



RESEARCH PAPER

# Vascular tissue in the stem and roots of woody plants can conduct light

Qiang Sun<sup>1,4</sup>, Kiyotsugu Yoda<sup>1,2</sup>, Mitsuo Suzuki<sup>1,3</sup> and Hitoshi Suzuki<sup>1,2</sup>

<sup>1</sup> Photodynamics Research Center, The Institute of Physical and Chemical Research (RIKEN), Sendai 980-0845, Japan

<sup>2</sup> Faculty of Science and Engineering, Ishinomaki-Senshu University, Ishinomaki 986-8580, Japan

<sup>3</sup> School of Life Science, Tohoku University, Sendai 980-0862, Japan

Received 1 July 2002; Accepted 20 December 2002

## Abstract

The role of vascular tissue in conducting light was analysed in 21 species of woody plants. Vessels, fibres (both xylem and phloem fibres) and tracheids in woody plants are shown to conduct light efficiently along the axial direction of both stems and roots, via their lumina (vessels) or cell walls (fibres and tracheids). Other components, such as sieve tubes and parenchyma cells, are not efficient axial light conductors. Investigation of the spectral properties of the conducted light indicated that far-red light was conducted most efficiently by vascular tissue. Light gradients in the axial direction were also investigated and revealed that conducted light leaked out of the light-conducting structures to the surrounding living tissues. These properties of the conducted light suggest a close relationship with metabolic activities mediated by phytochromes. The results therefore indicate not only that signals from the external light environment can enter the interior of stems above ground and are conducted by vascular tissue towards roots under ground, but also that the light conducted probably contributes directly to photomorphogenic activities within them.

Key words: Far-red light, gymnosperms, light conduction, optical properties of stem and root tissues, photomorphogenesis, phytochromes, vascular tissue, woody dicotyledons.

## Introduction

Light is one of the most important environmental factors exerting great influences on the growth and development

of plants via photosynthesis and photomorphogenesis. In this sense, plants are dependent on their light environment. However, plants themselves modify the light entering their interior to produce an internal light environment very different from that outside (for reviews, see Walter-Shea and Norman, 1991; Vogelmann, 1993). Because this internal light environment, as modified by plant tissues, is directly tuned to the light-related metabolic activities of the plant, knowledge of the optical properties of plant tissues is essential to understand the relationship between the internal light environment and the light-regulated metabolic activities inside plants.

The optical properties of plant tissues have so far been investigated mostly in the leaf and the seedling, because of their importance in photosynthesis and/or photomorphogenesis (for review see Vogelmann, 1994). The structures investigated have focused on leaf epidermis (Bone *et al.*, 1985; Vogelmann *et al.*, 1996) and structural modifications of its surface (Ehleringer *et al.*, 1976; Reicosky and Hanover, 1978), palisade parenchyma (Fukshansky *et al.*, 1991; Vogelmann and Han, 2000), spongy parenchyma (Terashima and Saeki, 1983; Fukshansky and Martinez, 1992), and foliar sclereids (Karabourniotis, 1998); and etiolated seedling tissues, such as those of cotyledons (Seyfried and Schäfer, 1983), mesocotyls (Kunzelmann and Schäfer, 1985) and coleoptiles (Parks and Poff, 1986; Kunzelmann *et al.*, 1988). These tissues or cells are known to contribute in different ways to the formation of the internal light environment by modifying the incident light from its original quality (Kazarinova-Fukshansky *et al.*, 1985; McClendon and Fukshansky, 1990; Turunen *et al.*, 1999), quantity (Parks and Poff, 1986; Piening and Poff, 1988; Cui *et al.*, 1991) and direction of conduction (Mandoli and Briggs, 1982*a, b*; Iino, 1990; Myers *et al.*,

<sup>4</sup> To whom correspondence should be addressed. Fax: +81 22 228 2164. E-mail: qiangsun@postman.riken.go.jp

1994). All these investigations are expanding an understanding of (i) the roles of plant tissues in dealing with the surrounding light environment, (ii) the characteristics of the modified internal light environment and (iii) the possible physiological significance of the internal light environment.

Vascular plants are composed of dermal, ground and vascular tissue systems (Esau, 1977). The tissues and cells investigated so far for their optical properties belong to the dermal and ground systems and have been restricted to those of the leaf and the seedling. Vascular tissue is present in the largest quantity in the stem and root of woody plants, as xylem and phloem, and is known mostly for its functions of transporting water and nutrients within the plant and providing mechanical support. There has been some research on 'bark and stem photosynthesis', but reference to the light environment inside the woody stems dealt mainly with that directly beneath the periderm or epidermis, where chlorenchyma are abundantly present (Pfan, 1999; Pfan and Aschan, 2001), not with that of the main vascular tissue. In the investigations of the optical properties of the leaf, and of the stem and root of seedlings, the possible influence of vascular tissue on the internal light environment has always been neglected, probably because of the relatively small volume that they occupy. Therefore, the optical properties of vascular tissue and the internal light environment of woody stems and roots have yet to be characterized. In the present study, the stems and roots of woody seed plants have been investigated, focusing on the relationship of the optical properties of their vascular tissue to the conduction of light inside them. The aim was to clarify (i) the involvement of vascular tissue in light conduction along the axial direction of stems and roots, and (ii) the influence of vascular tissue on the intensity and spectral properties of the conducted light.

