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Spatially limited clonality and pollen and seed dispersal in a characteristic climber of Central African rain forests: *Haumania danckelmaniana* (Marantaceae)

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ABSTRACT

Gene dispersal and clonality are important aspects of plant evolution affecting the spatial genetic structure (SGS) and the long-term survival of species. In the tropics these parameters have mostly been investigated in trees and some herbs, but rarely in climbers which frequently: (1) show clonal growth leading to a patchy distribution pattern similar to that of understory herbs; and (2) flower in the canopy where they may have access to long-distance dispersal like canopy trees. We thus hypothesize for climbers an intermediate genetic structure between herbs and trees. The study aims at assessing breeding system and spatial extent of clonality and gene dispersal in *Haumania danckelmaniana* (Marantaceae), a common climber in the tropical rain forests from western Central Africa. In eastern Cameroon, 330 ramets were sampled at three spatial scales and genotyped at seven microsatellite loci. Clonality was moderate (clonal extend: 15–25 m, clonal diversity 0.4–0.65) indicating the importance of recruitment from seeds at this locality. The low inbreeding (F_{IS}) suggested predominant outcrossing. The rate of decay of the relatedness between individuals with distance indicated limited gene dispersal distance (σ_g = 9–50 m, neighborhood sizes Nb = 23–67) in accordance with narrowly gravity dispersed seeds and restricted pollen transfer distance in densely flowering populations. The marked SGS (Sp = 0.011–0.026) was similar to that reported in tropical trees, but might increase with augmented clonality as in many herbs, especially under more severe disturbance regimes.

Key words: Cameroon; clonality; gene dispersal distance; microsatellites; perennial climbers; Sp statistic; tropical understory.

Gene dispersal and clonality are important aspects of plant evolution (Mallet 2001). Frequent long-distance gene dispersal (*i.e.*, high gene flow) will ensure relatively high genetic diversity within populations, which is important for the long-term survival of a species, including the preadaptation to a changing environment (Kremer *et al.* 2012). It may, however, prevent local adaptation and speciation and thereby evolutionary diversification (Ackerman & Ward 1999, Coyne & Orr 2004, but see also Smith *et al.* 2005). Restricted gene flow instead might allow for local adaptation and speciation (see Galen *et al.* 1991, Sambatti & Rice 2006, Akerman & Bürger 2014), but also carry along the risk of extinction due to an accumulation of deleterious alleles and/or the lack of appropriate variants preadapted to a changing environment (Couvet 2002). Although clonality is a means of vegetative propagation without genetic changes, its evolutionary advantage lies in the establishment of a local population able to establish and persist through times of adverse conditions where sexual reproduction is hindered by a temporal or spatial lack of suitable partners for reproduction (Haddadchi *et al.* 2014) and/or of pollen and dispersal agents (Ehrlén & Lehtilä 2002, Honnay & Bossuyt 2005, Honnay *et al.* 2006, Silvertown 2008). Thus, knowledge on the extent of gene dispersal, shaped by pollen and seed dispersal, and clonality is important for predicting the ability of a plant species to persist in the future and cope with environmental changes (Kremer *et al.* 2012).

In the tropical rain forest, gene dispersal has been mostly investigated in trees. As trees in this very species-rich environment typically occur at low population density and are mostly self-incompatible (Stacy *et al.* 1996, Huang *et al.* 2003, Fashing *et al.* 2004, Laurin *et al.* 2014, Peh *et al.* 2014), pollen is usually transferred over large distances, often by bees, resulting in extensive breeding areas (Bawa 1990, Ward *et al.* 2005, Born *et al.* 2008, Dick *et al.* 2008, Daïnou *et al.* 2014). The efficiency and distance of seed dispersal in tropical trees, in contrast, might vary considerably according to the dispersal vectors ranging from wind to large animals (Hamilton 1999, Dick *et al.* 2008, Bizoux *et al.* 2009, Ndiade-Bourobou *et al.* 2010).

In contrast to tropical trees, gene flow in tropical herbs and climbers (including lianas, 'woody'; and vines, 'non-woody'), which contribute substantially to rain forest plant diversity (Bobo *et al.* 2006, Schnitzer *et al.* 2012) has been far less investigated (but see for herbs: Rusterholz *et al.* 2009, Cuartas-Hernández *et al.* 2010, Vandepitte *et al.* 2010, Lasso *et al.* 2011, Schleuning *et al.* 2011, for woody climbers: Foster & Sork 1997, Wang *et al.* 2009, and for non-woody climbers: Terauchi 1990, Godt & Hamrick 1993). However, the spatial genetic structure (SGS), *i.e.*, the non-random distribution of alleles or genotypes in space or

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time (Loveless & Hamrick 1984), differs significantly among life forms, being generally stronger in herbs than in trees (Vekemans & Hardy 2004, Duminil *et al.* 2007, see also for herbs, *e.g.*, *Gst* in nuclear markers in Nybom 2004) with specific information on climbers still lacking (but see Terauchi 1990). The causal factors for a stronger genetic structure in herbs are as follows: (1) a more patchy population structure than in trees (Melendez-Ackerman *et al.* 2005), often shaped by clonal growth, *e.g.,* via adventives shoots, rhizomes, or bulbils (Sagers 1993, Kennedy 2000, Schleuning *et al.* 2008); (2) visits by less-mobile pollinators in the understory (compare for tropical trees: Carbone *et al.* 1999, Ward *et al.* 2005, Dick *et al.* 2008, for understory shrub: Westcott & Graham 2000, Zeng *et al.* 2012, for tropical understory herbs: Cuartas-Hernández *et al.* 2010, Lasso *et al.* 2011); (3) for wind-dispersed diaspores, less efficient dispersal from the understory than from the canopy which can be subject to strong winds; and (4) self-fertilization that tends to be more common in herbs than in trees (Duminil *et al.* 2009).

