Principes, 31(1), 1987, pp. 31–40

Shedding of Vines by the Palms Welfia georgii and Iriartea gigantea

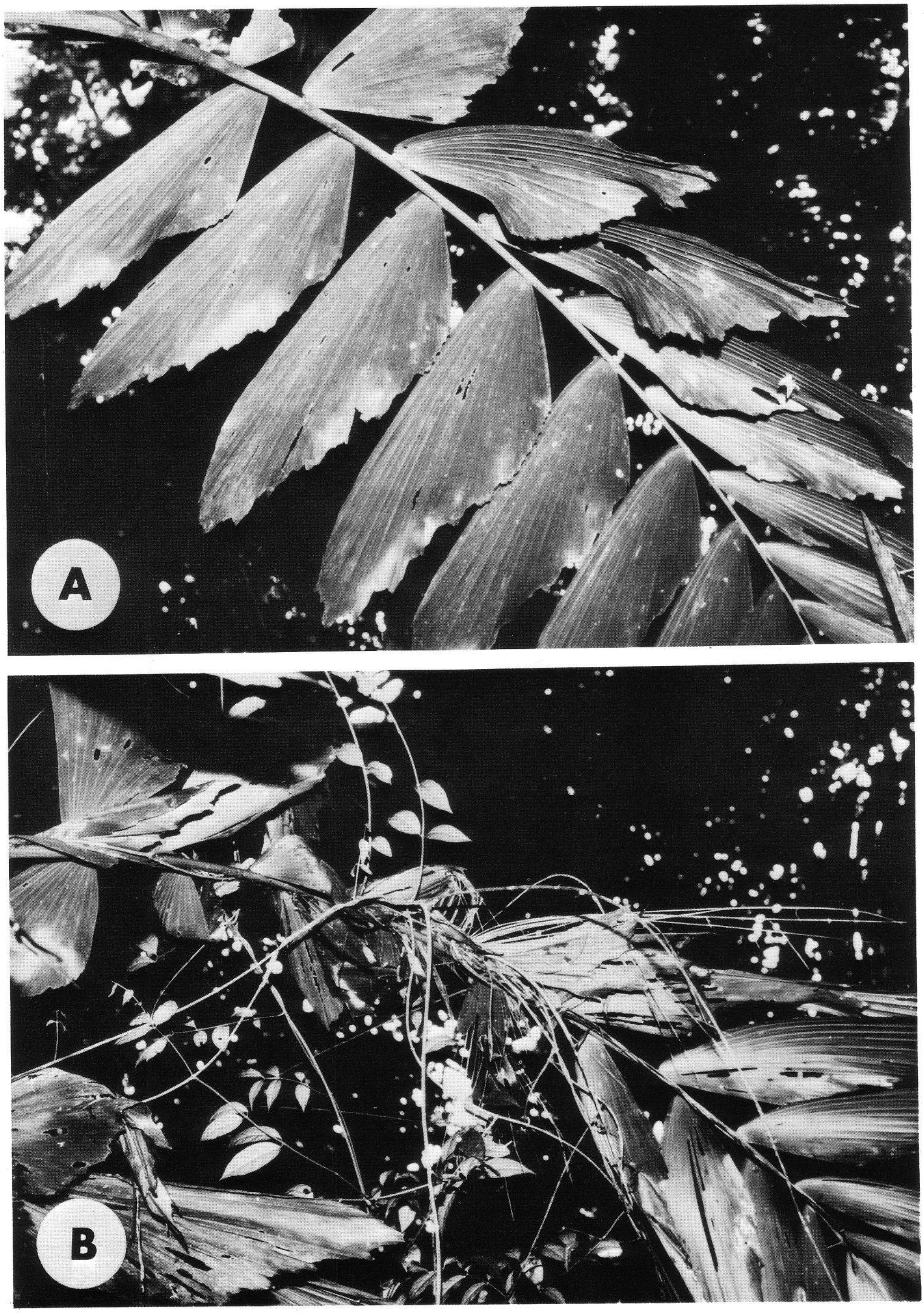
PAUL M. RICH,[1] SHAWN LUM, LEDA MUÑOZ E., AND MAURICIO QUESADA A.
Harvard University, Harvard Forest, Petersham, MA 01366;
Department of Botany, University of California, Berkeley, CA 94720; and
Organization for Tropical Studies, Apartado 676, 2050 San Pedro, Costa Rica