## Materials and methods

### *Species investigated and preparation of plant materials*

Twenty-one species of woody plants were used in the present investigation, chosen from different phylogenetic groups and representing a wide variety of structural characters of seed plants. There were six gymnosperms (*Ginkgo biloba* L., *Pinus densiflora* Siebold et Zucc., *Cryptomeria japonica* (L. F.) D. Don, *Abies firma* Siebold et Zucc., *Chamaecyparis obtusa* (Siebold et Zucc.) Endl. and *Metasequoia glyptostroboides* Hu et W.C. Cheng) and 15 woody dicotyledons, including 11 species with diffuse-porous xylem (vessels are diffuse and relatively uniform in transverse section)—*Acer sieboldianum* Blume, *Pourthiaea villosa* (Thunb.) Decne., *Fagus japonica* Maxim., *Aucuba japonica* Thunb., *Ilex serrata* Thunb., *Sapium japonicum* (Siebold et Zucc.) Pax et K. Hoffm., *Rhododendron obtusum* Planch., *Photinia glabra* × *P. serratifolia*, *Salix triandra* L. subsp. *nipponica* (Franch. et Sav.) A. K. Skvortsov, *Aesculus turbinata* Blume, and *Camellia japonica* L. var. *hortensis*) and four species with ring-porous xylem (large vessels are close to growth ring boundaries and small ones elsewhere)—*Zelkova serrata* (Thunb.) Makino, *Quercus crispula* Blume, *Akebia trifoliata* (Thunb.) Koidz., and *Wisteria floribunda* Willd. They were collected

freshly from woodlands near the laboratory in the summer and autumn of 2001 and 2002. Stem, root and stem–root transition zones (containing both lower stem and upper root) were investigated: three stem lengths for each species, two stem–root transition lengths for 12 species and two root lengths for six species. Each length was 20 cm long by 0.5–3.0 cm in diameter. A smooth transverse surface was made at the lower cut end with a sharp razor blade. Trimming and subsequent measurements were performed rapidly to obviate any effects of desiccation. After all the measurements, there was routine tissue sectioning of the materials investigated to identify the cell types involved in light conduction.

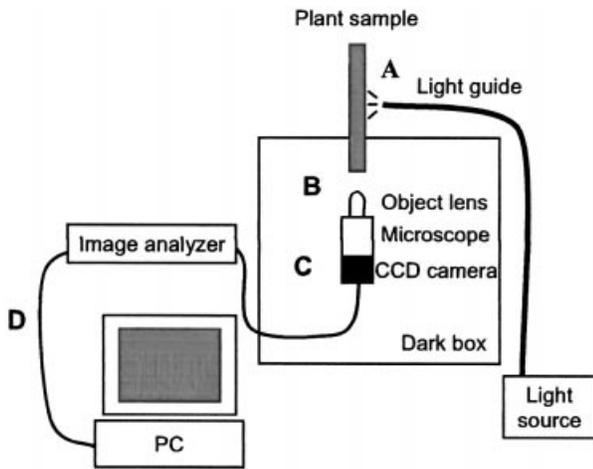
### *Experimental apparatus and measurements of optical properties of vascular tissue*

The apparatus for detecting light conduction in plant tissues is illustrated in Fig. 1. A length of stem, root, or stem–root transition zone with the transversely cut lower end downwards, was inserted into a box through a hole in the top and sealed with black gum to exclude extraneous light. The light source was a microscope halogen lamp, which unilaterally illuminated the protruding stump, via a light guide at a site 2–4 cm from the lower cut end. Illumination was performed at incident angles of 30° (oblique), 60° (oblique) and 90° (horizontal) with the axis of the stem or root. The image of the conducted light at the surface of the lower cut end was observed using a microscope attached to a far-red light-sensitive CCD camera (Wat-902H, Watec Corp., Japan). Video signals were fed into an image processing system (Argus-20 and Aquacosmos version 1.10, Hamamatsu Photonics K. K., Japan), which was used to clarify the differences in the efficiency of light conduction of the different cell types within the vascular tissue.

To evaluate the effect of vascular tissue on the quantitative and qualitative characteristics of the conducted light, the intensity gradients and spectra of the light transmitted through the stem or root lengths were measured with the same apparatus under the horizontal (90°) and oblique (30° and 60°) illuminations, respectively. Light intensity gradients were measured in units of  $W\ m^{-2}$  by fixing a light meter (LI-250, Li-Cor Inc., USA) directly under the cut end in place of the microscope lens and by adjusting the distance of the illumination site with respect to the cut end at intervals of 0.5 cm or 1.0 cm. The spectral properties of the transmitted light were investigated in the same way, by replacing the light meter with a photonic multi-channel analyser (PMA-11, Hamamatsu). In addition to the horizontal and oblique illuminations, axial illumination through a 15 mm long length was also made in the investigation of the spectral properties. Spectra of both the transmitted and incident light were measured and their ratio was calculated to analyse the transmission efficiency of the vascular tissue across the spectral region investigated during axial conduction. The spectrum of transmitted light was also measured using the horizontal, oblique (30° and 60°) and axial illumination with monochromatic incident light, from 410–880 nm at intervals of 10–20 nm, which was obtained, respectively, by inserting a series of narrow band pass interference filters (8–12 nm half band-width) between the light guide and the sample. The intensity of all monochromatic incident light was kept close using neutral density filters. The spectrum of the light transmitted from the 15 mm long length of the stem or root was also measured under sunlight, in order to verify the spectral properties of the light conducted in the stem and root in a natural light environment.

## Results

Vascular tissue in all the species investigated conducted light axially along both stem (Fig. 2A–C, H) and root



**Fig. 1.** Schematic drawing of the experimental apparatus. The light source illuminates a stem or root length through a light guide at a certain angle (A). Light conducted by the plant tissue reaches the surface of its cut end (B). Light transmitted from the cut surface is magnified by a microscope and recorded with a CCD camera (C). The acquired images are analysed with the aid of a personal computer (D).

(Fig. 3A, C), not only in the internodes but also through the nodes. Different cell types varied in their efficiency of axial light conduction (Figs 2, 3).

Vessel elements, tracheids, fibres, sieve tube elements, sieve cells, and parenchyma cells are the major components of vascular tissue. Vessel elements, the major cell type in xylem, are linked together axially by their dissolved end walls to form long continuous tubes: the vessels (Fahn, 1990). Despite the different patterns of vessel arrangement in the diffuse-porous and ring-porous xylem of the dicotyledons investigated, efficient light conduction axially along the vessels was observed in both groups (Fig. 2B, C). Light transmitted through vessels passed predominantly via the lumina, rather than via the walls, in both stems (Fig. 2D–F) and roots (Fig. 3A, B). The intensity of the transmitted light in the lumen generally showed no obvious difference, whatever the diameter of the vessel (Fig. 2B, C).