Climbers ascend to the forest canopy using other plants as support (Bongers *et al.* 2002). By flowering high up in the canopy, climbers might take advantage of the same long-distance dispersing vectors as canopy trees, but their local population structure might be more similar to some clonal understory herbs because their high rate of clonality and the fact that flowering individuals are mainly restricted to gaps and forest edges with favorable light conditions lead to a rather clumped spatial distribution (Terauchi 1990, Schnitzer *et al.* 2000, 2012, Nabe-Nielsen & Hall 2002, Ledo & Schnitzer 2014). Overall, clonality in climbers serves primarily to reduce competitors by impeding their recruitment (Penalosa 1982, Stevens 1987, Bongers *et al.* 2002, Doucet 2003). Thereby, climbers often show a particular vigorous clonal growth after environmental disturbance (*i.e.*, an opening of the closed forest canopy), resulting in a higher climber diversity and abundance in treefall gaps than in non-gap areas (Schnitzer & Carson 2001, Dalling *et al.* 2012, Ledo & Schnitzer 2014). The mating system has rarely been documented in climbers, but both predominantly outcrossing and selfing has been recorded (see Terauchi 1990, Foster & Sork 1997, Meeus *et al.* 2011).

The SGS of a climbing species might thus be expected to be intermediate between that found in herbs and trees with high structuring at small scale, due to the clumping of closely related ramets after cloning and low structuring at larger scale thanks to a large breeding area due to their flowering in the canopy with access to long-distance pollination vectors.

The aim of this study was to characterize, for the first time, the spatial extent of clonality and gene dispersal of a frequent Central African rain forest climber species: *Haumania danckelmaniana* (Marantaceae). To this end, the SGS of its populations was assessed at different scales using microsatellite markers to: (1) quantify clonal diversity and growth at a very local scale; (2) assess the breeding system (outcrossing rate) from the population inbreeding coefficient; and (3) estimate indirectly the mean gene dispersal distance using isolation by distance model predictions.

MATERIALS AND METHODS

Plant material, study area, and sampling design.—The study species *H. danckelmaniana* (J. Br. & K. Schum.) Milne-Redh. (Marantaceae) is a frequent perennial climber occurring in the understory, in gaps, and at the edges of tropical lowland rain forest in Cameroon, Equatorial Guinea, Gabon, and the Republic of the Congo (Dhetchuvi 1996). It can propagate clonally via rhizomes (Dhetchuvi 1996) just as all other species of the family Marantaceae (see also Kennedy 1978). As a perennial climber, *H. danckelmaniana* climbs to the tree canopy via zigzag shoots supported passively by the surrounding vegetation (Tomlinson 1961, Schönecker 2006). Growth rate of aboveground shoots can be very fast providing the capacity of sudden rapid growth in forest gaps (Schönecker 2006). Plants of this species flower massively for a few weeks only during the rainy season (Ley 2008). The flowers are pollinated by different species of large carpenter bees and sunbirds (see Ley & Claßen-Bockhoff 2009). Fruit set of the large and heavy brown capsular fruits is about 11 percent (Ley & Claßen-Bockhoff 2013) and the only dispersal mechanisms so far inferred for these fruits is by gravity, water (Ley 2008), and potentially rodents.

The study was conducted in Eastern Cameroon in the forest concession of the logging company Pallisco (Fig. S1). The area is characterized mostly by a dense humid semi-deciduous forest (Letouzey 1968, Doucet 2003, Sacipef 2004) with an average annual temperature around 24°C and an average annual precipitation between 1550 and 2000 mm with maxima reached during the two rainy seasons from April to May and September to October (Feteke 2007). The topography of the area is rather flat at an elevation of around 700 m (Feteke *et al.* 2004). The forest has been exploited through selective logging since the 1980s for about 20 tree species (Betti 2003, Pallisco 2007). The eight study sites (Fig. S1) were situated in areas where the time since last exploitation allowed the reestablishment of a closed canopy and a mixed understory.

For the determination of clonal size, we conducted an exhaustive sampling of 58 ramets in a central plot of 15 × 25 m in a forest (Fig. S1 inset within plot 5) of average light availability (secondary growth with numerous small trees). To assess the SGS at a local scale and verify whether extensive clones could occur, we sampled further 97 ramets every 20–150 m along four transects (0.6, 1.5, 3, and 4 km long) starting from the central plot in four different directions (Fig. S1). For analyses of gene flow at the landscape scale, we sampled 175 ramets in eight plots (about 20 ramets per 1 × 1 km² plot, minimum distance between adjacent ramets is 100 m to avoid collecting repeatedly the same clone, *i.e.,* this distance is considerably larger than the here estimated clonal size). The plots were distributed across the forestry concession Pallisco, separated by 1–100 km (Fig. S1). We collected silica gel dried leaf material from each ramet for genetic analyses.