Vines are abundant in tropical forests (Richards 1952) and can often be found growing on arborescent palms. Do vines have detrimental effects on the palms on which they grow? Do palms have characteristics that protect them from vines? Herein, we survey the occurrence of vines in natural populations of the arborescent palms *Welfia georgii* H. A. Wendl. ex Burret and *Iriartea gigantea* H. A. Wendl. ex Burret in Costa Rica and we discuss characteristics of palms that allow palms to avoid and shed vines.

Vines are climbing plants that require other plants for mechanical support. Vines include both woody forms, or lianas, and non-woody forms. In some cases, vines growing up tree trunks may become detached from the ground, as is common among aroids; and some may start growth on the trunk and secondarily become rooted in the ground, as in the case of some cyclanths. By using other plants for mechanical support, vines do not need to produce as much of their own support tissue, and thereby have increased resources available for extension growth, leaf production, and reproduction (Darwin 1867, Putz 1983, 1984). Vines can have various adverse effects on their tree hosts, including interference with light interception, interference with proper development of leaves, and increased mechanical load on the host's supporting stem. For instance, in palms, twining vines that reach the spear leaf can prevent proper leaf expansion (Fig. 1). Putz (1984) reviewed observed detrimental effects of lianas on their hosts, which included inhibition of growth (Featherly 1941, Trimble and Tryon 1974, Putz 1978), mechanical abrasion and passive strangulation (Lutz 1943), increased host susceptibility to ice and wind damage (Siccama et al. 1976), increased probability of host tree falling (Webb 1958, Putz 1984), and increased access to tree crowns by folivores and harmful arboreal animals (Montgomery and Sunquist 1978, Charles-Dominique et al. 1981).

Trees have evolved various means to avoid and shed vines. Symbiotic *Azteca* ants keep *Cecropia* free of vines (Janzen 1973). Black and Harper (1979) hypothesized that tree buttresses and smooth bark may deter lianas from climbing trees; however field observations by Boom and Mori (1982) found no inhibition of liana growth in trees with buttresses or smooth bark. Putz (1980) suggested that rapid stem thickening may enable trees to avoid lianas. Putz (1980) observed that most lianas on Barro Colorado Island, Panama, climb with twining stems, tendrils, or modified branches, which therefore constrains lianas to climb on other lianas and on small diameter trees and branches. Maier (1982) suggested that spines and thorns may protect palms from vines, and observed that vines were less abundant on *Bactris* and *Cryosophila* than on non-spiny palms in

[1] Current address: Mailstop K495, HSE-12, UC Los Alamos National Laboratory, Los Alamos, NM 87545.



1. Vines can interfere directly with proper leaf expansion in palms, as is shown in this pictoral sequence of A) a healthy leaf from a 6 m tall *Iriartea gigantea*; and B) a leaf from the same individual that did not expand properly because a twining vine constricted the leaf during the spear stage.

Panama. Putz (1984) suggested that trees with flexible stems and long leaves are able to avoid and shed lianas. Putz observed that the arborescent palms *Astrocaryum standleyanum* and *Scheelea zonensis* were free of lianas on Barro Colorado Island, Panama, and suggested that this was due to shedding of lianas when the long leaves abscissed. We examined the distribution of vines on palms in a Costa Rican tropical wet forest and tested the hypothesis that the shedding of palm leaves dislodges adherent vines.

