Physiology of shade loving plants: A comparative analysis with shade avoiding plants

^{1*}Dibyendu Sekhar Mahanty

¹Plant Physiology, Plant Biochemistry and Plant Molecular Biology Laboratory Post Graduate Department of Botany, Barasat Government College, Kolkata-700124 (India) ¹*Corresponding author: <u>dibyendu.mahanty@gmail.com</u>

Abstract

Shade loving plants have some distinguishing features vis-àvis shade-intolerant species. The adaptive features of shade plants can be anatomical, physiological, morphological etc. Shade leaves generally have more non green pigment content in comparison to the chlorophyll. They are mostly with variety of pigments in the leaves and often with showy leaves, also thus termed as foliage plants. They branch profusely, leaf blades orient according to light falling on them, often with pulvinous, low stomatal frequency, stomatal index.

In spite of these differences, they differ in pigment compositions, pigment content, habitat, mode of propagation, life cycle, whole plant senescence etc. If we delve deeper into the physiology of shade loving or shade tolerant plants, it is observed shade plants have adapted themselves to perform photosynthesis under compromised light level. They are programmed to invest heavily in solar technology, as if light was never in short reply. They take a very different method of capturing light for carbon assimilation. Such plants produce mostly are perennial and sexual reproduction in such plants are brief or absent. Unlike crop plants which are shade avoiding in particular shade plants do not have higher chlorophyll a:b ratio. They can capture and use low levels of light to make food. Due to reduced sexual reproduction they are dwarf perennials which are easily propagated, kept indoor in houses, banquets, hotels and various other common places of interest in urban areas. Foliage plants are therefore efficient from both economic, ecological and plant physiological point of view. Shade plants play an important role in human health, environment, ecology, psychology and can cumulatively act towards carbon dioxide sequestration and reduction at the local as well as global level.

Key words : Shade plants, Shade avoiding plants, foliage plants, non green pigments, chlorophyll.

¹Assistant Professor of Botany,

Light is the most important criteria for plant growth. Green plants convert light energy for carbon reduction and assimilation. Limitation to this phenomenon can endanger their growth, development, survival and evolution. Plants living under low light availability in the forest floor and other natural habitats have evolved mechanism and maximize light harvesting through change in their pigment composition, orientation of the leaves, low rate of metabolism and reproduction rate. Shade tolerance is a concept that refers to the capacity of a given plant to tolerate low light levels. From a physiological point of view, shade tolerance of a given plant is defined as the minimum light quantity under which a plant can survive⁵⁹.

Shade-loving plants (Figs 1-5) refer to those plants which thrive and proliferate under low light availability, as they are exposed to low intensity of light. To consider a plant to be shade tolerant or shade loving one criterion must be fulfilled; viz. the whole life cycle of the plant should take place under the shade. Shade loving plants or foliage plants (though all foliage plants cannot be considered as such) are mostly indigenous to the tropical and subtropical areas with warm temperature and abundant water. Most foliage plants grow as understory plants shaded by a canopy of giant trees. As a result, foliage plants native to this environment are tolerant to low light, sensitive to chilling temperatures, and day-neutral to photoperiod²⁸. The term sciophytes or sciophytic plants have been assigned to these plants owing to their prevalence in shade habitat. Such plants possess special ecological, anatomical, morphological and physiological adaptive features which help them survive and develop successfully under compromised sunlight. Due to prolonged period of low light intensity exposure, most of these plants are seen to occur under the canopies of large trees in forest floors where comparatively gloomy, hot and humid condition persist as in tropical rain forest biomes with immense humidity. Shade conditions can be generally two types i) partial shade (250 to 350 lux) and ii) full shade (175 to 200 lux). Partial shade plants need about 3-6 hours of direct sun per day, preferably morning and early afternoon sun and are with comparatively low sunlight need. Such plants are often with showy variegated leaves and serve as ornamentals in indoor, shaded corners and they are kept away from direct sunlight in hot afternoon so as to protect the foliages from photo-oxidation and physical stress caused due heat and ultraviolet rays of the sun. Partial shade plants may also be referred to as those that need filtered light. These plants perpetuate under the protection of other larger plants, trees or even a lattice structure in forest as well as artificial landscapes in various urban sites. Full shade refers to 2 hours of direct sunlight, less or no direct sunlight per day. An area with less than two hours of direct sunlight exposure is regarded as heavy shade. Shade plants which flourish in areas without direct sunlight receive light for regular photosynthesis in the form of reflected light from various directions or filtered light. North facing areas of landscapes, shades of large tress are some areas where shade plants are seen to thrive best.