Ramet density (D_r) was estimated by exhaustive counting of ramets within the central plot and within 32 subplots chosen

randomly (independently of the presence of *Haumania*) along the four transects in the area of plot 5 (subplots were 20 m long and 3 m or 6 m wide).

Microsatellite genotyping.—For DNA extraction and SSR genotyping we followed the protocol described in Ley and Hardy (2016) by using the seven primer pairs F2, F28, F62, F66, F70, F74, and F80 (Table S1). Raw data of SSR genotypes used in this study are available in Table S2 and S3.

Calculation of clone size and diversity.—To determine if identical genotypes consisting of seven microsatellite loci were necessarily clones, the probability P_{gen} (Parks & Werth 1993) that a non-inbred zygote would acquire a given diploid genotype by chance was calculated within the dataset of 155 genets from the central plot plus transects using GENALEX 6.4 (Peakall & Smouse 2006). $P_{gen} = (\Pi p_i)2^h$, where p_i is the frequency in the population of each allele (two per locus) presented in the genotype and h is the number of heterozygous loci (Parks & Werth 1993). The probability of observing at least one identical genotype by chance is calculated as the probability the genotype is *not* encountered among G genets subtracted from unity: $P_{sec} = 1-(1-P_{gen})^G$. Although the number of genets, G, cannot be known with certainty, in this case it can be approximated closely as the number of distinct genotypes obtained (Parks & Werth 1993).

Clones (genets) were delineated considering (1) only perfect genotypic matches using the multilocus matches function in GenAlEx v6 (Peakall & Smouse 2006) (strict clone delimitation); and (2) near-perfect genotypic matches, allowing a mismatch at no more than one locus for which there is one allele shared or alleles with sizes differing by at most two base pairs to account for possible genotyping errors (relaxed clone delimitation). In both approaches missing genotypes were considered as mismatches if the particular individual had more than one missing locus. Clonal diversity R was calculated as $R = (G-1)/(n-1)$, where n is the number of sampled ramets (Dorken & Eckert 2001). R varies from 0 when all n plants in a sample possess the same genotype and form thus a single clone, to 1, when all plants possess different genotypes.

Genetic diversity and differentiation in the eight plots.—The eight sampled plots were characterized by calculating the following measures of genetic diversity: the number of alleles, the allelic richness (R_S) corrected for sample size (El Mousadik & Petit 1996) as estimated in Fstat 2.9.3.2. (Goudet 1995), and the observed (H_o) and expected (H_e) heterozygosity (Nei 1978) using INEst (Chybicki & Burczyk 2009). To check for the presence of null alleles, *i.e.*, the false absence of alleles (*e.g.,* due to a mutation in the primer region), we also used the software INEst which jointly estimates inbreeding and null allele frequencies under the individual inbreeding model (IIM), yielding two values of F_{IS}, the second one being corrected for null alleles. In the presence of null alleles, diversity and differentiation values will be underestimated as potential heterozygotes will appear as homozygotes (Chapuis & Estoup 2007). To characterize how local stands are isolated by spatial distance, we estimated genetic differentiation between plots using pairwise $F_{ST}/(1-F_{ST})$ calculated in SPAGeDi (Hardy & Vekemans 2002) and regressed on the logarithm of distance. F_{ST} is a standard measure of genetic differentiation (Wright 1943) ranging from 0 at no differentiation to 1 at complete differentiation. Theoretical models of isolation by distance show that the ratio $F_{ST}/(1-F_{ST})$ is expected to increase linearly with the logarithm of the distance at a rate inversely proportional to gene dispersal distances (Rousset 1997).

Analyses of spatial genetic structure and gene dispersal distance.—The impact of clonality and gene dispersal distance on the fine-scale SGS was assessed by the pattern of decay of relatedness between individuals with spatial distance using the software SPAGeDi (Hardy & Vekemans 2002) (for more details see Appendix S1).

RESULTS

Clonality in *Haumania danckelmaniana*.—Using the strict versus the relaxed clone delimitation for the 58 ramets sampled in the central plot of 15 × 25 m, 38 and 23 genets were found, respectively (eight genets consisting of 2 to 8/11 ramets and 30/15 other genets with one ramet each; Table 1, Figs. 1A and B). Ramets belonging to the same genet were generally spatially aggregated with an average distance below 2 m and 7 m depending on the model of clone delimitation. Under the strict model only in two genets (C, F) the ramets appeared to be more widely dispersed (>2 m but <10 m between adjacent ramets), but being supported as coming from the same genet by their low P_{sec} values: P_{sec} (C) = 0.0023, P_{sec} (F) = 0.0065 (Table S2). The maximal genet extent was 17 m under the strict and 26 m under the relaxed clone delimitation. The probability of obtaining by chance the same genetic profile (P_{gen}) under the strict clone delimitation using seven loci (*i.e.*, only identical genotypes are clones) with the ramets from the central clonality plot and the adjacent transects in plot 5 is given in Table S2 (P_{gen} = 0.00056).