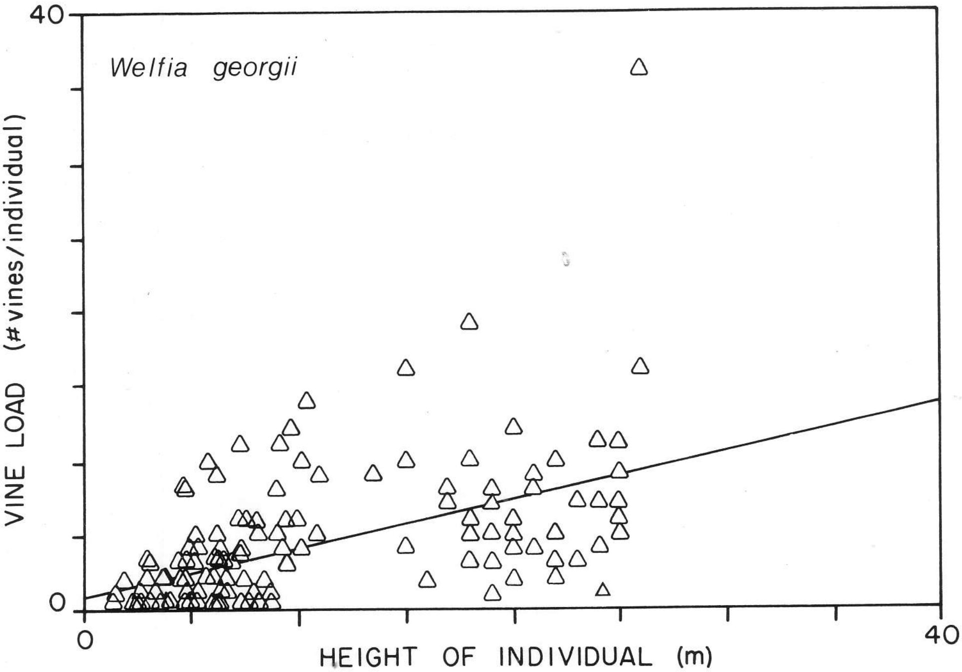
Methods

The occurrence of vines was surveyed for the arborescent palms *Welfia georgii* and *Iriartea gigantea* in tropical wet forest at La Selva Biological Station, Costa Rica. The study site is described in detail elsewhere (Hartshorn 1983, Chazdon 1985). In conjunction with studies of leaf production and height extension in arborescent palms (Rich 1985, 1986), we recorded the family identity of vines and the height to which individual vines grew on marked populations of 100 *Welfia* and 100 *Iriartea* with overall heights shorter than 13 m. We also surveyed family identity of vines growing on 50 individuals each for *Welfia* and *Iriartea* taller than 13 m, bringing the total sample size to 150 for each palm species. We recorded the height of each palm as measured to the top of the highest expanded leaf. Height was measured directly for shorter individuals and estimated for taller individuals. We noted the frequency with which vines grew into the crown and whether the vines grew into the lower crown, which we defined as the lowermost three leaves, or into the upper crown. For individuals less than 13 m tall, we recorded the occurrence of vines that were being carried to the ground by falling leaves. For tabulation of results, the samples of *Iriartea* and *Welfia* were divided into two groups, short palms (with individual heights less than 13 m) and tall palms (with individual heights greater than 13 m). For short *Welfia*, we recognized two subgroups, short individuals with no above-ground stem (generally individuals with heights less than 7 m tall) and short individuals with an above-ground stem (generally individuals with heights greater than 7 m tall). Vines were tabulated for seven taxonomic categories: Araceae, Cyclanthaceae, Melastomataceae, Piperaceae, Leguminosae, ferns, and a miscellaneous category.

Results

For both species, total vine load increased with palm height, though with a broad variance. For *Welfia georgii*, the linear regression of vine load as a function of height ($Y = 0.319X + 0.860$) had a low coefficient of determination ($r^2 = 0.26$), but a significant increase in vine load with height ($P < .01$) (Fig. 2A). For *Iriartea gigantea*, the linear regression of vine load as a function of height ($Y = 0.437X + 0.614$) also had a low coefficient of determination ($r^2 = 0.56$), but a significant increase in vine load with height ($P < .01$) (Fig. 2B).