Shade plants are mostly vulnerable to heavy or direct sunlight, may be due to deleterious effects of direct sunlight like photooxidation, elevated temperature, low rate of transpiration and variable pigment contents. They have in due course of time have evolved in themselves ability to survive under comparatively low temperature, low light intensity, high humidity. Quality and duration of sunlight also varies from habitat to habitat which has given rise to such plants in the natural environments. Plants which require maximum and direct sunlight for their optimum growth and development cannot survive in such compromised condition of low sunlight as seen in the case of common crop plants. In this situation low light intensity acts as an abiotic stress in them. For the preparation of the manuscript relevant literature¹⁻⁵⁹ has been consulted.

Shade plants in contrast if kept in direct sunlight fail to survive for long, lacking successful reproduction and propagation.

Aims and objectives :

The present study aimed at the -

- Identification some plants which can sustain and flourish in low luminance.
- Research and identification of important morphological characters like reduced life size, leaf orientation, presence of pulvinous, rolling of leaves, more branching formation reproduction *etc*.
- Anatomical characteristics involving reduced stomatal index, stomatal frequency, type of root, root system, thin cuticle, presence of poorly developed mechanical tissues.

- Study of physiological characteristics involving chlorophyll content, chlorophylla (chl-a), chlorophyll-b (chl-b), carotenoids content, rate of transpiration, mode of flowering, fruit development *etc*. in these plants flourishing under shade with low luminance.
- Optimum luminance for growth, mode or propagation.
- Find a solution towards carbon dioxide reduction through plantation in the urban areas like houses, hotels, banquets, meeting places as sustenance and maintenance of such shade loving plants is easy and less expensive.

Shade plants of some varieties were chosen, classified with botanical names (Table-1). Distribution and mode of propagation were studied. Photosynthetic pigments content and difference with normal plants were also studied. Shade plants are available in almost all classes except Gymnosperms, extending from bryophytes, pteridophytes, angiospermic dicotyledons and monocotyledons. The objective of the work was to do an extensive research and tabulate some shade loving plants and compare their characteristics with plants growing under optimum sunlight alos referred to as shade avoiding plants. Shade loving plants have immense commercial value in the local and global ornamental plants market. Orchids growing the natural habitats as well as artificial shade nets are important plants under this category. Quantification of chlorophyll-a, chlorophyll-b was done as per the Arnon³. Quantification of carotenoids was determined according to Yang et. al.,60.

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	Tuble 1 Fiant sumples taken for the study					
Sl.	Shade loving Plants	Plants living under direct				
No.	Shade loving I lands	sunlight (sun loving)				
1	Aglaonema costatum N.E.Br (Araceae)	Basella alba L. (Basellaceae)				
2	Stromanthe sanguinea Sond. (Marantaceae)	Carica papaya L. (Caricaceae)				
3	Aglaonema commutatum Schott (Araceae)	Zea mays L. (Poaceae)				
4	Calathea zebrina (Sims) Lindl. (Marantaceae)	Mangifera indica L.				
		(Anacardiaceae)				
5	Vanda tessellata (Roxb) Hook.	Neolamarckia cadamba (Roxb.)				
	(Orchidaceae)	Bosser syn Anthocephalus				
		cadamba (Roxb.) Miq. (Rubiaceae)				





Fig. 1. Aglaonema costatum



Fig. 3. Stromanthe sanguinea



Fig. 4. Calathea zebrina



Fig. 6. Sun loving crop plants Basella alba



Fig. 2. Aglaonema commutatum



Fig. 5. Vanda tessellata living as epiphyte



Fig. 7. Carica papaya

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Fig. 8. Sun loving crop plants *Zea mays*

^{is} Fig. 9. *Mangifera indica*

Physiological characteristics taken into account between shade plants and plants living under direct sunlight.