Clonal (genet) diversity within the 15 × 25 m central plot ranged therefore from R = 0.65 with a population density of 0.10 genets and 0.15 ramets per m² to R = 0.39 and a density of 0.06 genets per m^2, respectively. As the number of distinct genets is probably overestimated under the strict clone delimitation (because this neglects possible genotyping errors) and underestimated under the relaxed clone delimitation (because the probability of having different genets with very similar genotypes is not negligible), the true values are probably within their ranges, *i.e.*, between 23 and 38 genets.

At the fine-scale of the central plot (distance range 0.5–25 m), a marked SGS was found among all ramets (Fig. 2, $b_F = -0.049 \pm 0.008$). When kinship was computed only between ramets from distinct clones, the $F(d)$ curve was less marked ($b_F = -0.026 \pm 0.007$), especially under the relaxed clone delimitation ($b_F = -0.014 \pm 0.007$). No clones were detected within the four sampled transects (N = 97) with an average distance between adjacently sampled ramets of

TABLE 1. *Clone characteristics of* Haumania danckelmaniana *in eastern Cameroon in an exhaustively sampled central clonality plot (15 × 25 m) within plot 5 applying two different methods (M) considering either only perfect genotype matches or also near-perfect genotype matches. Only genets represented by multiple ramets are shown. ID of genets corresponds to Table S1. The same IDs of clones represent identical groupings of ramets.*

M	ID of clones	No. ramets	Max. extent (m)
Perfect genotype match	A	4	4.80
	B	2	1.70
	C	2	11.00
	D	2	1.80
	E	3	1.50
	F	5	16.60
	G	2	2.30
	H	8	8.10
	Average over eight clones	3.50	5.98
Near-perfect genotype match	A	4	4.80
	BCD	6	25.00
	EF + 2 ramets	10	21.00
	GH + 1 ramet	11	8.60
	I	6	23.00
	K	2	2.60
	L	2	26.00
	M	2	20.00
	Average over eight clones	5.38	16.38

57 ± 38 m. Ramet density in the area of the transects was on average 0.11 ± 0.09 ramets per m² (Table S4). Applying the ratio of ramets to genets from the central plot to the estimated ramet density of transects, the estimated genet density along the transects was $D_g = 0.11 \times (38/58) = 0.072$ or $D_g = 0.11 \times 23/58) = 0.044$ genets per m² depending on the chosen clone delimitation criterion (strict vs. relaxed, respectively).

Genetic characterization of sampled plots.—We compared genetic diversity (H_e) between plots ranging from 0.40 in plot 7 to 0.63 in plot 8 (Table S5) (average: 0.52 ± 0.06). Considerable heterozygote deficiency was detected in plot 4 due to a single locus bearing a null allele. However, when the effect of null alleles was factored out using INEst, corrected estimates of F_{IS} were always close to zero, as expected under a predominantly outcrossing mating system. Assessing differentiation between plots gave a global $F_{ST} = 0.09 \pm 0.014$ with pairwise F_{ST} between plots increasing with distance from 0 to 0.30 (Fig. S2; Table S6). The highest differentiation was reached between the two spatially most isolated plots 7 and 8 and all other ones.

Spatial genetic structure and dispersal distance.—At the local scale of the four transects within plot 5 (distance range *ca* 50 m to 3 km), the kinship–distance curve $F(d)$ between genets displayed a significant SGS ($b_F = -0.011 \pm 0.004$, Pval < 0.001), leading to $Sp = 0.011$ (Fig. 3A). Assuming that the effective population density, De, ranged between ½ and 1/20 of the mean genet density ($D_g = 0.044$ under the relaxed clone delimitation), the estimated gene dispersal parameter σ ranged between 14 and 50 m, and the neighborhood size Nb between 39 and 67.

At the landscape scale of the eight plots (distance between adjacent plots ranged from 1 to 100 km), F(d) displayed a regular decay ($b_F = -0.023 \pm 0.004$, Pval < 0.001, Fig. 3B), leading to $Sp = 0.026$. When gene dispersal was estimated at this scale, as done above, the estimated σ ranged between 9 and 32 m, and the neighborhood size Nb between 23 and 35.

DISCUSSION

Clonality and its impact on spatial genetic structure.—Within the exhaustively sampled central plot (15 × 25 m), clones of *H. danckelmaniana* were spatially restricted with a few ramets per genet only and a maximal extend of 17–26 m (depending on clone delimitation approach) which is similar to genets found in the woodland herb *Uvularia perfoliata* (Liliaceae) (2–10 m, Kudoh *et al.* 1999); the temperate deciduous mountain herb *Paris quadrifolia* (Melanthiaceae) (<5 m, Jacquemyn *et al.* 2005); and the forest understory herb *Convallaria majalis* (Liliaceae) (*ca* 6 m, Vandepitte *et al.* 2010), but much smaller than found in the bracken fern *Pteridium aquilinum* (Dennstaedtiaceae) from temperate mountains (*ca* 400 m, Parks & Werth 1993) and the perennial Amazonian herb *Heliconia metallica* (Heliconiaceae) (*ca* 55 m, Schleuning *et al.* 2011). Specific information on clonal sizes of other climbers is to our knowledge unavailable. No clones were detected in the four transects as ramets were sampled at a distance of >20 m, confirming that clonality in *H. danckelmaniana* is limited at this locality.