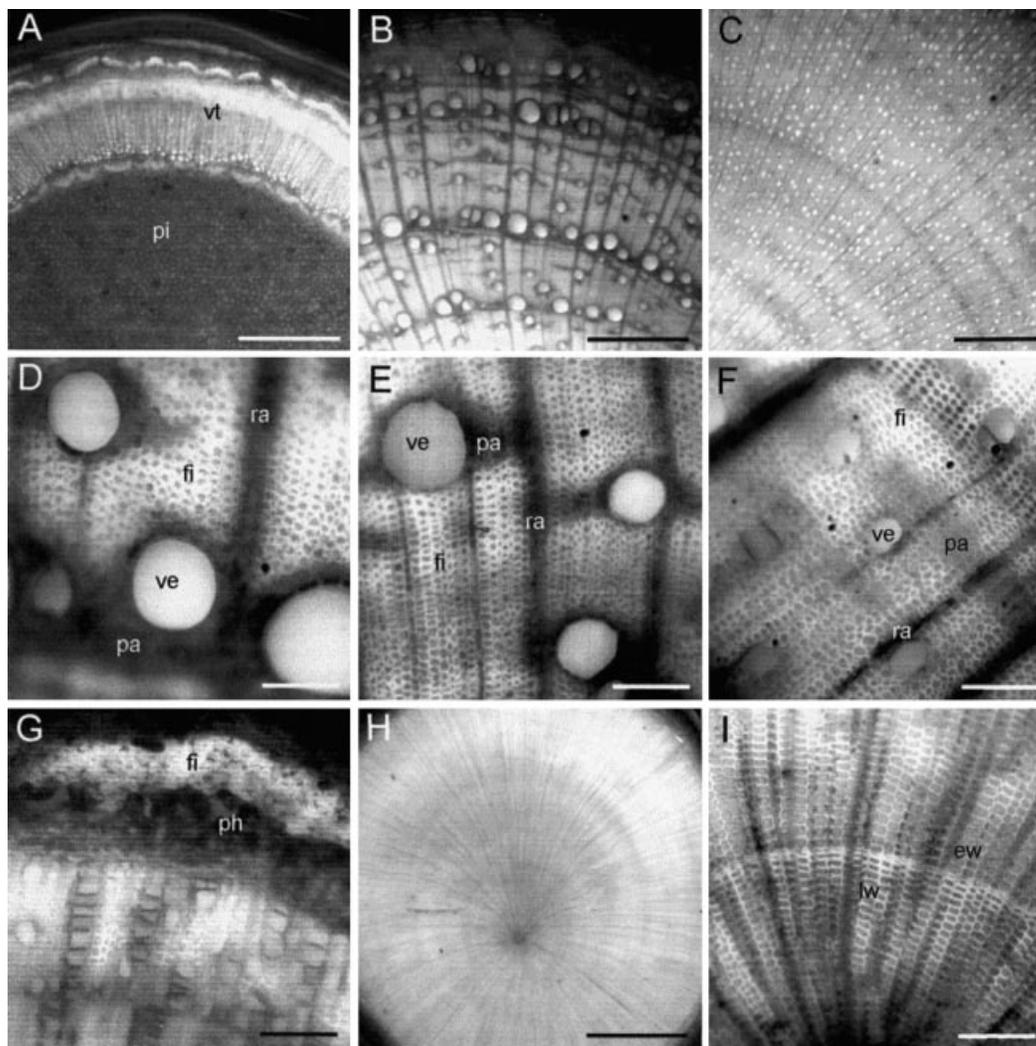
Fibres are axially-elongated thick-walled cells, forming the bulk of the vascular tissue of stems and roots of woody dicotyledons, especially in the xylem. Light conduction in both stem and root was clearly observed in both xylem fibres (Figs 2D–F, 3B) and phloem fibres (Fig. 2G), but predominantly via their thick walls as opposed to the lumina. The light conducted by phloem fibres was generally much brighter than that in xylem fibres, especially in young stems of the species investigated. In addition, the light-conducting efficiency of xylem fibres was dependent on the season of their formation in most cases: those formed in summer and autumn were thicker-walled and shone more brightly than those formed in spring.

Tracheids, the main cells in the xylem of gymnosperms, are also axially-elongated and usually thick-walled. Their light-conducting properties were found to be similar to those of the fibres of woody dicotyledons. In all six gymnosperms investigated, light was conducted most efficiently within the tracheid walls, and tracheid lumina did not conduct light efficiently in either stem (Fig. 2H, I) or root (Fig. 3C, D). Tracheids, too, generally showed a season-dependent capacity for light conduction, especially in stems: much more efficient light conduction occurred in the thicker-walled tracheids formed in summer and autumn than those formed in spring (Figs 2I, 3D).

In *Pinus densiflora*, efficient light conduction was also observed in the lumen of the resin canals in the vascular tissue of its stems and roots.

Parenchyma cells in the etiolated seedlings of some herbaceous species are known to function in the axial conduction of light (Mandoli and Briggs, 1982a, b, 1984a, b). In the vascular tissue of woody species, parenchyma cells include those in phloem, and the ray cells and axial parenchyma cells in xylem (Fahn, 1990). In the present study, parenchyma cells conducted light much less efficiently along the axial direction of both stems and roots (Figs 2D–F, 3B), compared with vessels and fibres. Other cell types classified as vascular tissue, such as sieve tube elements and companion cells, did not conduct light efficiently in either stems or roots (Fig. 2G).