Table 1 summarizes the mean vine loads and taxonomic distribution of vines encountered on palms. Short *Welfia* had a mean of 3.17 vines per individual, with a broad variance (sd = 2.97), whereas tall *Welfia* had a mean of 7.08 vines per individual (sd = 5.69). Among short *Welfia*, individuals with an above-ground stem had higher vine loads than did tall individuals and individuals without an above-ground stem. Tall *Iriartea* had a mean of 10.34 vines per individual (sd = 6.47), whereas short *Iriartea* had a mean of 2.31 vines per individual (sd = 2.56). For all palm groups, vines of the family Araceae comprised approximately 80% of the total vine load, with other less abundant vines including representatives in each of the other families. Vines of the family Cyclanthaceae comprised approximately 10% of the vine load. Vines in the Leguminosae


Welfia georgii
VINE LOAD (#vines/individual)
HEIGHT OF INDIVIDUAL (m)
40
0
0
40

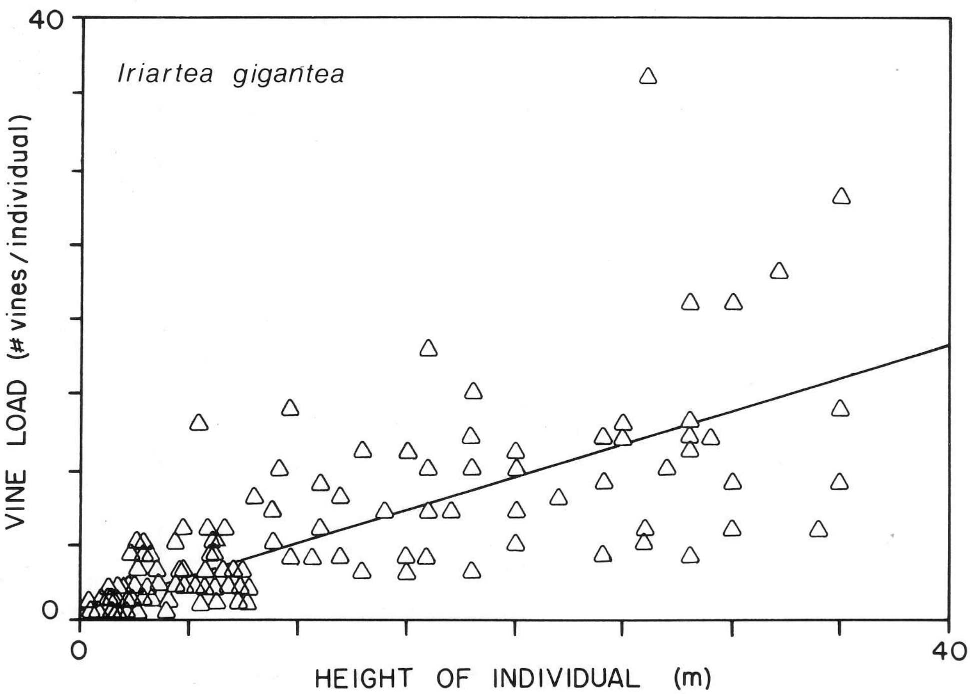

Iriartea gigantea
VINE LOAD (#vines/individual)
HEIGHT OF INDIVIDUAL (m)
40
0
0
40

Table 1. Taxa of vines on palms.[a]

Palm Group	n	Mean Vine Load	sd Vine Load	Proportion of Vine Load: Aro	Cycl	Mel	Pip	Fern	Leg	Other
Wg <13 m height	100	3.17	2.97	0.77	0.12	0.01	0.00	0.05	0.01	0.05
Without stem	66	1.94	1.99	0.85	0.01	0.00	0.00	0.08	0.02	0.05
With stem	34	4.97	4.00	0.70	0.20	0.02	0.00	0.03	0.00	0.05
Wg >13 m height	50	7.08	5.69	0.80	0.12	0.02	0.01	0.03	0.00	0.03
Ig <13 m height	100	2.31	2.56	0.82	0.10	0.01	0.03	0.02	0.00	0.02
Ig >13 m height	50	10.34	6.47	0.80	0.13	0.02	0.03	0.01	0.02	0.01

[a] Key to symbols: n = sample size; sd = standard deviation; Aro = Araceae; Cycl = Cyclanthaceae; Mel = Melastomataceae; Pip = Piperaceae; Fern = Polypodiaceae; Leg = Leguminosae; Wg = *Welfia georgii*; Ig = *Iriartea gigantea.*

(of which all were species of *Bauhinia*) and the miscellaneous category were small lianas (<0.5 cm stem diameter) and comprised only 2–7% of the vine load. In no case were larger lianas observed among the vine load. Most vines were root climbers, with the exception of some ferns, all Leguminosae, and all vines in the miscellaneous category, most of which were twiners.

