Comparative population studies in two *Cissus* species (Vitaceae) across fragmented and undisturbed rainforest habitats

Claire Arnold and Maurizio Rossetto

Claire Arnold[1,2] and Maurizio Rossetto[1,3] ([1]Centre for Plant Conservation Genetics, Southern Cross University, Lismore NSW 2480; [2] National Centre of Competence in Research Emile-Argand 11, CH-2007 Neuchâtel, Switzerland; [3] Royal Botanic Gardens and Domain Trust Sydney, Mrs Macquaries Rd, Sydney NSW 2000) 2002. Comparative population studies in two Cissus *species (Vitaceae) across fragmented and undisturbed rainforest habitats.* Cunninghamia *7(4): 683–693).*

This preliminary study investigated the interaction between ecological, environmental and genetic factors among two native vines, *Cissus hypoglauca* and *Cissus sterculiifolia* (family Vitaceae). Data from a number of fragmented populations within the Big Scrub and surrounding rainforest areas in northern NSW were used to investigate how closely related vines respond to habitat fragmentation. What has emerged is an account of two species occupying fairly distinct ecological niches, and consequently being differently affected by current environmental disturbances. *Cissus hypoglauca* appears to have greater ecological amplitude, including resilience to drier environmental conditions, while in the long term *Cissus sterculiifolia* is likely to be more extensively affected by rainforest degradation and fragmentation. Genetic analysis suggests that prior to extensive clearing the Big Scrub provided a continuum for gene flow across otherwise fairly disjunct rainforest areas. This pilot study illustrates how simple research can often support the development of long-term conservation and management strategies at the species and plant community level.

Introduction

Rainforest habitats worldwide are increasingly under pressure from degradation, over-exploitation and clearing. In north-eastern New South Wales, the Big Scrub Lowland Rainforest originally extended from the Richmond River to the Nightcap Range and across to the coastal escarpment. The area included the rich basalt and basalt alluvia denoting ancient volcanic activity in the region (Lott & Duggin 1993). Early vegetation cover occupied an area of more than 75 000 ha and, prior to European settlement, represented the largest continuous expanse of lowland sub-tropical rainforest in Australia (Adam 1992). The Big Scrub is included within a very important biodiversity region extending across the eastern border between NSW and Queensland; over 50 endemic genera are found in this region and more than 200 species are at their most southern or northern limits (Lott & Duggin 1993). Unfortunately, swift environmental degradation through logging and clearing resulted in the demise of most of the original rainforest cover by the early twentieth century (Connelly & Specht 1988). Today, less than 600 ha (approximately 0.7%) of the Big Scrub remain, arguably elevating it to the ranks of one the most endangered rainforest communities in the world. What is left is fragmented into around 40 isolated remnants, many under 10 ha in size but still containing remarkable species diversity (Lott & Duggin 1993). These rainforest fragments are small, under pressure from numerous external factors and unlikely to be evolutionary viable in the long term unless appropriate conservation and management actions are undertaken.

Lianas (or woody vines) play an important role in rainforest regeneration, maintenance of biodiversity and ecosystem processes. They are a polyphyletic group sharing a common strategy based on using the architecture of other plants to ascend the canopy (Schnitzer & Bongers 2002). The Vitaceae family is an important world-wide group of woody climbers with five genera and 30 species represented in Australia. Recent molecular studies have shown that *Cissus* (the largest genus with 14 Australian species, Jackes 1988) is not monophyletic, with five species being segregated from it (Rossetto et al. 2001, Rossetto et al. 2002). Two of these species, *Cissus hypoglauca* A. Gray and *Cissus sterculiifolia* Planch., are reasonably common in NSW and are the focus of this study. *Cissus hypoglauca* (Giant Water Vine) is a vigorous evergreen vine with thick stems, rusty-pubescent young shoot and tendrils, and five-foliate, palmately-compound leaves. Inflorescences are paniculate with terminal umbels and berries are purplish-black and globular. It occurs from southern New Guinea to Victoria in southern Australia, and is associated with rainforests, vine forests and occasionally eucalypt forest margins (Jackes 1988). *Cissus sterculiifolia* is also an evergreen, vigorous vine with palmately-compound leaves and a prominent yellowish-green midrib. Inflorescences are umbellate and the ovoid to elongate-falcate berries are purplish-black. This species occurs in rainforests from southern New Guinea to northern NSW (Australia) with occasional records as far south as Sydney (Jackes 1988).