Light intensity is a key parameter of the light environment within plant tissues. However, the exact measurement of light intensity at any particular location inside plant tissues has not yet been possible (Vogelmann *et al.*, 1991; Karabourniotis, 1998). By measuring the intensities of light transmitted axially by stems and roots, it has proved possible to evaluate the effect of vascular tissue on the intensity of the conducted light. In the species investigated, light was attenuated during its axial conduction along stems and roots whatever the angle of the illumination. There was a negative linear relationship between the logarithmic value of light intensity and the distance of conduction (Fig. 4). The slopes of the regression lines varied from  $-1.2$  to  $-0.8$  in the stems (Fig. 4A) and roots (Fig. 4B) of the species investigated. This pattern of attenuation demonstrates that vascular tissue is neither an efficient light guide, in which the intensity of light should change little during conduction, nor a complete scatterer of light, in which the attenuation of light should conform to Rayleigh scattering and occur to a much greater extent. This pattern of light attenuation indicates that vascular tissue in both stems and roots is best considered as a leaky light guide. Light leaks out of the light-conducting structures (i.e. vessels, fibres and tracheids) to the surrounding tissues, even reaching the outside of stems or roots, as it is conducted axially. Despite the same pattern of attenuation, it was found that more light



**Fig. 2.** Examples of images of light transmitted from the transverse end of stem vascular tissue under the horizontal illumination (incident angle at  $90^\circ$  to the stem axis). (A) More efficient axial light conduction in vascular tissue (vt) than in pith (pi) in one-year-old stem of *Aesculus turbinata*. (B) Light conduction in ring-porous xylem of *Wisteria floribunda*. (C) Light conduction in diffuse-porous xylem of *Salix triandra* subsp. *nipponica*. (D) Spring-formed xylem tissues in *W. floribunda*, showing efficient light-conducting fibres (fi) and vessels (ve), inefficient light-conducting rays (ra) and axial parenchyma (pa), and involvement of vessel lumina and fibre walls in light conduction. (E) More efficient light conduction in vessels (ve) and fibres (fi) than in rays (ra) or axial parenchyma (pa) in summer- and autumn-formed xylem tissues of *W. floribunda*. (F) Light conduction in diffuse-porous xylem of *Acer sieboldianum*, showing more efficient light conduction in fibres (fi) and vessels (ve) than in rays (ra) and axial parenchyma (pa). (G) Most efficient light conduction in phloem fibres (fi) in phloem (ph) of *Aesculus turbinata*. (H) Light conduction in stem of *Chamaecyparis obtusa*, a gymnosperm species. (I) Light conduction via tracheid walls in xylem of *C. obtusa*, showing more efficient light conduction in tracheids formed in summer (lw) than in those formed in spring (ew). Scale bars: 1 mm in (A), (B) and (H); 300  $\mu\text{m}$  in (C); and 100  $\mu\text{m}$  in (D–G) and (I).

was conducted in the stems and roots when the incident light was introduced at an angle more parallel to the axis.

The spectral properties of light have a direct influence on the light-related physiological activities of plants. To clarify the spectral properties of vascular tissue, the ratio of transmitted light (Fig. 5B) to incident light (Fig. 5A) at each wavelength was obtained in order to express the conducting efficiency of vascular tissue across the spectrum (Fig. 5D–I). In the spectral range investigated (192–952 nm), it was found that there were few obvious differences in the spectral properties of vascular tissue in

different parts of the stems or roots of the same species, among different species, and whatever the angle of illumination. The far-red and near infra-red region (beyond 720 nm) was always the most efficiently conducted region in both stems (Fig. 5D, F, H) and roots (Fig. 5E, G, I) of the species investigated. Relatively, light in the visible and ultraviolet regions was poorly conducted by vascular tissue despite the higher transmission efficiency in the ultraviolet region than in the visible region. However, solar radiation contains little ultraviolet light compared with the visible light, and also has a rapid intensity decrease beyond the red

and far-red regions. Experiments with sunlight as incident light verified that the spectral region, usually from 720–910 nm, was the predominant region conducted in the vascular tissue of the stems and roots (Fig. 5C).

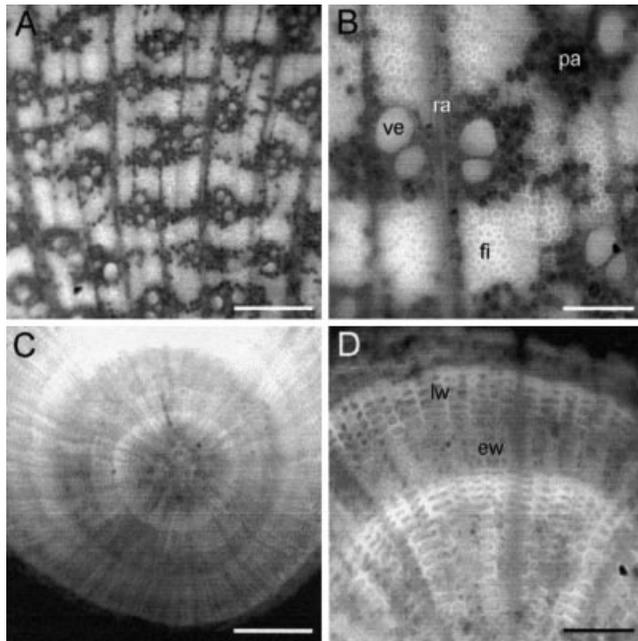
To verify that the far-red and near infra-red spectral properties of the conducted light are not derived from some

fluorescent effect of plant tissues, a selection of monochromatic light sources from 410–880 nm, at intervals of 10–20 nm, were used as the incident light, and the spectral properties of the light transmitted by samples of stems and roots were compared. It was found that far-red light and near infra-red light were detected in the transmitted light from the lower cut end of stems or roots only when they were included in the incident light source (Fig. 6A): no transmitted light was detected with incident monochromatic light outside this range (Fig. 6B, C). This result verifies that the far-red light and near infra-red light conducted in the vascular tissue of stems and roots comes from the surrounding solar radiation.