- i. Stomatal frequency
- ii. Stomatal index
- iii. Proportion of the area covered by the stomata with respect to the total leaf area
- iv. Size of the stomata
- v. Total chlorophyll versus carotenoids

content

vi. Chlorophyll-a versus chlorophyll-b content

Fig. 10. Anthocephalus

cadamba

- vii. Water requirement in shade plants versus plants growing under direct sunlight.
- viii. Rate of transpiration per gram of water transpired/square cm of leaf surface/hour
- ix. Mode of propagation mostly asexual mode of reproduction.
- x. Absence of sexual reproduction leading to delay or no senescence.

	Tuble 2. Stollatur requercy		Stomatal	Stomatal			
Sl.			Frequency *	Index*			
No.	Plants	Type of plant	(in thousand	(% of stoma per			
			per sq.cm)	total number of			
				cells)			
1	Aglaonema costatum	Shade loving	4.6-6.6	2.3%-5.46%			
2	Stromanthe sanguinea	Shade loving	4.2-6.7	2.76% - 5.67%			
3	Aglaonema commutatum	Shade loving	3.4-7.3	1.14% - 4.79%			
4	Calathea zebrina	Shade loving	3.8-7.6	2.3-3.4%			
5	Vanda tasselata	Shade loving	1.8-2.6	2.4-4.6%			
6	Anthocephalus cadamba	Sun loving	5.6-9.8	4.9-11.8%			
7	Basella alba Sun loving 4.6-7.19 9.01%-12						
8	Carica papaya	Sun loving	5.6-8.9	8.09-12.8			
9	Mangifera indica	Sun loving	4.8-8.3	6.4-8.3%			
10	Zea mays	Sun loving	5.4-9.7	7.84-12.36%			
* Cal	* Calculated as the average of both adaxial and abaxial surfaces, stomatal index was calculated as						
	Number of Stomata						
Stomatal Index = $\frac{1}{No. of stomata + Epidermal cells} X 100$							
	No.of stomata + Epiaermal cells						

Table-2. Stomatal frequency and index of the plants taken for the study

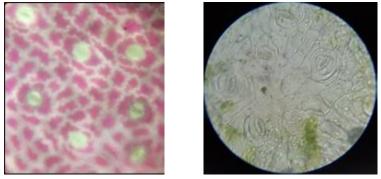


Fig. 11. Stomata in Stromanthe sanguinea (L) a shade loving; Basella alba (R) a sun loving plant

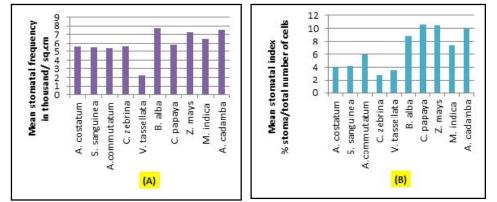


Fig. 12. Mean stomatal frequency and stomatal index of the plants taken for the study

	Table-3. List of plants with chlorophyll and carolenoid content and ratios						T-4-1
		Chl-a [mg/	Chl-b	Total		Carote	Total
Sl.	Plants	gm of	[mg/gm	chlorophyll	Chla:	noids[mg/	chloro-
No.		fresh	of fresh	[mg/gm of	chl-b	gm of	phyll :
		tissue]	tissue]	fresh tissue]		fresh tissue]	carotenoids
1	A. costatum	0.225	0.394	0.619	0.571	0.176	3.244
2	S. sanguinea	0.267	0.322	0.589	0.829	0.182	4.55
3	A. commutatum	0.288	0.274	0.562	1.05	0.205	5.121
4	C. zebrina	0.291	0.282	0.573	1.03	0.217	4.74
5	V. tassellata	0.074	0.037	0.111	0.111	0.1031	1.07
6	B. alba	0.301	0.412	0.713	0.73	0.178	4.10
7	C. papaya	0.371	0.459	0.830	0.80	0.191	4.18
8	Z. mays	0.312	0.344	0.656	0.906	0.201	4.5
9	Mangifera	0.412	0.432	0.844	0.953	0.198	4.81
	indica	0.712	0.752	0.01	0.755	0.170	т.01
10	A. cadamba	0.367	0.323	0.580	1.135	0.177	6.412