The importance of vines in the dynamics of forest community has been rarely investigated (Arnold 1999, Schnitzer & Carson 2001). As a result, the understanding of their role in forest dynamics has lagged behind that of other plant groups (Schnitzer & Bongers 2002). Within an undisturbed and well-structured forest edge or a mid-sized gap vines can produce a dense foliage cover, which protects the forest from damaging external factors such as wind, light, weeds and disease (Wiens et al. 1985). Forest disturbance, or 'edge effect', can be detected up to 500 m within the margin of a forest, with the first 200 m being the most affected (Sizer & Tanner 1999, Mesquita et al. 1999). Where large openings or significant edge disturbance occur, drying winds and sunlight penetration can have irreversible effects on shade and humidity-loving species (Winter et al. 1984). Furthermore, weed species are usually more competitive in disturbed habitat (Bungard et al. 1998) potentially increasing the loss of native species diversity (Connelly & Specht 1988). The rapid growth rates and spread of native vines make them efficient competitors as they rapidly close gaps. However they are sometimes considered as having a negative impact on tree regrowth, especially within smaller remnants and, as a consequence, are deliberately restrained.

Vines also play an important role in organic matter cycles and soil stabilisation. This is because lianas, unlike most trees, allocate greater biomass to photosynthetic tissues than to supporting structures (Roldan & Varela 1999). However, vines are different from other structural parasites in that they remain rooted to the ground (Schnitzer & Bongers 2002). As a result, their contribution to the leaf litter reaches up to 24 % in subtropical rainforests in North Eastern NSW (Hegarty 1988). Overall, vines have an important role in the regeneration and conservation of rainforests, particularly within disturbed habitats.

The aim of this study was a preliminary investigation of the ecological, genetic and environmental factors affecting distribution and persistence of *Cissus hypoglauca* and *C. sterculiifolia*. The data obtained from a mixture of fragmented sites from the Big Scrub and undisturbed sites from surrounding rainforest areas will represent a new insight into the effects of rainforest clearing on native vine species.

Materials and Methods

Sites description

Our study compared some of the biggest remaining Big Scrub fragments to undisturbed areas within northern and southern regions of north-eastern NSW. In data analysis, belonging to a rainforest area was measured as a binomial value. For each individual sampled for genetic analysis relevant ecological data was also recorded. The ecological descriptors were selected according to a previous study on vines in Europe (Arnold 1999). However, not all the populations considered in the genetic study could be used in the ecological investigation (Table 1). The Broken Head and Evans Head populations had had their structure significantly changed by fire, while the Nimbin, Lumley Park and Tuckombil populations were too small to be considered within the ecological analysis.

Table 1. Sites sampled for ecological and DNA analysis showing altitude and population size for *Cissus hypoglauca* and *Cissus sterculiifolia* (the shaded populations were removed from the ecological analysis — see text for explanation).

Population groups/regions	Sites	Altitude range (m)	Estimated population size for: *C. hypoglauca*	*C. sterculiifolia*
Big Scrub	Broken Head	5–50	> 20	10–20
	Duck Creek	51	> 20	0
	Davis Scrub	170	0	10–20
	Lumley Park	120	3	1
	Victoria Park	150	2	10–20
	Uralba	135	> 20	0
	Tuckombil	100	2	0
Southern Coast	Evans Head	4	> 20	0
	Iluka	5	> 20	> 20
Northern Ranges	Nimbin	230	2	0
	Terania Creek	100–190	> 20	10–20
	Whian Whian	200–400	> 20	> 20