Little can be said about the age of the observed *H. danckelmaniana* clones as rhizome growth rate is not yet documented in *Haumania*. However, it is documented in four related species from different genera of the African Marantaceae where rhizomes grow by about 0.2–0.5 m per year depending on light environment (Brncic 2002, compare also *H. metallica*: max. 0.65 m per year in Schleuning *et al.* 2008). Assuming a similar growth rate in *Haumania* at this locality of average light availability, the distances between ramets of the detected *H. danckelmaniana* clones indicate a minimum age of 30 years. However, this can only be a lower age estimate as Marantaceae have a nekrozom, *i.e.*, while the rhizome propagates in one direction, it dies at the other end (Tomlinson 1962, Brncic 2002, Schönecker 2006) so that the extent of the same clone in the past is no longer detectable.

Clonal diversity, *i.e.*, the proportion of ramets from distinct genets, in *H. danckelmaniana* was high ($R = 0.39–0.65$ in the 15 × 25 m central plot depending on the clone delimitation approach) compared to other clonal plants where the whole population was sometimes made of a single or a few clones only (see Vandepitte *et al.* 2010: *Convallaria majalis* R = 0–0.16 in 6 × 6 m plots, Schleuning *et al.* 2011: *H. metallica* R = *ca* 0.16 in

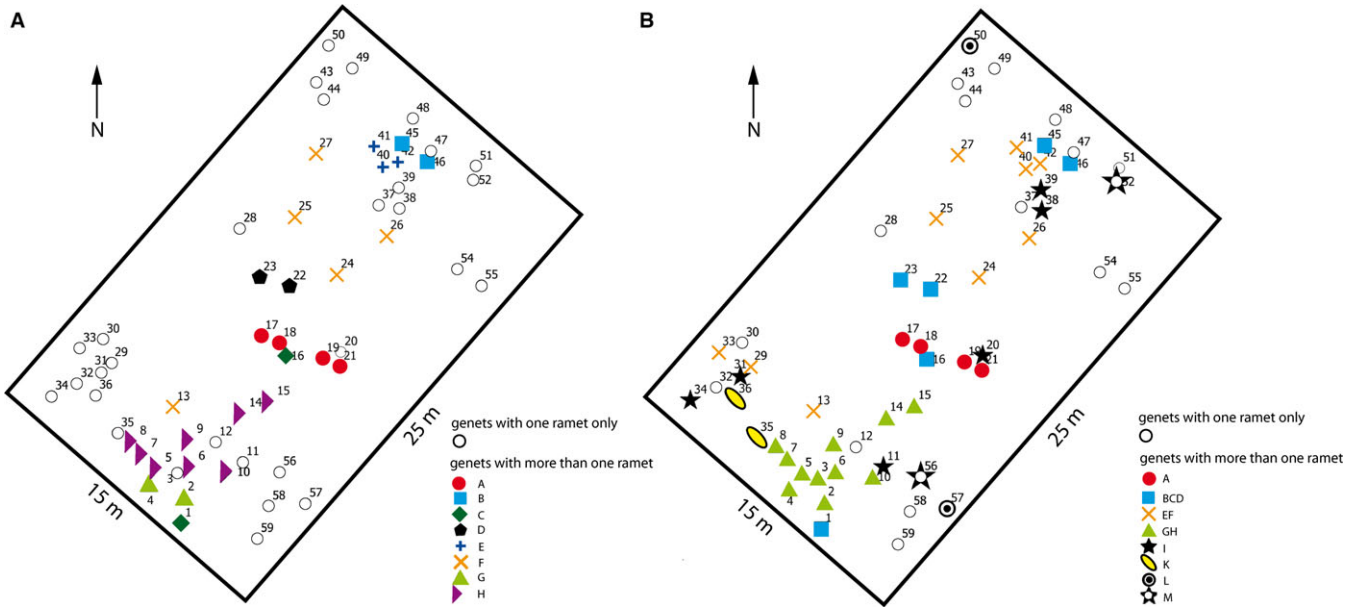

FIGURE 1. Clonality of 58 ramets (icons with ID) of *Haumania danckelmaniana* (Marantaceae) exhaustively sampled in a central clonality plot of 15 × 25 m situated in the center of plot 5 (see Fig. S1) based on seven microsatellites, allowing only perfect genotypic matches (A) and allowing also near-perfect genotypic matches (B). Ramets belonging to the same clone are illustrated by the same icon (see legend for clonal ID) except for white circles which represent genets with one ramet only.

