Journal of Tropical Ecology (2013) **29**:357–360. © Cambridge University Press 2013
doi:10.1017/S0266467413000308

SHORT COMMUNICATION

Global distribution of root climbers is positively associated with precipitation and negatively associated with seasonality

Jaqueline Durigon*,[1], Sandra Milena Durán† and Ernesto Gianoli‡,§

* Programa de Pós-Graduação em Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil
† Earth and Atmospheric Sciences Department, University of Alberta, Edmonton, Alberta T6G 2E9, Canada
‡ Departamento de Biología, Universidad de la Serena, La Serena, Chile
§ Departamento de Botánica, Universidad de Concepción, Concepción, Chile

(*Received 22 February 2013; revised 2 May 2013; accepted 2 May 2013; first published online 23 May 2013*)

Abstract: Root climbers constitute a distinctive group within climbing plants and some evidence suggests that they are associated with high precipitation and low light availability at local scales, which is in contrast with general patterns of liana distribution in the tropics. The influence of precipitation and seasonality on the occurrence of root climbers was evaluated both globally and in the tropics. The presence/absence of root climbers was recorded in 174 sites of Alwyn H. Gentry Forest Transect Data Set. The effects of mean annual precipitation and dry-season length (and temperature) on their occurrence were analysed using logistic regressions. Root climbers were significantly more frequent in sites with greater precipitation and reduced seasonality. Increasing temperature reduced root-climber occurrence in tropical sites, but this effect was marginally significant at a global scale. Dry and open habitats appear unsuitable for root climbers. This can be explained by the susceptibility to desiccation of adventitious roots and/or the low acclimation ability of these climbers to high irradiance.

Key Words: climbing mechanism, distribution patterns, environmental constraints, lianas

Lianas (woody climbers) play a key role in the structure and function of forest ecosystems (Schnitzer & Bongers 2002), representing 10–40% of woody stems in tropical forests (Gentry 1991). General patterns of liana distribution, abundance and species richness in the tropics have been documented (DeWalt *et al.* 2010, Gallagher & Leishman 2012, Schnitzer 2005, van der Heijden & Phillips 2008). Precipitation and seasonality have been identified as major drivers of liana abundance in tropical regions, with lianas increasing with decreased annual rainfall and increased dry-season length (DeWalt *et al.* 2010, Schnitzer 2005). However, in a study across Neotropical forests, van der Heijden & Phillips (2008) found no relationship between liana abundance and both mean annual rainfall and dry-season length, suggesting that this issue deserves further study.

The climbing habit has evolved many times during plant evolution (Gianoli 2004), and a variety of mechanisms are utilized by climbers to access the support structure (Isnard & Silk 2009, Putz & Holbrook 1991). The relative frequency of climbing mechanisms varies with the availability of suitable supports and with light levels (Carrasco-Urra & Gianoli 2009, Hegarty & Caballé 1991, Putz 1984). However, the distribution of climbing mechanisms at global scales has received little attention; the single study performed to date took into account the proportion of twiners relative to tendril-bearers only, and evaluated the relationship between this proportion and latitude (Gallagher & Leishman 2012). The association between climbing mechanisms and the environmental factors that influence liana distribution has yet to be evaluated at a global scale.

Root climbers constitute a distinctive group within climbing plants. Whereas other guilds have constraints concerning the maximum support diameter they can use (e.g. tendril-bearers), root climbers are free from this limitation (Hegarty 1991, Putz 1984, Putz & Holbrook 1991). Lianas are often considered light-demanding plants (Hegarty & Caballé 1991, Putz 1984, Schnitzer