Table 2 summarizes the proportion of individual palms with vines growing into the crown, the proportion of total vine load in the crown, and among the vines that grew into the crown, the proportion that was restricted to the lower crown. Although tall individuals had greater vine loads than short individuals, tall individuals had fewer vines growing into the crown. Among vines that grew into the crown, most were restricted only to the lower crown. In none of the 300 cases did we observe substantial blockage of light by leaves of vines. We did observe several cases where vines interfered with leaf expansion, all of which involved vines that grew into the upper crown (Fig. 1). We have observed some palms, not included in this study, that had crowns that were inundated by vines and had definite light blockage and interference with leaf development.

Table 2 also summarizes the proportion of individuals that were shedding leaves with vines attached. Among short individuals, 3–15% were shedding leaves with vines attached. Typically, the lowermost leaf was brown and beginning to fall, carrying any attached vines with it (Fig. 2). Short *Welfia* with an above-ground stem had a lower proportion of individuals with vines growing into the crown than either short *Welfia* without an above-ground stem or tall *Welfia*; and this same group had the highest proportion of individuals (15%) that were shedding leaves with vines attached. On numerous occasions we encountered recently fallen leaves on the forest floor that had vines attached to them (Fig. 3), however these cases were not systematically recorded. Entire vines were not necessarily torn from the trunk of a palm when a leaf fell, but rather were partially dislodged or broken. This disruption of the leading end of vines was especially prevalent among vines in the Araceae, and many aroids showed branching from secondarily released lateral buds.

←

2. Vine load, expressed as the total number of vines per individual palm, increases significantly with height ($P < .01$) within the arborescent palms A) *Welfia georgii* (n = 150; $r^2 = 0.26$; Y = 0.319X + 0.860) and B) *Iriartea gigantea* (n = 150; $r^2 = 0.56$; Y = 0.437X + 0.614). In both cases there is broad variance in the vine load for a particular height individual, especially among taller individuals.

Table 2. Palms that had vines growing into the crown and palms with vines falling with leaves. (Palm groups are as in Table 1.)

Palm Group	n	Proportion of Palms with Vines in Crown	Proportion of Vines in Crown	Proportion of Crown Vines in Lower Crown[a]	Proportion of Palms with Vines Falling with Leaves
Wg <13 m height	100	0.60	0.57	0.92	0.07
Without stem	66	0.70	1.00	0.93	0.03
With stem	34	0.47	0.24	0.90	0.15
Wg >13 m height	50	0.08	0.01	0.75	—
Ig <13 m height	100	0.37	0.29	0.87	0.03
Ig >13 m height	50	0.06	0.02	0.55	—

[a] The lower crown is here defined as the lowermost three leaves.

Table 3 summarizes findings concerning the taxa of vines that grew into palm crowns. Aroids comprised the majority of the vine load in palm crowns (75–97%), except in the case of tall *Iriartea* (22%). Only the aroid and miscellaneous categories were encountered in the crowns of tall *Welfia* and in the crowns of both short and tall *Iriartea*. Cyclanths, ferns, and legumes were encountered at low frequency in the crowns of short *Welfia*. Melastomes and pipers were not encountered in palm crowns.

Discussion

The greater vine loads on taller palms resulted from an accumulation of vines over time. The wide variance in vine loads among palms probably resulted because of differences in the microsites provided by the trunk, the rate of colonization by new vines, and the rate of death and detachment of vines. Tall palms had fewer vines growing into their crowns than short palms because the crowns grew above suitable microsites for some vines and because vines were shed with the leaves.

The prevalence of root climbers and absence of large lianas supports the hypothesis of Putz (1984) that the thick trunk of many palms deters attachment of lianas with twining stems and tendrils. *Welfia* shows little increase in stem diameter during height growth, and has a stem diameter at breast height of 15–25 cm even in short individuals, whereas stem diameter in *Iriartea* rapidly increases from 4 cm in short individuals to more than 20 cm in tall individuals (Rich 1985, 1986, Rich et al. 1985). In addition, the lack of branches in palms prevents colonization by lianas growing on surrounding trees. Palm stems are stiff near the base and flexible toward the crown (Rich 1985, 1986, in press), a characteristic that may also contribute to the exclusion of lianas (Putz 1984).