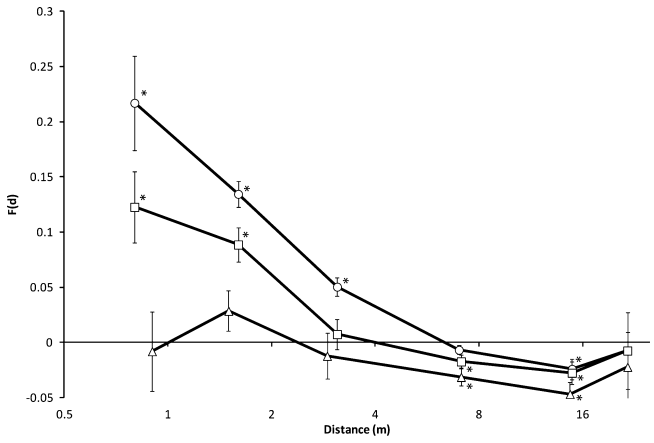

FIGURE 2. Kinship–distance curve between all ramets (circles), between genets under the strict clone delimitation (square) and between genets under the relaxed clone delimitation (triangle) in an exhaustively sampled central clonality plot (15 × 25 m) within plot 5 (for position see Fig. S1). Error bars indicate standard errors obtained by jackknifing over loci; *, indicate significance of $F(d)$ at $P < 0.01$.

6 × 9 m plots). The individual clones of *H. danckelmaniana* at the investigated site did not establish clear boundaries, but different genets were usually intermingled. The finding of small clone sizes and spatial mixing of distinct clones of *H. danckelmaniana* indicates a frequent recruitment from seeds at this locality. Multiclonal populations have been found elsewhere in clonal plants (see review of 21 clonal plants in Ellstrand & Roose 1987, *U. perfoliata* in Kudoh *et al.* 1999). The observed moderate clonal growth in *H. danckelmaniana* at this site might be due to the intermediate light regime at the study locality. An intermediate light regime enhances neither an uncontrolled growth of a single clone (Nabe-Nielsen 2000, Doucet 2003, Schnitzer & Bongers 2011), or a 'waiting' strategy of individual genets under a closed canopy (waiting strategy = long-term survival of small individuals with a very slow growth rate until a canopy opening occurs which incites their accelerated clonal growth, see Kudoh *et al.* 1999).

Currently, our conclusions are limited to forest conditions of average light availability (secondary growth with numerous small trees). In the future, clonal structure would have to be investigated under different environmental disturbance regimes (Vandepitte *et al.* 2010, Schleuning *et al.* 2011) and light conditions to estimate its ecological and evolutionary role for the *Haumania* species. Brncic (2002) found that environmental conditions considerably influence rhizome growth rate in other Marantaceae species, and other studies have shown that climbers might respond with vigorous clonal growth to forest disturbance that lead to an opening of the canopy and thus increased light availability (Schnitzer *et al.* 2012). In extreme cases maximal clonal size of climbers might attain over 500 m (Putz 1984). From *H. liebrechtsiana,* the close relative of *H. danckelmaniana* (Dhetchuvi 1996), it is known that it can establish large and dense stands (however, clonal size and diversity remain unknown) after forest disturbance (*e.g.*, logging), *e.g.,* at Lope, Gabon (White & Abernethy 1997) or in the Democratic Republic of the Congo (pers.

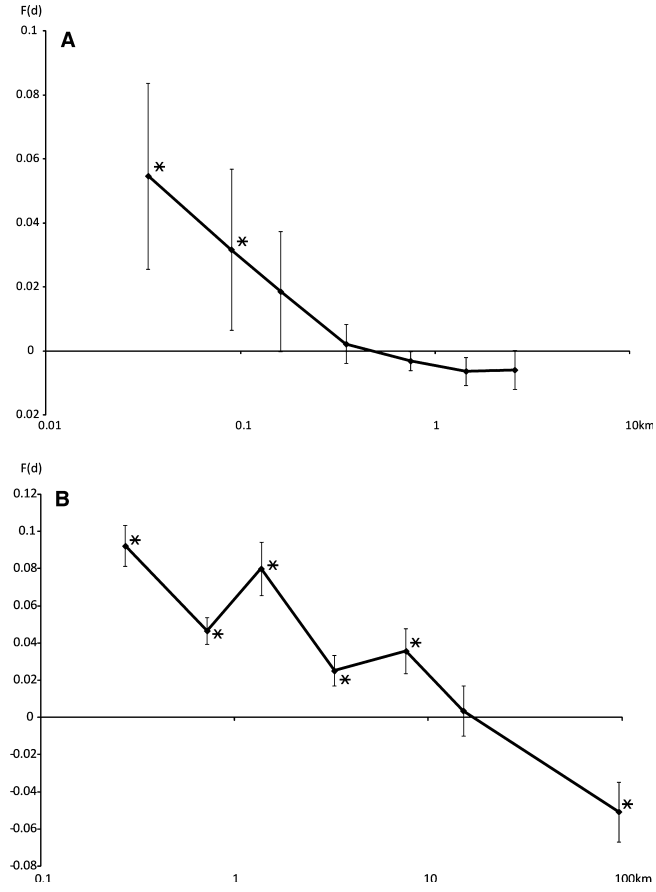

FIGURE 3. Average kinship between individuals of *Haumania danckelmaniana* (Marantaceae) at the local scale (*ca* 50 m to 3 km) with 105 ramets from the central plot and the four transects (A) and at the landscape scale (*ca* 1–100 km) with 175 ramets from eight plots (B) at Pallisco (Cameroon) according to geographical distances (log scale) based on seven microsatellites. Kinship coefficients between individuals are standardized relative to the unweighted average allele frequencies over all individuals. Error bars indicate standard errors obtained by jackknifing over loci; *, indicate significance of $F(d)$ at $P < 0.01$.