[1] Corresponding author. Email: jaquelinedurigon@gmail.com

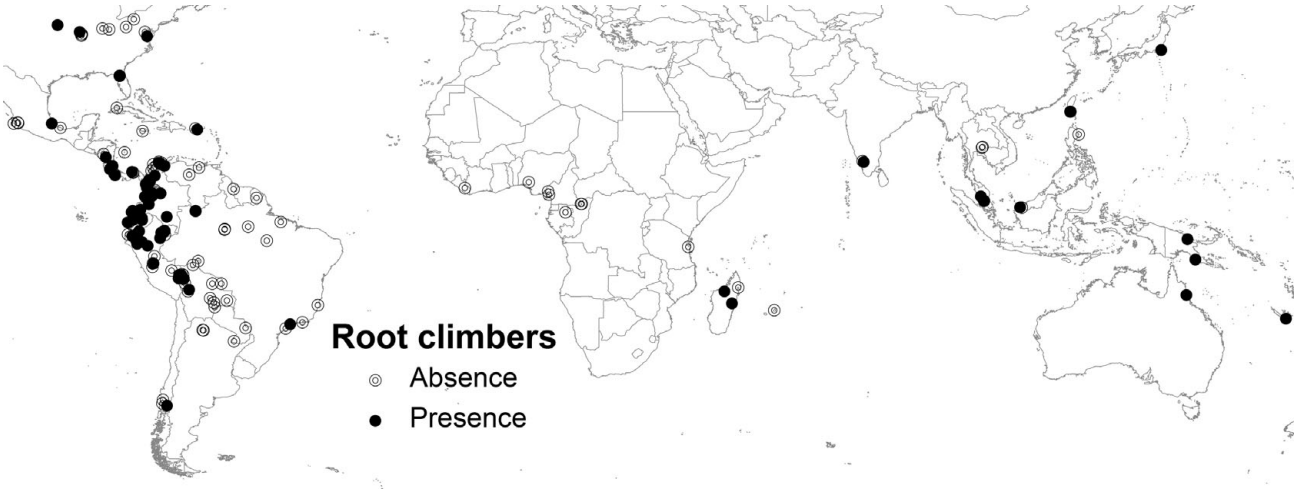

Figure 1. Spatial distribution of Gentry's forest plots used in the current study (n = 174). Presence/absence of root climbers is indicated.

& Bongers 2002, but see Gianoli *et al.* 2010), while root climbers comprise mostly shade-tolerant species (Hegarty 1991, Valladares *et al.* 2011). At least at local scales, root climbers seem to be associated with high precipitation and low light availability (Hegarty 1991, Orihuela 2010, Teramura *et al.* 1991). In extratropical regions of South America, root climbers were only recorded in rain forests, being absent from seasonal forests (Durigon *et al.* unpubl. data). In seasonal forests, many tree species lose their leaves in the dry season, resulting in high light penetration in the understorey (Kalacska *et al.* 2008). This may be an unfavourable condition for root climbers in view of their low potential for acclimation to high irradiance (Carter & Teramura 1988, Teramura *et al.* 1991). In the present study, we tested whether root climbers mainly occur in areas with high precipitation and low seasonality across forests worldwide, a pattern which is contrary to general patterns of distribution and abundance of lianas in the tropics. We also included the effect of temperature on the occurrence of root climbers because there is evidence that temperature may influence distribution limits of lianas (Jiménez-Castillo *et al.* 2007).

In order to test our hypothesis, we constructed a matrix of presence/absence data of root climbers in 174 sites distributed in tropical and temperate areas. These sites correspond to a subset of the Alwyn H. Gentry Forest Transect Data Set (Phillips & Miller 2002), which comprises forest plots of 0.1 ha distributed across the globe (Figure 1). Gentry quantified all trees, shrubs, lianas and hemiepiphytes with stems $\geq$2.5 cm diameter at breast height in 225 plots worldwide. Each plot consists of 10 transects of 2 $\times$ 50 m distributed across mature forest. We used only those plots that had lianas. Some sites had more than one plot, but they were considered independent sampling units as they had contrasting soil types. From this database, we selected the species identified by Gentry as lianas, and determined which of these species climb using adventitious roots by searching the literature and herbarium collections. Environmental data for each site, i.e. mean annual precipitation, length of the dry season, and mean annual temperature, were taken from the WorldClim dataset (www.worldclim.org). Dry-season length was defined as the number of consecutive months with average precipitation <100 mm (DeWalt *et al.* 2010).