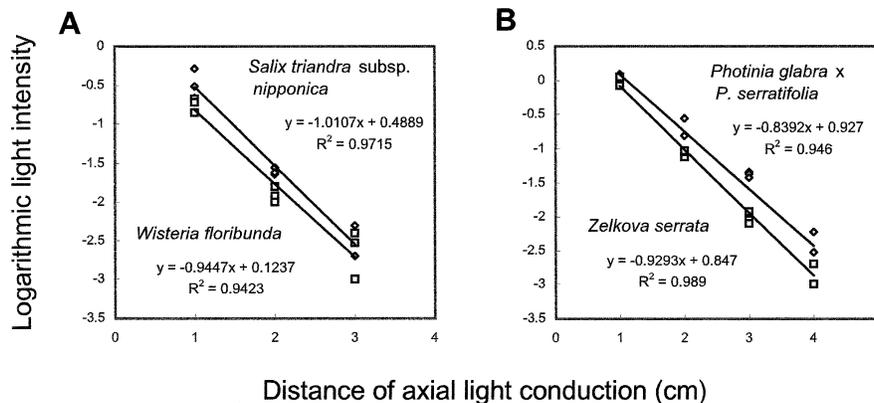
## Discussion

### *The involvement of vascular tissue in light conduction and axial light-conducting paths in stems and roots*

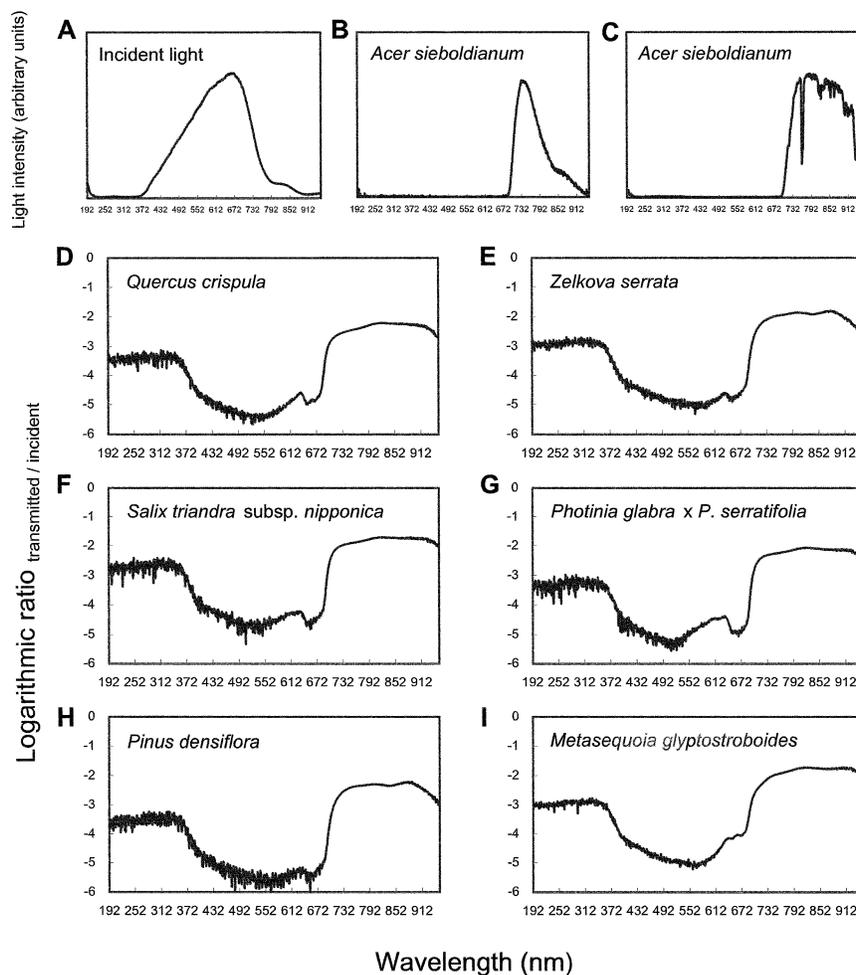
It is well known that vascular tissue functions to transport water and nutrients and to support plants mechanically, and that these functions depend greatly on the structural specializations of certain of its components (Esau, 1977; Fahh, 1990). Vessels are formed by the axial linkage of vessel elements and the dissolution of their end walls, and are thus long, continuous tubes of relatively large diameters, facilitating axial water conduction within plants. Fibres and tracheids are axially-elongated, thick-walled cells, considered to contribute mainly to the mechanical strength of both stem and root. Tracheids are also the main route for water conduction in gymnosperms. The present investigation demonstrates a newly discovered role of vascular tissue in the stems and roots of woody plants: involvement in axial light conduction. The components of vascular tissue (vessels, fibres and tracheids) conduct light via their lumina (vessels) and lateral walls (fibres and tracheids) (Figs 2, 3). Thus, it is suggested



**Fig. 3.** Examples of images of light transmitted from the transverse end of root vascular tissue under the horizontal illumination (incident angle at 90° to the root axis). (A, B) *Zelkova serrata*, a dicotyledon species. (C, D) *Cryptomeria japonica*, a gymnosperm species. (A) Light conduction in xylem. (B) More efficient light conduction in fibres (fi) and vessels (ve) than in rays (ra) and axial parenchyma (pa). (C) Light conduction in xylem. (D) More efficient light conduction in tracheids formed in summer and autumn (lw) than in those formed in spring (ew). Scale bars: 300 µm in (A) and (C), and 100 µm in (B) and (D).



**Fig. 4.** Attenuation patterns of light in stems and roots of some representative species under oblique illumination (incident angle at 60° to the stem or root axis). (A) Stems of *Wisteria floribunda*, a dicotyledon species with ring-porous xylem, and *Salix triandra* subsp. *nipponica*, a dicotyledon species with diffuse-porous xylem. (B) Roots of *Zelkova serrata*, a dicotyledon species with ring-porous xylem, and *Photinia glabra* x *P. serratifolia*, a dicotyledon species with diffuse-porous xylem. Light intensities were measured in units of  $W m^{-2}$ .