obs.). These stands might consist of a single or a few clones only with many ramets belonging to the same genet extended over a much larger area and resulting in a much lower clonal diversity. Such stands are so far unknown from *H. danckelmaniana* and might indicate a different potential for invasion between the two closely related species. This might be an important life-history trait explaining the different expansion histories assumed for the two *Haumania* species in Central Africa (see Ley & Hardy 2010).

Breeding system.—The close to zero F_{IS} estimates (corrected for null alleles) support the assumption of a low level of selfing (auto- and geitonogamous) in *H. danckelmaniana* in contrast to a Cameroonian woody climber which is highly inbred ($F_{IS} = 0.455$ in *Ancistrocladus korupensis,* Ancistrocladaceae, Foster & Sork 1997). Additional genetic studies in different populations of *H. danckelmaniana* from Cameroon and Gabon showed similarly low F_{IS} values (Ley & Hardy, unpubl. data). The results here for *H. danckelmaniana* are consistent with hand self-pollination experiments which in contrast to cross-hand pollination experiments did not yield any fruits (Ley & Claßen-Bockhoff 2013). The low selfing rate in *H. danckelmaniana* is probably based on an unknown, but effective mechanism of self-incompatibility. Given that pollinators often visit successively flowers from the same massively flowering individual, a high inbreeding would be expected if the species was self-compatible (Ley & Claßen-Bockhoff 2009). With its low rate of selfing, *H. danckelmaniana* differs strikingly from other family members which are largely self-compatible to even autogamous (Ley & Claßen-Bockhoff 2013). Levels of (in)compatibility are not uniform in climbers. While self-incompatibility is documented in a tristylos woody climber from La Reunion (Meeus *et al.* 2011), moderate selfing has been found in *Passiflora mollissima* from Hawaii (La Rosa 1992) and predominant outcrossing in *Dioscorea tokoro* (Terauchi 1990). However, the paucity of examples here shows that the breeding system of climbers is still insufficiently documented (see also the sexual system database for plants: The tree of sex consortium 2014, http://datadryad.org/resource/doi:10.5061/dryad.v1908).

Spatial genetic structure shaped by limited seed and pollen dispersal.—The SGS of *H. danckelmaniana* was significant at all scales investigated in agreement with isolation by distance expectations (Wright 1943). At a very local scale (15 × 25 m plot), clonality contributed substantially to this apparent strong genetic structure as demonstrated by the considerably less steep slope in the $F(d)$ curves when excluding comparisons between ramets of a same genet $Fg(d)$ vs. $Fr(d)$ curves). However, as even the $Fg(d)$ curves displayed a significantly negative slope, limited clonal growth alone could not explain the SGS of *H. danckelmaniana* at this scale (Fig. 2). Hence, it indicates additionally a rather limited seed (and possibly pollen) dispersal (see below for additional evidence).

Restricted seed and pollen dispersal was further corroborated by the very limited gene dispersal distance estimates (σ_g = 14–50 m, neighborhood size Nb = 39–67). Gene dispersal includes both seed and pollen dispersal and the contribution of each component to σ_g can be appreciated through the relationship $\sigma_g^2 = \sigma_s^2 + \frac{1}{2}\sigma_p^2$, where σ_s and σ_p represent the spatial extent of seed and pollen dispersal, respectively (Crawford 1984). Thus, even if σ_s was much smaller than σ_p ($\sigma_s \sim 0$), the extent of pollen dispersal could not be above *ca* σ_p = 70 m (using σ_g = max. 50 m). This can explain why population samples 100 km apart can reach an F_{ST} up to 0.3 despite a relatively continuous species distribution and even topography without any geographic barriers.

Narrow seed dispersal matches the ecological observations of *H. danckelmaniana*. Their large, heavy, and inconspicuously brown fruits without any adaptations for long-distance dispersal (*e.g.*, no means for ecto- or endozoic dispersal) are probably gravity and sometimes additionally rodent dispersed. The main seed dispersal vector in *H. danckelmaniana* might actually be

plant clonal growth: by producing and dropping a seed at the end of a long flowering shoot it might reach beyond the original position of the mother. Here, dispersal must be understood as the distance separating the progeny and its mother at the time of their respective establishment (germination; Gliddon *et al.* 1987).

Contrary to the narrow seed dispersal, narrow pollen dispersal was not expected in *H. danckelmaniana* because its main pollinators (large carpenter bees) are known to be able to perform long-distance flights when foraging (Ley & Claßen-Bockhoff 2009). The spatially limited effective pollen dispersal is probably induced by the high population density of *H. danckelmaniana*. Here, populations and individuals flower abundantly and in synchrony (Ley 2008), so that even pollinators able to cross long distances will probably perform a majority of short-distance flights because this strategy is more energetically cost effective (Cibuola & Zimmerman 1984). Flights between flowers of a same genet are probably ineffective because of the self-incompatibility system (see Ley & Claßen-Bockhoff 2013), but as we have shown that clones are highly intermingled locally, even short flights can lead to effective cross-pollination between genets.