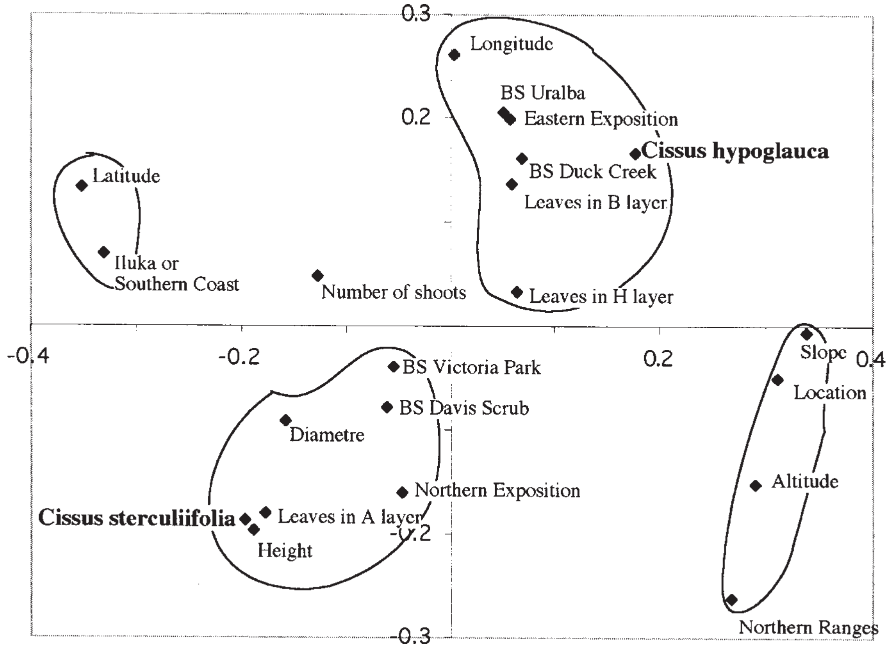

Fig. 1. Projection of the 21 descriptors on the first two axes of the correspondence analysis (CA). BS denotes sites within the Big Scrub area.

Environmental descriptors

Latitude and longitude were determined using a GPS (Garmin type) or estimated on a 1: 25 000 map when tree coverage was too dense for efficient satellite reception (degrees were converted into decimal numbers). Altitude was measured using an altimeter of the type Thommen Classique 6000 and confirmed on the same maps. Slope was described as a semi-quantitative descriptor varying from 0 for a flat landscape to 2 for a slope of more than 30 degrees. Exposure was measured with a compass and divided into two quantitative components: Expo N and Expo E. These values correspond to the sine and cosine of the angle read on the compass and deferred on a circle of radius 1 (East (1; 0), North (0; 1), West (-1; 0) and South (0; -1)).

A semi-quantitative descriptor ('Disturbance' on Figure 1) varying from 0 to 6 was used to describe the condition of the forest edge. The following values were used: 0 = inside the rainforest; 1 = in a gap; 2 = non-cultivated edge opening; 3 = edge close to a plantation or an open agricultural area; 4 = edge bound by a pathway; 5 = edge bound by an unsealed road; 6 =edge bound by a sealed road.

Structural descriptors

The circumference of vine trunks was measured as close to the ground as possible (breast height was not always suitable as vines often grew along the ground). If many shoots were present, the largest in circumference was measured. The precision of this measurement was rounded to 0.5 cm (quantitative variable). Number of shoots was scored as a semi-quantitative variable: 1 = 1 to 5 shoots; 2 = 5 to 10 shoots; 3 = 10 to

20 shoots; 4 = over 20 shoots. Height (quantitative variable) was estimated when possible but for individuals of more than ten metres measures were generally obtained using an eclimetre as the top of the vines was masked by tree foliage. The abundance of *Cissus* foliage in each of the three vegetation layer (H layer = herbaceous <1m; B layer = bush 1 m to 6 m; A layer = tree > 6 m) was noted as a semi-quantitative variable coded from 0 (absent) to 3 (very abundant).

Population size of *C. sterculiifolia* and *C. hypoglauca* within each site was described as a semi-quantitative value varying from 0 to 5: 1 = 1 individual; 2 = 2 to 5 individuals; 3 = 6 to 10 individuals; 4 = 11 to 20; 5 = over 20 individuals.

Analysis of ecological data

In order to compare the interactions between descriptors, populations and species multivariate analysis was performed. The square matrix used for the analysis consisted of 106 individuals and 21 descriptors. The ecological data were standardised using Progiciel R4.0 developed by Philippe Casgrain and Pierre Legendre at Montréal University (Legendre & Legendre 1998). A correspondence analysis (CA) was performed on standardised data using Canoco (Ter Braak 1991). This analysis was completed by further multivariate analyses using Progiciel R 4.0. An euclidian distance matrix was used for the two Mantel tests. For all these, 999 permutations were performed and a Bonferroni correction was made on the multiple-tests bootstrap.