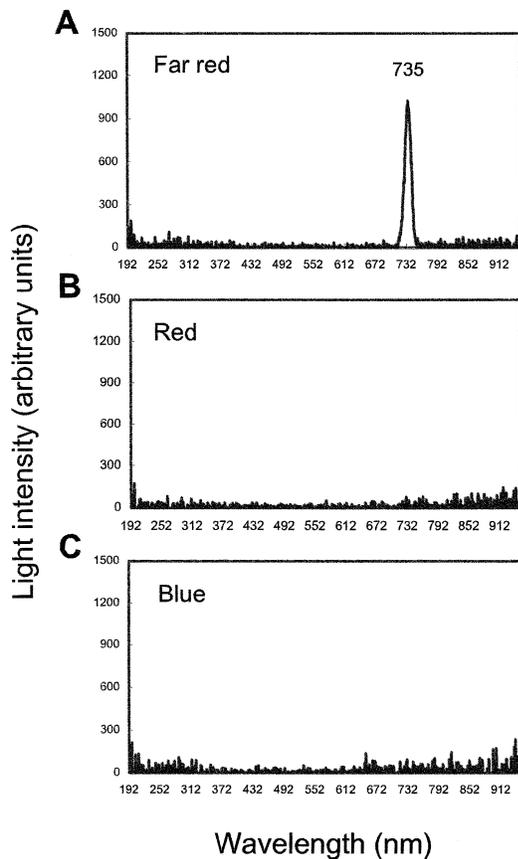


**Fig. 5.** Examples of spectral region-specific light conduction in stems and roots of several representative species. (A) Spectrum of incident light source (a microscope halogen lamp). (B) Transmission spectrum of a 15 mm long stem length of *Acer sieboldianum* under the axial illumination of the incident light (A). (C) Transmission spectrum of a 15 mm long stem length of *A. sieboldianum* under sunlight. (D–I) Ratio of transmission spectra to incident light spectra on axial illumination of a 15 mm long length of stem or root, showing the differences of light-conducting efficiency of vascular tissue across the spectral region investigated. (D), (F) and (H) are stems. (E), (G) and (I) are roots. (D) *Quercus crispula*, a dicotyledon species with ring-diffuse xylem. (E) *Zelkova serrata*, a dicotyledon species with ring-porous xylem. (F) *Salix triandra* subsp. *nipponica*, a dicotyledon species with diffuse-porous xylem. (G) *Photinia glabra* × *P. serratifolia*, a dicotyledon species with diffuse-porous xylem. (H) *Pinus densiflora*, a gymnosperm species. (I) *Metasequoia glyptostroboides*, a gymnosperm species. Arbitrary units in light intensity are used for comparison of spectral shapes.

here that the structural specializations of the vessels, fibres and tracheids can also be considered as adaptations for axial light conduction, in both stems and roots, in addition to those for water transport and mechanical support.

Light conduction in plant tissues and cells has not yet been clarified, but recent investigations strongly suggest that the efficiency of plant tissues for light conduction is closely related to their structural characteristics. Efficient light conduction has so far been reported in the sclereids of leaves (Karabourniotis *et al.*, 1994; Karabourniotis, 1998) and the axial parenchyma cell rows of etiolated seedlings (Mandoli and Briggs, 1982a, b). It is believed that thick walls are relatively homogeneous and have a higher refractive index, compared with the cytoplasm. The thick-

walled structures of foliar sclereids have light-conducting properties similar to those of a light guide, and light may be propagated by internal reflections within their thick walls (Karabourniotis *et al.*, 2000). The light conduction observed in the thick walls of fibres and tracheids probably occurs by a similar mechanism to that in the walls of foliar sclereids. Furthermore, the axially elongated structure of individual fibres and tracheids presumably facilitates the conduction of light over longer distances, and their tapered and intertwining ends should also facilitate light conduction from one fibre to another. All these structural characteristics of fibres and tracheids may be believed to contribute to efficient light conduction along the axial direction of stems and roots.



**Fig. 6.** Examples of differences in the conducting efficiency of monochromatic lights in a stem of *Salix triandra* subsp. *nipponica* under the horizontal illumination (incident angle at  $90^\circ$  to the stem axis) of incident monochromatic lights obtained from narrow band pass interference filters. (A) Far-red light (using a '733 nm' interference filter) as the incident light (peak transmission through the tissue obtained at 735 nm). (B) Red light (using a '662 nm' interference filter) as the incident light. (C) Blue light (using a '449 nm' interference filter) as the incident light. Black bars to around 150 units are background noise. Arbitrary units in light intensity are used for comparison of spectral shapes.

In the coleoptiles and mesocotyls of etiolated seedlings, axially-elongated parenchyma cells form long axial rows by the connections of their end walls. When light enters the interior of these cell rows at certain angles, it can be efficiently propagated via their cytoplasm and vacuoles by multiple reflections between the lateral walls (Mandoli and Briggs, 1982*a, b*, 1984*a, b*). Vessel elements have a similar structural arrangement to that of these axial parenchyma cells. Meanwhile, the end walls of vessel elements dissolve as they mature, and their diameter is much larger. It is therefore reasonable to assume that light conduction in vessels occurs by similar means; that is, light entering the vessel interior should travel along the lumen by the reflections between the lateral walls.

These results also revealed that the parenchyma cells, sieve tube elements and companion cells etc. in vascular tissue are not involved in axial light conduction (Figs 2, 3).

That may also be attributed to their structural characteristics. These cells are similar in some structural respects to the parenchyma cells in leaves: they vary in size, are spherical, oval or irregular in shape, have an irregular arrangement with diverse orientations of cell walls, contain pigments and have inhomogeneous cytoplasm. In leaves, these characteristics of parenchyma cells are believed to lead to the existence of many interfaces within and between cells when light passes through them. At these interfaces, multiple reflections and refractions scatter even the collimated incident light into an isotropic light environment just within a very short distance below the epidermis (DeLucia *et al.*, 1992). Absorption due to the presence of pigments in parenchyma cells greatly attenuates the internal light intensity (Cui *et al.*, 1991; Myers *et al.*, 1994). The similarities of both foliar parenchyma cells and those cells of the vascular tissue, render them inefficient at conducting light.

In summary, the present study demonstrates that (i) incident light striking stems and roots can penetrate into the interior; and (ii) there are structural axial light-conducting paths within the stems and roots of woody plants. Light entering the cell walls of fibres and tracheids at certain angles can be conducted along the axial direction of stems and roots because of their light-guiding properties. Light entering the vessel lumina at certain angles is also conducted along vessels via reflections between their lateral walls, while light passing through parenchyma cells, etc. is scattered by multiple reflections and refractions and is not efficiently conducted. Also, incident light arriving at different angles is finally propagated axially along the stem and root. However, illumination that is more parallel to the stem axis always leads to the conduction of more light in vascular tissue.