Table-3. List of plants v	vith chlorophy	Il and caroter	noid cont	ent and ratios

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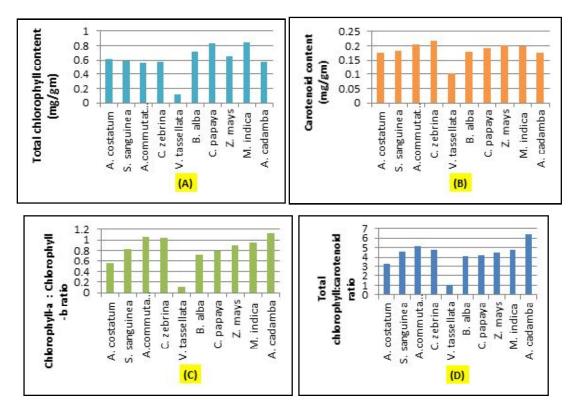


Fig. 13. Chart showing (A) Total chlorophyll content (B) Carotenoid content (C) Chlorophyll-a : Chlorophyll-b ratio (D) Total chlorophyll : carotenoid ratio in shade loving versus sun loving plants taken for the study

• Shade tolerance or shade loving of some plants is a complex property that is achieved by different sets of responses in different species, such as alterations in leaf physiology and biochemistry leaf anatomy, morphology and/ or plant architecture. In general, under low light, shade loving plants have propensity to adapt to low utilization of resources as most of these plants lack explicit sexual reproduction, fruit development, seed formation, accompanied by very low growth rates and many structural and biochemical changes so as to enhance the efficiency of photosynthetic energy transduction^{54,59}. Shade loving species under low

light conditions gives thinner leaves, absence of vigorous growth with apical dominance, profuse branching, slow growth rate and decreased elongation rates⁵⁹. Whereas shade avoiding or sun loving plants show higher growth rate, greater rate of transpiration, stomatal frequency, stomatal index, apical dominance and growth of the branches with longer internodes which often render these plants ability to escape shade areas. Two groups of plants taken for the study had contrasting characters as discussed in the previous section. Sun loving plants like *B. alba*, *C. papaya, Z. mays, M. indica, A. cadamba* (Figs. 6-10) are mainly crop plants which have distinct sexual reproduction followed by fruit, seed development. This physiological processes require higher amount of energy transduction and the thus the quantity of principal pigments (chlorophyll a and b) was comparatively higher than the shade loving plants (Fig. 13, Table-3). Plant living under shades possess comparatively less quantity of chlorophyll-a and chlorophyll-b, whereas higher quantity of carotenoids which increases the light harvesting more efficiently. Thus in shade loving plants there was higher quantity of carotenoids/gm of tissue and in sun loving plants mg of chlorophyll/gm of tissue was higher. Shade tolerant plants are adapted to be efficient energy-users. These plants by their appearance they are less green and mostly with variegated leaves. These plants grow broader, thinner so that they can harvest higher sunlight even though thriving under low light intensity. Reduced growth- The hypothesis that leaf growth was limited by photoassimilate availability⁵. Low-light acclimation of this plant has a considerable limiting effect on biomass production⁵⁸. Rolling of leaf in these was observed so as to reduce water loss and in many of the there was pulvinous controlling leaf movement. Some of the morphological adaptations in shade loving plants are reduced leaf size, branching, slow growth etc. Anatomical changes observed in such plants less amount of mechanical tissues, low stomatal frequency, stomatal index (Table-2, Figs. 11 and 12) in case of shade loving plants. Physiological feature no apical dominance and and less pronounced growth absence of elaborate sexual reproduction and fruit development were some features which are entirely different from the sun loving crop plants like Z. mays and others. Amount of accessory pigments per gm of fresh tissues are higher than the principal pigments. Accessory pigments (carotenes and xanthophylls) serve as the antennae pigments which after harvesting light energy passes on to Chlorophyll-a and finally to chlorophyll-b in the reaction center. Shade loving plants are observed to contain higher amount of carotenoids in comparison to chlorophyll molecules may be in order to obtain or harvest greater light energy living in partially shaded areas. Thus plant possesses higher antennae pigments which can harvest more light due their placement in shaded areas with lower light intensity. Plants living in the direct sunlight possess higher number of stomata in both the sides of the leaf lamina as observed in case of the crop plants like rice, wheat, maize, sunflower and they in many cases move their leaf blades in order to harvest higher amount of light energy. These plants often have isobilateral leaves. With higher sunlight the rate transpiration also increases in such plants in order to cool the leaf whole plants as a strategy against heat or abiotic stress conditions. In Pinus, Abies it has been observed that these plants living in the direct sunlight are in possession of higher quantity on chlorophylla, b as well as carotenoids. Leaves of such plants deep green and leathery³⁹. Leaf size is observed to be higher in case of the foliar plants or shade loving plants, even if it is small then compound leaves with leaflets account for higher photosynthetic surface. Leaf movement in relation to the direction and intensity of incoming light on the leaf surfaces. Shade plants transpire comparatively less in contrast to the normal plants as they do not get heated up during the day.