Genetic analysis

Microsatellites, or simple sequence repeats (SSRs), are often used as the genetic marker of choice for population studies. Abundant and uniform distribution throughout the genome, codominant inheritance, simple screening requirements and reproducibility make SSRs particularly attractive to a multitude of applications. Initially described as species-specific, an increasing number of studies are showing that SSRs can be efficiently transferred across related taxa (Rossetto et al. 2000, Scott et al. 2000, Arnold et al. 2002). In fact, close to 80 % transfer success can be expected within genera and around 35 % within families (Rossetto 2001). A recent study by Arnold et al. (2002) showed that a number of SSRs characterised for *Vitis vinifera* could be successfully transfer across *C. hypoglauca* and *C. sterculiifolia* and produce meaningful population data. Four of these loci were used to assess genetic diversity across the selected populations of the two vine species (Table 2).

Table 2. Name, repeat type, optimal annealing temperature and numbers of alleles for each vine species for the four SSR loci. Two loci were used for *Cissus hypoglauca* (scu15vv and vmc8D11) and three for *Cissus sterculiifolia* (scu06vv, scu08vv and scu15vv). Not analysed loci are indicated as na.

Locus	Repeat type	Annealing temperature	Number of alleles for *C. hypoglauca*	Number of alleles for *C. sterculiifolia*
scu06vv	AT	50ºC	na	8
scu08vv	GGT	58ºC	na	5
scu15vv	GAA	54ºC	11	6
vmc8D11	GA	61ºC	9	na

When possible, leaf material from fully-grown vines, was sampled from a number populations representing three distinct geographic groups: Big Scrub, Northern Ranges and Southern Coast (Table 1). Total DNA was extracted using a CTAB method previously described by Rossetto et al. (2001). PCR amplifications were performed in 25 μl reaction volumes containing 10 μmol/L Tris-HCl, 50 μmol/L KCl, 2.5 μmol/L $MgCl_2$, 0.5 unit Taq polymerase (Roche), 0.2 μmol/L of each dNTP, 5 μmol/L of each forward and reverse primer, 25 ng of template DNA plus DNA-free water to make up the total volume. PCRs were run under the following conditions: an initial denaturation step of 94°C for 4 min., followed by 30 steps of 94°C for 30 sec, 48°C–61°C (depending on the primer used — see Table 2) for 30 sec, 72°C for 30 sec, with a final extension step at 72°C for 7 min.

PCR products were initially run on a 2% agarose gel and visualised using ethidium bromide in order to verify amplification success. If amplification was successful, the PCR products were run on a laser-scanning polyacrylamide gel system, the Gel-Scan 2000 (Corbett Research) and visualised with ethidium bromide in order to assess the size range. Samples were run on an 18 cm long, 0.1 mm thick 6% polyacrylamide non-denaturing gel at 1200 V. Descriptive population statistics for the two study species were obtained using GDA 1.1 (Lewis & Zaykin 2002).

Results and disussion

Ecological data

The first three axes of the correspondance analysis (CA) performed on a square matrix composed of 106 individuals and 21 descriptors, explain 53.1% of the total variance (25.9% for axis 1; 15.8 % for axis 2; 11.4 % for axis 3). Figure 1 represents the projection of these 21 descriptors on the first two axes of the CA. Along the first axis a notable gradient of altitude and slope can be observed, while the second axis appears to be more influenced by structural descriptors. This preliminary ecological study shows differences in the ecology and performance of these two species.

If the relationships among structural descriptors are considered independently of the presence or abundance of both *Cissus* species, a correlation between diameter, plant height and the leaf abundance in the tree layer can be observed. This correlation is confirmed by a Mantel test (p=0.001) between the diameter matrix and a matrix grouping the other two descriptors. Vines usually reach the highest canopies after long persistent growth tracking that of the supporting species. If only a low quantity of light reaches the base of a tendril climber, the production of exploring shoots or ramets close to the base would result in a loss of energy. As a result, within such conditions vines attempt to put most of their growth efforts into maintaining their position within the canopy and in colonising more than one tree within the tree layer where light supply is higher (Putz & Mooney 1991). In order to counterpart the hydraulic constraints, the vine needs to develop an increasingly thicker stem resulting in the positive correlation between height, leaf production in the tree layer and diameter. On the other hand if a large quantity of light reaches the base of a tendril climber, the production of exploring shoots does not represent a loss of energy.

