent, environment plays an important role in sweet gum colour changes. In this study, leaf-reddening events in the individual leaves and crowns of sweet gum trees were studied by analysing the ecology of sweet gum trees planted on a gradient of soil types, by comparing pruned and unpruned trees, by severing certain leaf veins and by measuring the snapping strength of the petiole. High-temperature areas on the severed leaves were detected using thermography. Low stomatal conductance and high leaf temperature rapidly appeared at the stressed area in severed lobes because of water stress and a related transpiration-cooling failure, especially in direct sunshine or on dry, hot summer days. The consistent relationship between the reddened and high-temperature areas indicates that a persistent transpiration-cooling failure resulted in local-area reddening on sweet gum leaves and the formation of a protective layer with high anthocyanin content. A significant relation between the snapping strength of the petiole and leaf reddening suggests that a persistent water imbalance during the formation of the abscission zone accelerates the sweet gum leaf reddening. Namely, a persistent transpiration-cooling failure during the defoliation process induces protective responses of the leaf. The rapid water loss of sweet gum juvenile leaves indicates that the reddening of the leaves may be a sensitive response to the changing properties of the leaf cuticle.

## 1. Introduction

Many tree species possess ornamental value because of their particular colour of leaves, flowers and/or other organs at certain developmental stages. The juvenile leaf on the twig tip and the mature leaf before shedding often show red or purplish-red colours (Feild et al., 2001). The red autumn leaves of most tree species are caused by the synthesis of a large quantity of anthocyanins in the epidermal and/or palisade leaf layers. It is still unclear why anthocyanins are synthesised in autumn just before the leaf falls. This synthesis has been considered a warning colour in the context of co-evolutionary interaction with insects (Archetti, 2000), a by-product of physiological function (Matile, 2000) or a means of eliminating toxins (Ford, 1986), among others. Leaf reddening has also been widely recognised as an environmentally driven, species adaptative mechanism with such functions as photoprotection (Feild et al., 2001; Gould et al., 1995; Hughes et al., 2007), protection from low-temperature stress (Close et al., 2002; Pietrini and Massacci, 1998) and osmotic regulation (Chalker-Scott, 1999, 2002). Although the autumn leaf colour of many tree species was considered the result of photoperiod (Howe et al., 1995) or nutrition-induced metabolic change, the leaf colour change of certain tree species was found to be sensitive to water imbalance during growth. For example, under the influence of the east Asian monsoon climate, leaves of the sweet gum tree (*Liquidambar styraciflua* L.) do not redden every year in Japan (Wang et al., 2009b), especially in years with plentiful rainfall and reduced light irradiation. During the present study, we found that persistent transpiration-cooling failure and water stress induced by leaf severing, coarse sandy soil, overgrowth and the shedding process can trigger leaf reddening of sweet gum trees. Therefore, water stress and transpiration-cooling failure may be the major triggers of leaf reddening in sweet gum.

## 2. Materials and methods

The studied sweet gum trees are street trees planted along an arch-like street near a previous riverbed in Yamaguchi, Japan. As indicated in Fig. 1a, the right side of the area has fine gley soil, the left side has coarse lowland soil, and the curve lies at the transition between the two soil types. In all, 86 eight-year-old plants were studied by analysing photographic images of the trees. The photographs were taken on the ground

---

☆ Supported by the National Natural Science Funds of China, ID number 31170671 and the Project of Science and Technology Development in Shandong, China; ID number 2012GNC11107.

* Corresponding author. Tel.: +86 531 88557594; fax: +86 531 88932824.
*E-mail address:* wf-126@126.com (F. Wang).

1574-9541/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.ecoinf.2013.12.008

**Fig. 1.** Sweet gum trees along an arch-like street in Ogoriheiseimachi, Yamaguchi, Japan. Crown coloration response of the trees to a gradient of soil conditions from normal to sandy. On the minimised map in the upper left corner, the red line (1) represents the arch-like street, and the grey area (2) is the Fushino River.

from the southern side with a Canon CCD camera (IXY 6.0) on a cloudy day in the middle of Oct. 2009, and then the images were analysed with the RGB colour system in Photoshop software (Wang et al., 2009a). The same methodology was used to compare sweet gum trees pruned in the previous year with unpruned trees lying along opposite sides of a highway. The green (G) and luminance (L) values were directly read from the RGB colour system in Photoshop, and the G/L ratio was calculated to analyse the colour status of the images (Wang et al., 2008, 2009a). Camellia (*Camellia sasanqua* Thunb.) ground shrubs were also studied using this type of digital image analysis.

To study the water stress at localised areas on the leaf, special experiment was designed to sever the leaf veins. During the study after Jun 2009, more than 30 typical palmate sweet gum leaves with five lobes were selected on the sunny side of several crowns, and the major veins of the top three lobes were severed at their bases. Using the degree of stress, each treated leaf was divided into three areas: unsevered (N), transitional (T) and stressed areas (S) (Wang and Yamamoto, 2010), where the leaf colour, temperature, stomatal conductance and water content of the leaves were measured.