We used logistic regression (R-software) to evaluate the effects of mean annual precipitation, dry-season length and mean annual temperature on the occurrence of root climbers (binary data: presence = 1, absence = 0). The analyses were performed using both the global dataset and tropical sites only.

A total of 174 plots in Gentry's dataset had liana species, with 151 plots located in the tropics and 23 plots in temperate ecosystems. We retrieved 116 liana species bearing adventitious roots as climbing mechanism. Root climbers occurred in 79 of the 174 plots considered in the study, being present in only seven plots from temperate forests (Figure 1). As expected, root climbers were positively associated with mean annual precipitation and negatively associated with dry-season length across forests worldwide; the same patterns were found for tropical forests only (Table 1). Higher temperatures reduced the probability of root-climber occurrence in tropical sites and had a marginally significant effect at the global level (Table 1). The inclusion of plots with no lianas (n = 5) did not alter the patterns found (data not shown).

Whereas overall liana abundance across the tropics decreases with increasing precipitation and decreasing seasonality (DeWalt *et al.* 2010, Schnitzer 2005), we found that root climbers occurred more frequently in sites with greater precipitation and shorter seasonality. This

https://doi.org/10.1017/S0266467413000308 Published online by Cambridge University Press

Table 1. Logistic regressions to evaluate the effects of mean annual precipitation (MAP), dry-season length (DSL) and temperature on the occurrence of root climbers across forests distributed worldwide and in tropical forests only. β denotes the standardized regression coefficients, and SE their standard error.

Dataset	Variable	Range	β	SE	*z*-value	df	P-value
All sites	MAP (mm y^{-1})	494–7426	0.007	0.001	4.05	173	< 0.001
	DSL (mo)	0–10	−0.181	0.063	−2.88	173	< 0.001
	Temperature (°C)	7.7–28	−0.060	0.031	−1.94	173	0.05
Tropical sites	MAP (mm y^{-1})	494–7426	0.007	0.002	3.60	151	< 0.001
	DSL (mo)	0–10	−0.154	0.065	−2.73	151	0.017
	Temperature (°C)	12–28	−0.20	0.052	−3.80	151	< 0.001

pattern held both at the tropical and global scales. Gentry (1988, 1991) noted that in sites with higher precipitation the species richness and abundance of root climbers tend to increase. Besides utilizing data of a different type, Gentry included hemiepiphytes in his analysis, while in our quantitative analysis we took into account the presence/absence of root climbers only.

Open and dry habitats appear unsuitable for root climbers. This could be related to physiological adaptations to low light developed by many species from this group of climbers (Carter & Teramura 1988, Teramura *et al.* 1991). Shade-tolerant lianas preferentially allocate resources to traits that enhance survival in light-limited understorey environments, sacrificing carbon gain and shoot growth, which are maximized by light-demanding species (Ichihashi *et al.* 2010, Valladares *et al.* 2011). Susceptibility to desiccation of adventitious roots (Hegarty 1988, Wilder 1992) may explain the exclusion of root climbers from sites with high potential evapotranspiration and high temperatures.

The increased liana abundance in dry and seasonal forests has been attributed to a greater competitive advantage of lianas over trees, which allows the former to show higher growth rates during the dry season (Schnitzer 2005). The higher light levels in the understorey throughout the year and the increase in light when deciduous trees shed their leaves in the dry season are likely to favour lianas (DeWalt *et al.* 2010, Schnitzer 2005). However, the physiological adaptability and light acclimation potential of lianas are likely to be associated with their particular climbing mechanism (Carter & Teramura 1988, Teramura *et al.* 1991). Whereas tendril climbers show broad physiological plasticity in response to variation in light availability, most root climbers have low capacity of acclimation to high irradiance (Teramura *et al.* 1991). Stems of root climbers grow away from sources of strong light (Hegarty 1991) and chances of survival are greater when they grow on the less-exposed side of a tree, thus avoiding desiccation (Hegarty 1988). Root climbers cope with deep shade by intercepting light efficiently and reducing gas-exchange rates (photosynthesis and dark respiration) (Gianoli & Saldaña 2013, Kusumoto *et al.* 2013, Valladares *et al.* 2011); the strategy of maximization of light capture and minimization of metabolic costs is typical of shade-tolerant plants (Valladares & Niinemets 2008).