In such circumstances, lateral expansion of the vine will lead to a greater production of leaves in the herbaceous and bush layer. A Mantel test performed between a matrix containing the number of shoots and a matrix representing the abundance of leaves in the bush and herbaceous layer, confirmed the existence of a positive correlation between these values ($p=0.004$). These results suggest the presence of a correlation between leaf number across the various layers, shoots size and shoot number. A greater number of leaves in the tree layer corresponds to greater height and larger stem size. A greater number of leaves in the bush and/or herbaceous layers corresponds to a greater number of shoot.

Figure 1 clearly segregates between the abundance of *Cissus hypoglauca* and *C. sterculiifolia* as they occupy opposed positions on the graph. This segregation is independent of altitude, latitude and shoot number but is likely to be accentuated by the uneven abundance of these two species within the Big Scrub remnants. Uralba and Duck Creek contain only *C. hypoglauca*, while Victoria Park and Davis Scrub have greater numbers of *C. sterculiifolia*. This study shows a link between *C. sterculiifolia*, northern exposure of the slope and higher abundance of leaves in the tree layer (Fig. 1). *C. sterculiifolia* vines were mostly found inside rainforests and on flat areas (or areas with a weak slope). Conversely, *C. hypoglauca* was more abundant along the coast as indicated in Figure 1 by the link to longitude. *C. hypoglauca* produced most of its leaves in the herbaceous and bush layers indicating that it was mainly found on forest edges (Fig. 1).

In contrast to the Big Scrub sites, the sites within the Northern Ranges and Southern Coast regions were bigger and contained both species. These two regions are diametrically opposed (Fig. 1) as Northern Ranges sites are at high altitude while Southern Coast sites are at sea level. The Iluka site is within littoral rainforest with trees kept relatively small as a consequence of the ocean winds blowing over the sand dunes (Specht & Specht 1999). Within this rainforest type both *Cissus* species have a tendency for greater vegetative dynamic as suggested by an increased number of shoots.

In the Northern Ranges, *Cissus sterculiifolia* was mainly found within tall rainforests, while *C. hypoglauca* was mainly found at rainforests edges or in wet sclerophyll forests. Thus this preliminary ecological study suggests that *C. hypoglauca* can occupy drier environmental conditions than *C. sterculiifolia*, which is more closely dependent on humid rainforest habitats.

Non-disturbed edges or tree-fall gaps usually offer vertical structure for all sorts of climbers with a higher density of trees of different height and diameters (Putz & Chai 1987). If the supply of light, temperature and humidity is sufficient, there is no need for vines to invest in vertical growth. As a result, they can concentrate leaf production within the herbaceous and bush layer as observed in the present study and corroborated by other studies (Arnold 1999, Avalos & Mulkey 1999). Furthermore, the ability to form secondary rooting points allows vines to increase leaf area without necessitating excessive stem thickening. This strategy reduces mortality risks, as each stem has the potential to independently continue lateral and vertical exploration.

However, extreme environmental disturbances such as edge effect can lead to excessive moisture losses. Within these drier conditions *C. hypoglauca* seems to be able to adapt better than *C. sterculiifolia* which appears to be more vulnerable to such changes. This lower ability to adapt to changed environmental conditions could explain why *C. sterculiifolia* plants appears to be consistently larger in size (possibly suggesting greater age) and show limited signs of active vegetative reproduction.

Genetic data

As vine populations within the Big Scrub remnants are small, highly significant data on current population dynamics can be difficult to obtain. Yet despite the limitations imposed by sampling size, some very interesting trends were observed. Of particular interest is the comparative data on population genetics obtained from the Big Scrub, Northern Ranges and Southern Coast.

Table 3: SSR data for the *Cissus hypoglauca* populations analysed (using two loci, scu15vv and vmc8D11). For each group, the number of sites investigated (Sites), overall number of individuals (N), overall number of alleles (A_T), mean number of alleles per locus (A), expected (H_E) and observed (H_O) heterozygosity, inbreeding coefficient (F_{is}) and fixation index (F_{st}) are shown.