#### *Photomorphogenic significance of the internal light environment in stems and roots*

Vessels, fibres and tracheids enable far-red light and near infra-red light to be efficiently conducted along stems and roots, and the spectral properties of the surrounding solar radiation enable the light from 720–910 nm to be the predominant spectral region conducted in stems and roots in the terrestrial light environment (Figs 5, 6). There are presumably a number of factors contributing to this specific spectrum of internally transmitted light, but few details are clear. Chlorophylls are among the candidates for the absorption of visible light, leaving light of longer wavelengths to be conducted axially. Further investigations are now in progress.

Despite the efficient light conduction in stems and roots, the main light-conducting components (vessels, fibres and tracheids) of vascular tissue are dead by the time maturation is complete, so no light-related metabolic activities are possible. However, the attenuation patterns of the conducted light in an axial direction indicate the leaky

light guide properties of these light conductors, and the conducted light can leak to the surrounding tissues (Fig. 4). The other living tissues in the phloem and xylem are thus bathed in an internal far-red and near infrared light environment. The far-red composition contained in the internal light environment suggests some photomorphogenic significance in the stems and roots.

There are several intrinsic photoreceptors in plants that regulate their processes of growth and development, with specific photoreceptors reacting to certain specific wavelengths (Briggs and Olney, 2001). Phytochromes are a family of photoreceptors related to far-red light, and perceive light signals by red light ( $P_r$ ) and far-red light absorbing ( $P_{fr}$ ) forms with a maximal absorption at 660 nm and 730 nm, respectively. Phytochrome-mediated responses are classified into three main types according to the energy and duration of irradiance necessary: low-fluence response (LFR), very low-fluence response (VLFR) and high-irradiance response (HIR). Far-red light is involved in all of these phytochrome-mediated photomorphogenic responses at these different energy levels by changing  $P_{fr}$ : $P_r$  ratio in LFR (for a review see Fankhauser, 2001), triggering VLFR directly as one of the spectral compositions (Botto *et al.*, 1996; Shinomura *et al.*, 1996), and causing FR-HIR (Hartmann, 1966; Whitelam *et al.*, 1993; Shinomura *et al.*, 2000).

The present study has revealed the existence of the far-red light inside stems and roots under the natural light environment, which bathes the living cells and is therefore likely to drive certain phytochrome-mediated responses. Since the light is attenuated during axial conduction, there will be an axial far-red light gradient when light is conducted from the stems to the roots, below ground. This light gradient may be expected to relate to various phytochrome-mediated photomorphogenic responses according to the energy of irradiance, and in the axial direction along roots, light environments suitable for the various kinds of phytochrome responses (HIR, LFR and VLFR) should thus exist. Consequently, the different photomorphogenic responses probably all occur in roots, of juvenile woody plants at least, at different depths in the ground. In recent investigations, similar properties of light conduction have been clarified in many herbaceous species, and have been shown to influence the expression levels of some specific genes in *Arabidopsis thaliana* (Q Sun, K Sato-Nara, H Suzuki *et al.*, unpublished data). Thus, the regulation of growth and development of stems and roots in woody plants should be understood not only in terms of the indirect consequences of the physiological effects in other parts (such as buds and leaves), but also in terms of the direct contribution of light signal perception within the stems and roots themselves. Stems and roots themselves, therefore, require careful investigation for direct effects on phytochrome-mediated growth and development.

## Acknowledgements

We are grateful to Drs Fumio Takahashi and Kumi Sato-Nara for laboratory assistance and useful discussions, and to Dr Ian G. Gleadall for critical reading and comments on the manuscript.

## References

- Bone RA, Lee DW, Norman JM. 1985. Epidermal cells functioning as lenses in leaves of tropical rain-forest shade plants. *Applied Optics* **24**, 1408–1412.
- Botto JF, Sanchez RA, Whitelam GC, Casal JJ. 1996. Phytochrome A mediates the promotion of seed germination by very low fluences of light and canopy shade light in *Arabidopsis*. *Plant Physiology* **110**, 439–444.
- Briggs WR, Olney MA. 2001. Photoreceptors in plant photomorphogenesis to date. Five phytochromes, two cryptochromes, one phototropin, and one superchrome. *Plant Physiology* **13**, 85–88.
- Cui M, Vogelmann TC, Smith WK. 1991. Chlorophyll and light gradients in sun and shade leaves of *Spinacia oleracea*. *Plant, Cell and Environment* **14**, 493–500.
- DeLucia EH, Day TA, Vogelmann TC. 1992. UV-B and visible light penetration into needles of two species of subalpine conifers during foliar development. *Plant, Cell and Environment* **15**, 921–929.
- Ehleringer J, Björkman O, Mooney HA. 1976. Leaf pubescence effects on absorptance and photosynthesis in a desert shrub. *Science* **192**, 376–377.
- Esau K. 1977. *Anatomy of seed plants*, 2nd edn. New York: J Wiley & Sons, 61–181.
- Fahn A. 1990. *Plant anatomy*, 4th edn. Oxford: Butterworth-Heinemann, 332–381.
- Fankhauser C. 2001. The phytochromes, a family of red/far-red absorbing photoreceptors. *Journal of Biological Chemistry* **276**, 11453–11456.
- Fukshansky L, Fukshansky-Kazarinova N, Martinez von RA. 1991. Estimation of optical parameters in a living tissue by solving the inverse problem of the multiradiative transfer. *Applied Optics* **30**, 3145–3153.
- Fukshansky L, Martinez von RA. 1992. A theoretical study of the light microenvironment in a leaf in relation to photosynthesis. *Plant Science* **86**, 167–182.
- Hartmann KM. 1966. A general hypothesis to interpret 'high energy phenomena' of photomorphogenesis on the basis of phytochrome. *Photochemistry and Photobiology* **5**, 349–366.
- Iino M. 1990. Phototropism: mechanisms and ecological implications. *Plant, Cell and Environment* **13**, 633–650.
- Karabourniotis G. 1998. Light-guiding function of foliar sclereids in the evergreen sclerophyll *Phillyrea latifolia*: a quantitative approach. *Journal of Experimental Botany* **49**, 739–746.
- Karabourniotis G, Bornman JF, Nikolopoulos D. 2000. A possible optical role of the bundle sheath extensions of the heterobaric leaves of *Vitis vinifera* and *Quercus coccifera*. *Plant, Cell and Environment* **23**, 423–430.
- Karabourniotis G, Papastergiou N, Kabanopoulou E, Fasseas C. 1994. Foliar sclereids of *Olea europaea* may function as optical fibers. *Canadian Journal of Botany* **72**, 330–336.
- Kazarinova-Fukshansky N, Seyfried M, Schäfer E. 1985. Distortion of action spectra in photomorphogenesis by light gradients within the plant tissue. *Photochemistry and Photobiology* **41**, 689–702.
- Kunzelmann P, Iino M, Schäfer E. 1988. Phototropism of maize coleoptiles. Influence of light gradients. *Planta* **176**, 212–220.
- Kunzelmann P, Schäfer E. 1985. Phytochrome-mediated