The *Sp* statistic, as a quantification of the strength of the SGS, ranged in *H. danckelmaniana* between 0.010 at a local (50 m to 2 km) scale and 0.026 at a landscape (1–100 km) scale. The reason for the higher *Sp* value at the landscape scale remains unclear and inverse to our expectations but as the time needed for the kinship–distance curve to reach an equilibrium increases with the spatial scale investigated (Hardy & Vekemans 1999), there is more risk that the landscape-scale *Sp* value may be out of equilibrium and influenced by peculiar historical demographic events.

In any case, these *Sp* values of *H. danckelmaniana* are intermediate values when compared to tropical tree species (mean $Sp = 0.0173$; $N = 15$ species; Dick *et al.* 2008). In fact, tropical trees are also generally predominantly outcrossing and pollen is mostly animal dispersed. However, SGS tends to be related more to seed dispersal with lower values in trees with fruits dispersed by birds, bats, or monkeys (mean $Sp = 0.009$, $N = 6$) than by gravity, wind, and/or scatter-hoarding rodents (mean $Sp = 0.023$, $N = 9$) (Dick *et al.* 2008).

The reason why the strength of SGS remains similar despite contrasted gene dispersal distances between trees ($N = 10$, range 141–1180 m; Hardy *et al.* 2006) and our climber model (mean $\sigma_g = 40.6$ m) can be explained by their contrasted densities: *ca* one to six adult trees per ha in the tree populations studied by Hardy *et al.* (2006) compared to *ca* 500 genets per ha around plot 5 in *H. danckelmaniana*. Indeed, SGS results from a balance between gene dispersal distance and local genetic drift, which both correlate somehow negatively with adult density, so that measures of SGS must be scaled to population densities to compare the strength of SGS between species.

In contrast to trees, the SGS for some tropical herbs and shrubs such as *Piper* spp. is much stronger (*Sp* from 0.03 to 0.136) suggesting considerable substructuring due to a combination of limited seed and pollen dispersal, clonality, and selfing (Lasso *et al.* 2011). In a review of (mostly temperate) plants, Vekemans and Hardy (2004) also reported a trend of much stronger SGS in terrestrial herbaceous life forms (mean $Sp = 0.046$, $N = 26$) than in trees (mean $Sp = 0.010$, $N = 17$), suggesting less efficient seed and pollen dispersal relative to population densities in the former. The SGS of other canopy dwelling species, *i.e.*, epiphytes, are quite variable and depend very much on the individual life-history traits. Although a strong structure is found in most epiphytic bromeliads (clonal growth, vertebrate pollination, diverse breeding system from predominant inbreeding to predominant outbreeding in Gonzalez-Astorga *et al.* 2004, Zanella *et al.* 2011, Zanella *et al.* 2012, Cascante-Marín *et al.* 2014), a low structure is reported in most orchids (Murren & Ellison 1998, Ackerman & Ward 1999) and another wind-dispersed perennial climber (*Dioscorea tokoro*, Terauchi 1990), probably due to considerable gene flow by wind-borne seeds that may disperse over long distances.

CONCLUSION

This is, to our knowledge, only the second study on clonality and gene flow in a tropical African climber (see Foster & Sork 1997) with several genetic measures for a climber reported here for the first time. It demonstrates very limited seed and pollen dispersal distances in the studied climber and a SGS similar to trees. This is contradictory to our initial hypothesis that climbers would present a SGS intermediate between the ones of trees and herbs. The fact that our studied model appears more similar to the case of trees may be explained by the following factors: (1) it is mainly an outcrossing species; (2) clonal growth remains limited; and (3) the effect of limited pollen and seed dispersal is partly reversed by limited drift due to a high population density.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Geographic position of the study area and the eight sampled plots within the forestry concession Pallisco in the

East of Cameroon.

FIGURE S2. Pairwise $F_{ST}/(1-F_{ST})$ versus distance (km) comparing eight plots with about 20 individuals each of *Haumania danckelmaniana* at Pallisco, Cameroon.

APPENDIX S1. Analyses of spatial genetic structure and gene dispersal distance.

TABLE S1. *Microsatellite primers used in this study.*

TABLE S2. *Probabilities of random occurrence of a diploid genotype identical at the 7 microsatellite markers used in each of the 155 Haumania danckelmaniana individuals sampled.*

TABLE S3. *Genotypes from 7 microsatellites for 175 individuals from 8 plots at Pallisco, eastern Cameroon.*

TABLE S4. *Ramet density in 32 random plots along the four transects established in plot 5.*

TABLE S5. *Genetic characterization of eight plots of Haumania danckelmaniana at Pallisco, Cameroon based on calculations in ° FSTAT and # INEst.*

TABLE S6. *Matrix of pairwise* F_{ST} *and spatial distance of eight populations of* Haumania danckelmaniana *at Pallisco, Cameroon.*

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