Aroids are the most abundant vines growing on palms in the forest at La Selva. Various characteristics favor aroids on the palm stems, including their ability to form root attachments to the broad, smooth surface of the palm trunks; their flexible, non-woody stems that allow bending with the palm stem; their ability to form leaves of different size and shape suitable for the different microhabitats at different heights (Givnish and Vermeij 1976); and their ability to continue growth after mechanical damage. Aroids that are broken or partially detached by falling palm leaves are often able to continue growth because axillary buds are released and efficient vascular connections are formed at these branching regions (French and Tomlinson 1984). The year-round rainfall and high humidity at La Selva provide an environ-

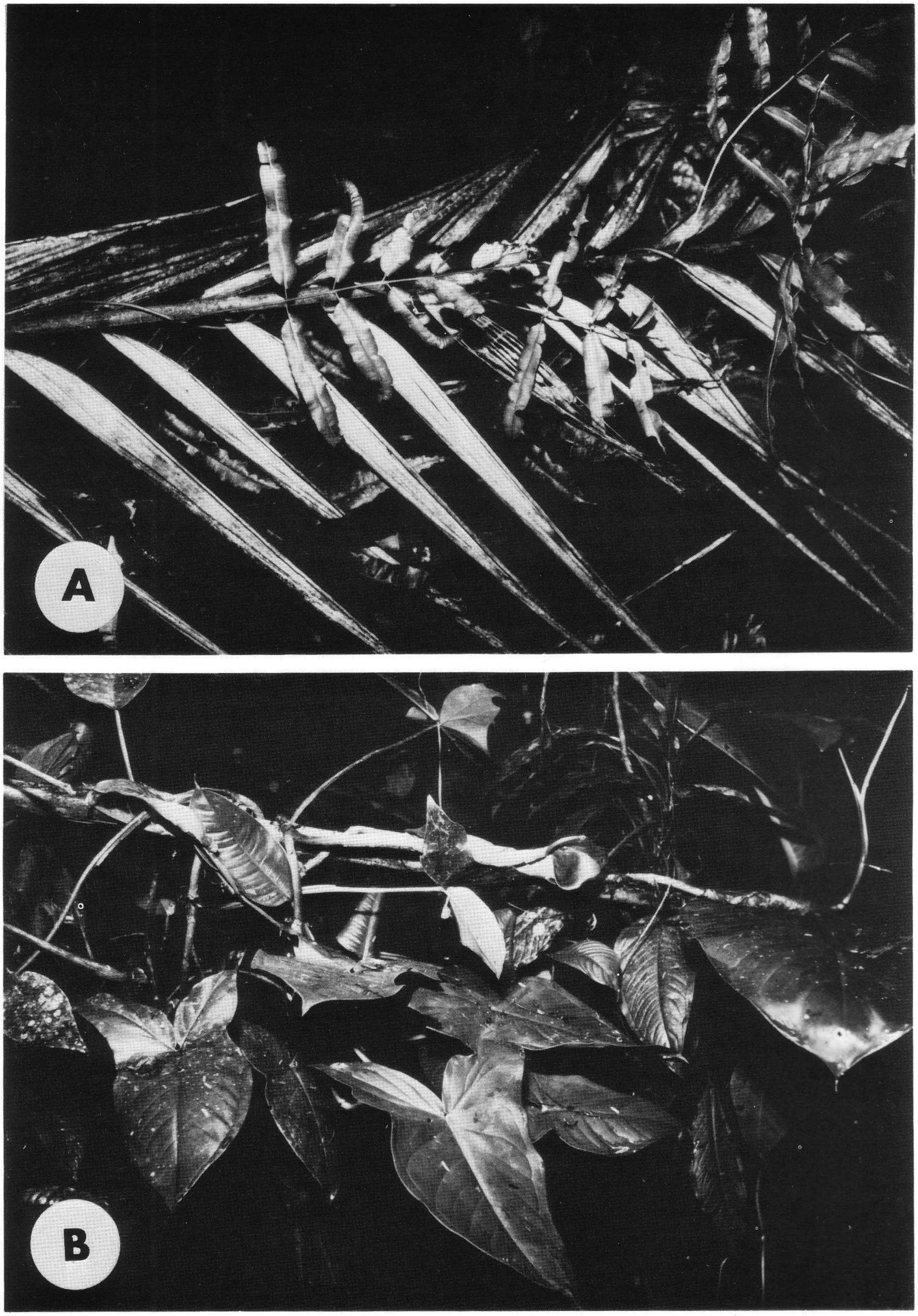
3. A) Palms can accumulate large vine loads at La Selva Biological Station, Costa Rica, as can be seen on the trunk of the palm *Welfia georgii*. Vines of the family Araceae comprising more than 80% of the vine load. B) When leaves are shed, they often carry adherent vines with them.