Climbing by adventitious roots is a mechanism employed by relatively few climber taxa (Gallagher & Leishman 2012, Hegarty 1991). However, some species of root climbers can be locally very abundant, both in tropical and temperate rain forests (Durigon & Waechter 2011, Gianoli *et al.* 2010, Kusumoto *et al.* 2013). We have shown that root climbers have distinctive environmental requirements and constraints, which make their pattern of association with precipitation and seasonality contrary to the one proposed for all lianas as a group. Consequently, whereas lianas are predicted to increase in abundance and biomass with increasing frequency or duration of seasonal droughts associated with climate change (Schnitzer & Bongers 2011), we can expect that root climbers will decline if the rain forests where they occur become drier in the future.

ACKNOWLEDGEMENTS

We thank the Missouri Botanical Garden for making available the valuable dataset of Alwyn H. Gentry. JD thanks CAPES (PDSE 7138-12-1) for the scholarship during the "Sandwich" PhD Program at Universidad de la Serena, Chile. EG thanks funding by FONDECYT grant 1100585.

LITERATURE CITED

CARRASCO-URRA, F. & GIANOLI, E. 2009. Abundance of climbing plants in a southern temperate rain forest: host tree characteristics or light availability? *Journal of Vegetation Science* 20:1155–1162.

CARTER, G. A. & TERAMURA, A. H. 1988. Vine photosynthesis and relationships to climbing mechanics in a forest understory. *American Journal of Botany* 75:1011–1018.

DEWALT, S. J., SCHNITZER, S. A., CHAVE, J., BONGERS, F., BURNHAM, R. J., CAI, Z. Q., CHUYONG, G., CLARK, D. B., EWANGO, C. E. N., GERWING, J. J., GORTAIRE, E., HART, T., IBARRA-MANRIQUEZ, G., ICKES, K., KENFACK, D., MACIA, M. J., MAKANA, J. R., MARTINEZ-RAMOS, M., MASCARO, J., MOSES, S.,

https://doi.org/10.1017/S0266467413000308 Published online by Cambridge University Press

MULLER-LANDAU, H. C., PARREN, M. P. E., PARTHASARATHY, N., PÉREZ-SALICRUP, D. R., PUTZ, F. E., ROMERO-SALTOS, H. & THOMAS, D. 2010. Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica* 42:309–317.

DURIGON, J. & WAECHTER, J. L. 2011. Floristic composition and biogeographic relations of a subtropical assemblage of climbing plants. *Biodiversity and Conservation* 20:1027–1044.

GALLAGHER, R. V. & LEISHMAN, M. R. 2012. A global analysis of trait variation and evolution in climbing plants. *Journal of Biogeography* 39:1757–1771.

GENTRY, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75:1–34.

GENTRY, A. H. 1991. The distribution and evolution of climbing plants. Pp. 3–52 in Putz, F. E. & Money, H. A. (eds.). *The biology of vines*. Cambridge University Press, Cambridge.

GIANOLI, E. 2004. Evolution of a climbing habit promotes diversification in flowering plants. *Proceedings of the Royal Society B – Biological Sciences* 271:2011–2015.

GIANOLI, E. & SALDAÑA, A. 2013. Phenotypic selection on leaf functional traits of two congeneric species in a temperate rainforest is consistent with their shade tolerance. *Oecologia*, in press (doi: 10.1007/s00442-013-2590-2).