From the present work it may be said that shade tolerant species has some unique adaptations rather than the sun-loving plants. Many of them are indoor plants. These plants have evolved in due course of time the strategy to withstand low light availability. Harvesting optimum light present in such shaded places by alteration of their pigment composition, comparatively lower number of stomata per unit area of the leaf surface, leaf lamina, delay in sexual reproduction, altered method of propagation etc. Due change in plant physiological, plant biochemical a, anatomical and morphological features in these plants they are efficient carbon dioxides sequesters in shaded places, indoor areas.

Adequate knowhow regarding such plants through identification, classification, and their optimum growth requirements can throw light towards establishing and managing such plants in urban environments like, small houses, balcony, offices, banquets, hotels and various other indoor areas. Shade plants can sustain more efficiently to drought as they do not transpire extensively. This can give a cumulative effect on carbon dioxide reduction and sustainable living in the urban milieu. Rearing and cultivation of urban shade trees can thus play a significant role in improving urban air quality.

References :

- Anthony P.A., J.A.M. Holtum, and B.R. Jackes (2002). Shade acclimation of rainforest leaves to colonization by lichens. Functional Ecology *16*: 808–816.
- Araus, J.L., L. Alegre, L. Tapia, R. Calafell, and M.D. Serret (1986) *American Journal* of Botany, Columbus, 73: p.1760-1770.
- 3. Aron D., (1949). Plant Physiology. 24:

1-15.

- Barros V.R., C.B. Field, D.J. Dokke, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova and B. Girma (2015). Climate change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge (UK): Cambridge University Press.
- 5. Benedetto D. A., C. Boschi, R. Klasman and J. Molinari (2005). *Cientifica, Jaboticabal 33*(2): 160-164.
- 6. Boardman K.N. (1977) Comparative Photosynthesis of Sun and Shade Plants, *Ann. Rev. Plant Physiol.*
- Brooker R.W., F.T. Maestre, R.M. Callaway, C.L. Lortie, L.A. Cavieres, G. Kunstler, P. Liancourt, K. Tielbörger, J.M. Travis, F. Anthelme and C. Armas (2008). *Journal* of Ecology 96: 18–34.
- Bugmann H.K., X. Yan, M.T. Sykes, P. Martin, M. Lindner, P.V. Desanker, and S.G. Cumming (1996). *Climatic Change* 34: 289–313.
- 9. Callaway R.M. (1995). *The Botanical Review 61:* 306–349.
- Callaway R.M. (2007). Positive interactions and interdependence in plant communities. New York (NY): Springer-Verlag
- Canham C.D., A.C. Finzi, S.W. Pacala, and D.H. Burbank (1994). Canadian Journal of Forest Research 24: 337– 349.
- Cramer W., A. Bondeau, F.I. Woodward, I.C. Prentice, R.A. Betts, V. Brovkin, P.M. Cox, V. Fisher, J.A. Foley, A.D. Friend, and C. Kucharik (2001). *Global Change Biology* 7: 357–373.