- phototropism in maize mesocotyls. Relation between light and  $P_{fr}$  gradients, light growth response, and phototropism. *Planta* **165**, 424–429.
- Mandoli DF, Briggs WR.** 1982a. Optical properties of etiolated plant tissues. *Proceedings of the National Academy of Sciences, USA* **79**, 2902–2906.
- Mandoli DF, Briggs WR.** 1982b. The photoperceptive sites and the function of tissue light-piping in photomorphogenesis of etiolated oat seedlings. *Plant, Cell and Environment* **5**, 137–145.
- Mandoli DF, Briggs WR.** 1984a. Fiber-optic plant tissues: spectral dependence in dark-grown and green tissues. *Photochemistry and Photobiology* **39**, 419–424.
- Mandoli DF, Briggs WR.** 1984b. Fiber optics in plants. *Scientific American* **251**, 90–98.
- McClendon JH, Fukshansky L.** 1990. On the interpretation of absorption spectra of leaves. I. Introduction and the correction of leaf spectra for surface reflection. *Photochemistry and Photobiology* **51**, 203–210.
- Myers DA, Vogelmann TC, Bornman JF.** 1994. Epidermal focussing and effects on light utilization in *Oxalis acetosella*. *Physiologia Plantarum* **91**, 651–656.
- Parks BM, Poff KL.** 1986. Altering the axial light gradient affects photomorphogenesis in emerging seedlings of *Zea mays* L. *Plant Physiology* **81**, 75–80.
- Pfanz H.** 1999. Photosynthetic performance of twigs and stems of trees with and without stress. *Phyton* **39**, 29–33.
- Pfanz H, Aschan G.** 2001. The existence of bark and stem photosynthesis in woody plants and its significance for the overall carbon gain. *Progress in Botany* **62**, 477–510.
- Piening CJ, Poff KL.** 1988. Mechanism of detecting light direction in first positive phototropism in *Zea mays* L. *Plant, Cell and Environment* **11**, 143–146.
- Reicosky DA, Hanover JW.** 1978. Physiological effects of surface waxes. I. Light reflectance for glaucous and nonglucous *Picea pungens*. *Plant Physiology* **62**, 101–104.
- Seyfried M, Schäfer E.** 1983. Changes in the optical properties of cotyledons of *Cucurbita pepo* during the first seven days of development. *Plant, Cell and Environment* **6**, 633–640.
- Shinomura T, Nagatani A, Hanzawa H, Kubota M, Watanabe W, Furuya M.** 1996. Action spectra for phytochrome A- and B-specific photoinduction of seed germination in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences, USA* **93**, 8129–8133.
- Shinomura T, Uchida K, Furuya M.** 2000. Elementary processes of photoperception by phytochrome A for high-irradiance response of hypocotyl elongation in *Arabidopsis*. *Plant Physiology* **122**, 147–156.
- Terashima I, Saeki T.** 1983. Light environment within a leaf. I. Optical properties of paradermal sections of *Camellia* leaves with special reference to differences in the optical properties of palisade and spongy tissues. *Plant and Cell Physiology* **24**, 1493–1501.
- Turunen MT, Vogelmann TC, Smith WK.** 1999. UV screening in lodgepole pine (*Pinus contorta* ssp. *latifolia*) cotyledons and needles. *International Journal of Plant Science* **160**, 315–320.
- Vogelmann TC.** 1993. Plant tissue optics. *Annual Review of Plant Physiology and Plant Molecular Biology* **44**, 231–251.
- Vogelmann TC.** 1994. Light within the plant. In: Kendrick RE, Kronenberg GHM, eds. *Photomorphogenesis in plants*, 2nd edn. Netherlands: Kluwer Academic Publishers, 491–535.
- Vogelmann TC, Bornman JF, Yates DJ.** 1996. Focusing of light by leaf epidermal cells. *Physiologia Plantarum* **98**, 43–56.
- Vogelmann TC, Han T.** 2000. Measurement of gradients of absorbed light in spinach leaves from chlorophyll fluorescence profiles. *Plant, Cell and Environment* **23**, 1303–1311.
- Vogelmann TC, Martin G, Chen G, Buttry D.** 1991. Fiber optic microprobes and measurement of the light microenvironment within plant tissues. *Advances in Botanical Research* **18**, 256–296.
- Walter-Shea EA, Norman JM.** 1991. Leaf optical properties. In: Myneni RB, Ross J, eds. *Photon-vegetation interactions*. Berlin: Springer-Verlag, 229–251.
- Whitelam GC, Johnson E, Peng J, Carol P, Anderson ML, Cowl JS, Harberd NP.** 1993. Phytochrome A null mutants of *Arabidopsis* display a wild-type phenotype in white light. *The Plant Cell* **5**, 757–768.