GIANOLI, E., SALDAÑA, A., JIMÉNEZ-CASTILLO, M. & VALLADARES, F. 2010. Distribution and abundance of vines along the light gradient in a southern temperate rain forest. *Journal of Vegetation Science* 21:66–73.

HEGARTY, E. E. 1988. *Canopy dynamics of lianes and trees in subtropical rainforest*. Department of Botany, University of Queensland, Brisbane. 241 pp.

HEGARTY, E. E. 1991. Vine–host interactions. Pp. 357–376 in Putz, F. E. & Money, H. A. (eds.). *The biology of vines*. Cambridge University Press, Cambridge.

HEGARTY, E. E. & CABALLÉ, G. 1991. Distribution and abundance of vines in forest communities. Pp. 313–336 in Putz, F. E. & Money, H. A. (eds.). *The biology of vines*. Cambridge University Press, Cambridge.

ICHIHASHI, R., NAGASHIMA, H. & TATENO, M. 2010. Biomass allocation between extension- and leaf display-oriented shoots in relation to habitat differentiation among five deciduous liana species in a Japanese cool-temperate forest. *Plant Ecology* 211:181–190.

ISNARD, S. & SILK, W. K. 2009. Moving with climbing plants from Charles Darwin's time into the 21st century. *American Journal of Botany* 96:1205–1221.

JIMÉNEZ-CASTILLO, M., WISER, S. K. & LUSK, C. H. 2007. Elevational parallels of latitudinal variation in the proportion of lianas in woody floras. *Journal of Biogeography* 34:163–168.

KALACSKA, M., SANCHEZ-AZOFEIFA, G. A., RIVARD, B., CALVO-ALVARADO, J. C. & QUESADA, M. 2008. Baseline assessment for environmental services payments from satellite imagery: a case study from Costa Rica and Mexico. *Journal of Environmental Management* 88:348–359.

KUSUMOTO, B., ENOKI, T. & KUBOTA, Y. 2013. Determinant factors influencing the spatial distributions of subtropical lianas are correlated with components of functional trait spectra. *Ecological Research* 28:9–19.

ORIHUELA, R. L. 2010. *Diversidade e abundância de hemiepífitos em um gradiente altitudinal na Floresta Atlântica no sul do Brasil*. Universidade Federal do Rio Grande do Sul, Porto Alegre. 29 pp.

PHILLIPS, O. & MILLER, J. S. 2002. Global patterns of plant diversity: Alwyn H. Gentry's forest transect data set. *Monograph in Systematic Botany from the Missouri Botanical Garden* 89:1–319.

PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.

PUTZ, F. E. & HOLBROOK, N. M. 1991. Biomechanical studies of vines. Pp. 73–98 in Putz, F. E. & Money, H. A. (eds.). *The biology of vines*. Cambridge University Press, Cambridge.

SCHNITZER, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* 166:262–276.

SCHNITZER, S. A. & BONGERS, F. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17:223–230.

SCHNITZER, S. A. & BONGERS, F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* 14:397–406.

TERAMURA, A. H., GOLD, W. G. & FORSETH, I. N. 1991. Physiological ecology of mesic, temperate woody vines. Pp. 245–285 in Putz, F. E. & Money, H. A. (eds.). *The biology of vines*. Cambridge University Press, Cambridge.

VALLADARES, F. & NIINEMETS, U. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution and Systematics* 39:237–257.

VALLADARES, F., GIANOLI, E. & SALDAÑA, A. 2011. Climbing plants in a temperate rainforest understorey: searching for high light or coping with deep shade? *Annals of Botany* 108:231–239.

VAN DER HEIJDEN, G. M. F. & PHILLIPS, O. L. 2008. What controls liana success in Neotropical forests? *Global Ecology and Biogeography* 17:372–383.

WILDER, G. J. 1992. Comparative morphology and anatomy of absorbing roots and anchoring roots in three species of Cyclanthaceae (Monocotyledoneae). *Canadian Journal of Botany* 70:38–48.