- De Frenne P., F. Rodríguez-Sánchez, D.A. Coomes, L. Baeten, G. Verstraeten, M. Vellend, M. Bernhardt-Römermann, C.D. Brown, J. Brunet, J. Cornelis, and G.M. Decocq (2013). *Proceedings of the National Academy of Sciences 110*: 18561–18565.
- Dent D.H., S.J. DeWalt and J.S. Denslow (2013). *Journal of Vegetation Science* 24: 530–542.
- Devlin P.F., P.R.H. Robson, S.R. Patel, L. Goosey, R.A. Sharrock and GC. Whitelam (1999) *Plant Physiol 119*: 1479–1487.
- Devlin P.F., M.J. Yanovsky, and S.A. Kay (2003) *Plant Physiol 133*: 1–13.
- 17. Di Benedetto, A. H. and D. H. Cogliatti, (1990). *Journal of Horticultural Science, Ashford, 65:* 689-698.
- Di Benedetto, A. H., and A. F. Garcia, (1992) *Journal of Horticultural Science, Ashford,* 67: 179-188.
- 19. Franceschini T., and R. Schneider (2014). *Oecologia 176:* 739–749.
- 20. Garcia, A.F. (2003) *Cientifica, Jaboticabal, 31:* 73-79,
- 21. Germino M.J., and W.K. Smith (1999). Plant, Cell & Environment 22: 407–415.
- 22. Givnish T.J. (1988). Functional Plant Biology 15: 63–92.
- 23. Glazer A.N. (1984) *Biochim Biophys Acta.*, 768: 29–51.
- 24. Glazer, A.N. (1989). J. Biol. Chem., 264(1): 1-4.
- Goldberg D.E. (1990). Components of resource competition in plant communities. In: Grace JB, Tilman D, editors. Perspectives on plant competition. San Diego (CA): Academic Press. p. 27–49.
- Hallik L., Ü. Niinemets, and I.J. Wright (2009). Are species shade and drought tolerance reflected in leaf level structural

and functional differentiation in Northern Hemisphere temperate woody flora? New

- 27. Hättenschwiler S. (2001). *Oecologia 129:* 31–42.
- 28. Henny, R. J., and J. Chen. (2003). *Plant Breed. Rev.* 23: 245–290.
- 29. Henry, H.A., and L.W. Aarssen (1997). *Oikos 80:* 575–582.
- Holmgren M., L. Gómez-Aparicio, J.L. Quero and F. Valladares (2012). *Oecologia* 169: 293–305.
- 31. Holzwarth A.R. (1991) *Plant Physiol*, 83: 518–528.
- Jacobs A.F.G., J.H. Van Boxel and R.M.M. El-Kilani (1994). Boundary-Layer Meteorology 71: 375–391.
- Jucker T., O. Bouriaud, and D.A. Coomes (2015). *Functional Ecology 29*: 1078-1086.
- Kitajima K. (1994). Oecologia 98: 419– 428.
- Kneeshaw D.D., R.K. Kobe, K.D. Coates, and C. Messier (2006). *Journal of Ecology* 94: 471–480.
- Kunstler G., T. Curt, M. Bouchaud and J. Lepart (2005). *Canadian Journal of Forest Research 35:* 1657–1668.
- Laanisto L., and Ü. Niinemets (2015). *Global Ecology and Biogeography 24:* 571–580.
- Lichenthaler, H. K. (1985) Differences in morphology and chemical compo-sition of leaves grown in different light intensities and qualities. In: BAKER, N. R.; DAVIES, W. J.; ONG, C. K. (Ed.). Control on leaf growth. Cambridge: Cambridge University Press, p. 201-221. (Society of Experimental Biology Seminar Series, 27).
- 39. Lichtenthaler H.K. *et al.* (2007) Differences in pigment composition, photosynthetic rates and chlorophyll fluorescence images

of sun and shade leaves of four tree species Elsevier Plant Physiology and Biochemitry.