ment that is favorable for aroids and other non-woody evergreen vines. Most of the vines that were common on palm trunks, including aroids and cyclanths, are able to reproduce and complete their life cycle without growing into the crown.

The crown development and architecture of palms provide a mechanism for shedding vines. The large compound leaves expand at the top of the crown. Each leaf shifts from the top to the bottom of the crown and is sequentially shed (Tomlinson 1979, Hallé et al. 1978). When the weighty leaves fall, they dislodge any adherent vines (Putz 1984). The lack of branches and continual turnover of leaves helps to prevent palms from accumulating vines in the crown. Givnish (1978) observed that compound leaves, with leaflets arranged about a rachis, serve as tem-

Table 3. Taxa of vines that grew into palm crowns. (Palm groups and symbols are as in Table 1.)

Palm Group	n	Aro	Cycl	Mel	Pip	Fern	Leg	Other
Wg <13 m height	100	0.83	0.02	0.00	0.00	0.09	0.01	0.05
Without stem	66	0.85	0.01	0.00	0.00	0.08	0.02	0.05
With stem	34	0.78	0.05	0.00	0.00	0.13	0.00	0.05
Wg >13 m height	50	0.75	0.00	0.00	0.00	0.00	0.00	0.25
Ig <13 m height	100	0.97	0.00	0.00	0.00	0.00	0.00	0.03
Ig >13 m height	50	0.22	0.00	0.00	0.00	0.00	0.00	0.78



4. Fallen palm leaves on the forest floor at La Selva Biological Station, Costa Rica, often have vines attached to them. A) A leaf of *Welfia georgii* carried a twining fern (*Salpichlaena volubilis*) to the ground. B) Another

porary "throw-away branches" that are favored in many circumstances over presumably more expensive branches with similar arrangements of simple leaves. In arborescent palms, the large compound leaves not only serve as "throw-away branches" that form a parasol-shaped crown and enable exploitation of light in canopy openings, but also serve to help keep palm crowns free of vines.

Conclusion and Summary

Vine loads increased with individual height in *Welfia georgii* and *Iriartea gigantea*, but the proportion of vines reaching the crown decreased with height. About 80% of vines were in the family Araceae. Other vines included representatives of the Cyclanthaceae, Melastomataceae, Piperaceae, Leguminosae, and ferns. Most vines that grew on palms were root climbers. Vines that grew into palm crowns usually only grew on the lowermost leaves. Some vines that grew into the palm crowns interfered with proper leaf expansion, especially in younger palms. As palm leaves were shed from the base of the crown, adherent vines were dislodged. The lack of branches, thick stem, flexibility of the upper stem, and continual shedding of large compound leaves of palms all appear to contribute to keeping palm crowns relatively free of vines.

Acknowledgments

We thank Francis Putz and P. B. Tomlinson for their comments and the staff of the Organization for Tropical Studies for logistical support. Research was supported by the Atkins Garden Fund of Harvard University, the Jesse Noyes Foundation through the Organization for Tropical Studies, a Fulbright Graduate Fellowship, and National Science Foundation Doctoral Dissertation Improvement Grant #BSR84-13187.

Literature Cited

BLACK, H. L. AND K. T. HARPER. 1979. The adaptive value of buttresses to tropical trees: additional hypotheses. Biotropica 11: 240.

BOOM, B. M. AND S. A. MORI. 1982. Falsification of two hypotheses on liana exclusion from tropical trees possessing buttresses and smooth bark. Bulletin of the Torrey Botanical Club 109: 447–450.