Thermography has been increasingly used in the study of stressed plants and trees (Chaerle and Van Der Straeten, 2000; Grant et al., 2006; Jones, 1999; Jones et al., 2002; Jones and Leinonen, 2003), and this technology was used in the present study as well. Thermal images of the severed leaves were taken with a NEC TH7100 thermal infrared (8–14 μm) camera (NEC company, Tokyo, Japan), with the temperature ranging from −20 to 100 °C and a minimum sensible temperature of 0.06 °C. The camera was handheld approximately 50 cm above the objective leaves and focused to a clear image. An active heat method under the direct sunshine in the field was used for the thermal image temperature measurement and the thermal images were taken from 9:00 to 12:00 a.m. Smoothly expanded leaves were selected to first take a thermal image, and then single thermal infrared images were continually taken after the major leaf veins were severed. The RGB images of the leaves from the thermography were extracted by using the lasso tool in Photoshop.

The leaf stomatal conductance was measured on different parts of the same leaf with a Decagon Sc-1 leaf porometer on a clear day in the natural field environment. The conductance measurements were performed with the sensor clip fixed on half lobes using the automatic measurement setting. Ten duplications were completed for each sample ($n = 10$).

The relative water content (WC) of leaf half lobes was measured using a rapid weighing method in a room equipped with an electronic balance (Shimadzu Auw220, 1/10,000 g). The water loss of sweet gum leaves was measured under room conditions (53–58% RH and 20–25 °C) by weighing leaf pieces at the beginning and end of a timed interval. The water loss of branches was measured by the same method in a circulating-air oven at 75 °C.

The vigour of the sweet gum trees was estimated by measuring their trunk diameters at breast height (DBH) with a tape measure and referencing the concentration of their crowns based on the Waring theory for estimating tree vigour (Blanche et al., 1985; McCullough and Wagner, 1987).

The leaves on the same tree were classified as purple, red, yellow or green, and each group of 20 samples was selected randomly. Their snapping strength was measured using a QIE strength metre with an accuracy of 0.1 kg. To measure the target leaves, each was held with the left hand, the metre was hooked onto the base of the leaf petiole, and the petiole was pulled until it broke from the petiole base or snapped into two sections. The instant force shown on the metre was considered the snapping strength of the leaf.

The leaf anthocyanin content was extracted with methanol containing 1% hydrochloric acid over a 24-hour period and measured by optical density (OD) readings at 525 nm with an ultraviolet and visible spectrometer (UV-2102). Then, the ratio of anthocyanin to chlorophyll was estimated by the ratio of the optical density at 525 nm to that at 645 nm (Rac 525/645).

The data were statistically analysed using Kaleidagraph 4.0 and Excel 2003.

## 3. Results and analysis

### 3.1. Leaf reddening under different site conditions and vigour states

In modern cities, the planting of trees with coloured leaves in an asymmetric design and of different tree species along the same street is common. Fig. 1 shows an Oct. image of sweet gum trees planted in an asymmetric design along a gradient of site conditions in Yamaguchi, Japan, and the geographic position of the trees (Fig. 1 insets 1 and 2). From Fig. 2a, the G/L values of the crowns of the sweet gum trees were larger on the right side, smaller on the left side and intermediate at the curve area in the street, and these differences were statistically significant ($F = 39.9$ and $P < 0.01$). The smaller G/L values indicated more red leaves on the trees to the left, the larger values indicated more green leaves on the trees to the right (Fig. 1a), and the middle values represented the transitional situation at the curve area in the street. Therefore, the dissimilar crown coloration of the trees on the left and right sides of the curve was due to the different frequencies of the red and green leaves on the two sides of the arch-like street.

From Fig. 2b, a statistically significant difference in the DBH of the sweet gum trees among the left, right and curved areas along the arch-like street can also be seen ($F = 46.0$ and $P < 0.01$). This difference indicates that larger trees have greener leaves (Fig. 2b) and that leaf coloration is related to the vigour of the trees. There was also a statistically significant difference in the vigour of the camellia hedge under the sweet gum crown between the left and right sides of the arch-like street (Fig. 2d). With a denser crown coverage, larger leaf area and longer stems, the camellia shrubs on the right side appeared more vigorous and deeper green in leaf colour than those on the left side. This pattern demonstrates that the site conditions at the left linear portion of the arch-like street are indeed poorer than at the right linear portion. On the left side with the coarse sandy soil, the sweet gum trees suffered more severe stresses and showed red or purplish-red colours early.

The autumn leaf colour of the sweet gum trees varied with their vigour because of the influence of different environmental stresses.