- 40. Lilles E.B., R. Astrup, M.L. Lefrançois, and K.D. Coates (2014). *Tree Physiology tpu092 34*: 1334–1347.
- Lin J., P.A. Harcombe, M.R. Fulton, and R.W. Hall (2002). *Oecologia 132:* 428– 435.
- Lintig, J von, R Welsch, <u>M Bonk</u>, G Giuliano, A Batschauer, and H Kleinig. (1997). *The Plant Journal for Cell and Molecular Biology 12*(3): 625-34. doi: 10.1046/j.1365-313x.1997.00625.x.
- 43. Lusk C.H., D.S. Falster, Jara C.K. Vergara, Jimenez M. Castillo and A. Saldaña Mendoza (2008). *Functional Ecology 22:* 454–459.
- Lusk C.H., M.A. Jorgensen, P.J. Bellingham (2015). *Journal of Ecology 103*: 479-488.
- 45. Markesteijn L., and L. Poorter (2009). Journal of Ecology 97: 311-325.
- 46. Martin P.H., and P.L. Marks (2006). Journal of Ecology 94: 1070–1079.
- 47. McCONNELL, D. B., P. RUGABER, T. J. SHEEHAN, and R. J. HENNY, (1984) Journal of the American Society for Horticultural Science, Alexandria, 109: 298-301.
- Meehl G.A., T.F. Stocker, W.D. Collins, P. Friedlingstein, A.T. Gaye, J.M. Gregory, A. Kitoh, R. Knutti, J.M. Murphy, A. Noda, and S.C. Raper (2007). Global climate projections. Climate change, 283. In: Solomon S, *et al.* editors. Climate change 2007: the physical science basis. Cambridge (UK): Cambridge University Press; p. 747–847.
- 49. Modrzynski J., D.J. Chmura, and M.G. Tjoelker (2015). Seedling growth and biomass allocation in relation to leaf habit

and shade tolerance among 10 temperate tree species. Tree Physiology tpv053 *35*: 879–893.

- 50. Nieto Lugilde D., J. Lenoir, S. Abdulhak, D. Aeschimann, S. Dullinger, J.C. Gégout, A. Guisan, H. Pauli, J. Renaud, J.P. Theurillat, and W. Thuiller (2014). Tree cover at fine and coarse spatial grains interacts with shade tolerance to shape plant species distributions across the Alps. Ecography 38: 578–589.
- 51. Roig-Villanova, Irma, (2007) Jordi Bou-Torrent^{1,‡}, Anahit Galstyan⁺, Lorenzo Carretero-Paulet¹, Sergi Portolés¹, Manuel Rodríguez-Concepción^{1,2} and Jaime F Martínez-García Interaction of shade avoidance and auxin responses: a role for two novel atypical bHLH proteins *The Embo Journal*.
- 52. Sims, D. A., and R. W. Pearcy, (1992) *American Journal of Botany, Columbus,* 79: 449-455.
- 53. Smith, H. (1982) Annual Review of Plant Physiology, 33: 481-518.
- 54. Spence I. (2007) Garden Plants and Flowers Through The Year, Royal Horticultural Society.
- 55. Tian Q., and J.W. Reed (2001) *J Plant Growth Regul 20:* 274–280.
- 56. Turgeon, R. (1989) Annual Review of Plant Physiology and Plant Molecular Biology, Palo Alto, 40: 119-138.
- 57. Vidal, D., E. Griera, P. Marin and J. Sabido (1990) *American Journal of Botany, Columbus, 77,* 1149-1158.
- 58. Valladares, F., and U. Niinemets, (2008) Annual Review of Ecology and Evolution and Systematics 39(1): 237-257.
- 59. Yang, C.M., K.W. Chang, M.H. Yin, and H.M. Huang, (1998). *Taiwania 43*(2): 116-122.