CHARLES-DOMINIQUE, P., M. ATRAMENTOWICZ, M. CHARLES-DOMINIQUE, H. GERARD, A. HLADIK, C. M. HLADIK, AND M. PREVOST. 1981. Les mammiferes frugivores arboricoles nocturnes d'une foret guyanaise: interrelations plantes-animaux. Rev. Ecol. (Terre Vie) 35: 341–435.

CHAZDON, R. L. 1985. The palm flora of Finca La Selva. Principes 29: 74–78.

DARWIN, C. 1867. On the movements and habits of climbing plants. Journal of the Linnean Society, Botany 9: 1–118.

FEATHERLY, H. T. 1941. The effect of grapevines on trees. Oklahoma Academy of Science Proceedings 21: 61–62.

FRENCH, J. C. AND P. B. TOMLINSON. 1984. Patterns of stem vasculature in *Philodendron*. American Journal of Botany 71: 1432–1443.

GIVNISH, T. J. 1978. On the adaptive significance of compound leaves, with particular reference to tropical trees. In P. B. Tomlinson and M. H. Zimmermann (eds.). Tropical trees as living systems. Cambridge University Press. pp. 351–380.

——— AND G. J. VERMEIJ. 1976. Sizes and shapes of liane leaves. American Naturalist 100: 743–778.

HALLÉ, F., R. A. A. OLDEMAN, AND P. B. TOMLINSON. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, New York.

HARTSHORN, G. S. 1983. Plants: introduction. In D. H. Janzen (ed.). Costa Rican natural history. University of Chicago Press, Chicago. pp. 118–157.

JANZEN, D. H. 1973. Dissolution of mutualism between *Cecropia* and its *Azteca* ants. Biotropica 5: 15–28.

LUTZ, H. J. 1943. Injuries to trees caused by *Celastrus* and *Vitis*. Bulletin of the Torrey Botanical Club 70: 436–439.

MAIER, F. E. 1982. Effects of physical defenses

←

leaf of *Welfia georgii* carried several aroids to the ground. In this case, some of the aroids broke off, with a portion remaining attached to the palm trunk.

on vine and epiphyte growth in palms. Tropical Ecology 23: 212–217.

MONTGOMERY, G. G. AND M. E. SUNQUIST. 1978. Habitat selection and use by two-toed and three-toed sloths. In G. Montgomery (ed.). The ecology of arboreal folivores. Smithsonian Institution Press, Washington.

PUTZ, F. E. 1980. Lianas vs. trees. Biotropica 12: 224–225.

———. 1983. Liana biomass and leaf area of a "Tierra Firme" forest in the Rio Negro Basin, Venezuela. Biotropica 15: 185–189.

———. 1984. How trees avoid and shed lianas. Biotropica 16: 19–23.

RICH, P. M. 1985. Mechanical architecture of arborescent rain forest palms in Costa Rica. Ph.D. Dissertation. Harvard University.

———. In press. Mechanical structure of the stem of arborescent palms. Botanical Gazette.

———. 1986. Mechanical architecture of arborescent rain forest palms. Principes 30: 117–131.

———, K. HELENURM, D. KEARNS, S. MORSE, M. PALMER, AND L. SHORT. 1986. Height and stem diameter relationships for arborescent palms and dicotyledonous trees of Costa Rican tropical wet forest. Bulletin of the Torrey Botanical Club. 113: 241–246.

RICHARDS, P. W. 1952. The tropical rain forest: an ecological study. Cambridge University Press, Cambridge.

SICCAMA, T. G., G. WEIR, AND K. WALLACE. 1976. Ice damage in a mixed hardwood forest in Connecticut in relation to *Vitis* infestation. Bulletin of Torrey Botanical Club 103: 180–183.

TOMLINSON, P. B. 1979. Systematics and ecology of the Palmae. Annual Review of Ecology and Systematics 10: 85–107.

TRIMBLE, G. R. JR., AND E. H. TRYON. 1974. Grapevines, a serious obstacle to timber production on good hardwood sites in Appalachia. Northern Logger 23: 22–23.

WEBB, L. J. 1958. Cyclones as an ecological factor in tropical lowland rain forest, North Queensland. Austr. J. Bot. 6: 220–228.