Group	Sites	N	A_T	A	H_E	H_O	F_{is}	F_{st}
Big Scrub	6	34	17	2.79	0.63	0.61	0.10	0.29
Northern Ranges	3	35	12	3.00	0.53	0.62	-0.01	0.25
Southern Coast	2	24	13	4.75	0.76	0.59	0.22	0.12
Overall	13	93	20	3.15	0.62	0.61	0.09	0.25

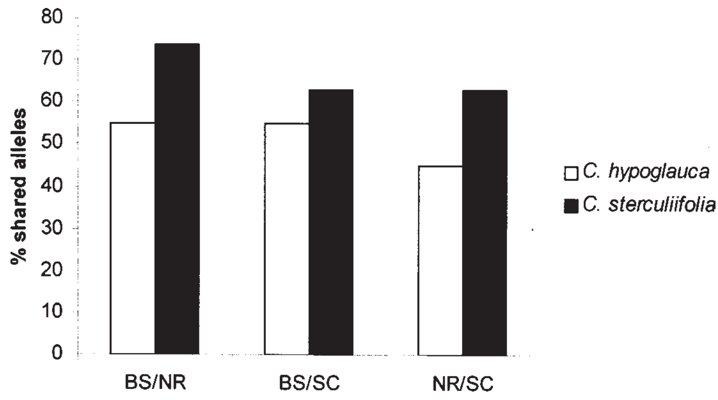

Fig. 2. Shared alleles between the Big Scrub (BS), Northern Ranges (NR) and Southern Coast (SC) population groups for *Cissus hypoglauca* and *Cissus sterculiifolia*.

Single *C. hypoglauca* populations had the lowest levels of diversity, as measured by the mean number of alleles per locus, within the Big Scrub (Table 3). This is not surprising, as most of these populations are extremely small and disjunct. As well as low within-population diversity, high fixation index in the Big Scrub (0.29 F_{st}, considered as very high by Hartl & Clark 1997) emphasised the structuring caused by population disjunction and habitat fragmentation. However, when grouping single populations within their respective regions, the overall number of alleles was higher in the Big Scrub than in the other two comparative regions (Table 3). Possible explanations for this result are the incomplete sampling of undisturbed populations within the Northern Ranges and Southern Coast, and the presence of residual rare alleles within the small Big Scrub populations. Similar sampling sizes for the Big Scrub and the Northern Ranges produced similar A and F_{st} as well as corresponding levels of heterozygosity (Table 3). Interestingly, more alleles are shared between the Big Scrub populations of *C. hypoglauca* and each of the two other regions, than between the Northern Ranges and Southern Coast (Figure 2). As the Big Scrub is geographically intermediate between these two otherwise distinct areas such allele-sharing patterns suggest that the Big Scrub provided an important corridor for gene flow among geographically disjunct rainforests in northern NSW.

The smaller number of samples available for the genetic investigation on *Cissus sterculiifolia* make population studies even more arduous. Sampling was not an under-representation of the true distribution of *C. sterculiifolia* but reflected a genuine scarcity of this vine at the study sites. Genetic data were more homogeneous than for *C. hypoglauca*, with moderate F_{st} values indicating lower inter-population distinction (Table 4). Overall genetic diversity measured as the total number of alleles was also lower in *C. sterculiifolia* (19 alleles across three loci — Table 4) than in *C. hypoglauca* (21 alleles across two loci — Table 3) with lower heterozygosity levels being also recorded (Table 4). Lower diversity and lesser population structure could be attributed to the fact that *C. sterculiifolia* is more restricted in habitat preferences (as previously suggested by Jackes 1988 and Benson & McDougall 2001). It is possible that this vine has undergone more extreme bottlenecks during recent glaciation events and/or has recently colonised northern NSW from rainforest refugia outside this area.

Table 4. SSR data for the *Cissus sterculiifolia* populations analysed (using three loci, scu15vv, scu08vv and scu06vv). For each group, the number of sites investigated (Sites), overall number of individuals (N), overall number of alleles (A_T), mean number of alleles per locus (A), expected (H_E) and observed (H_O) heterozygosity, inbreeding coefficient (F_{is}) and fixation index (F_{st}) are shown.

Group	Sites	N	A_T	A	H_E	H_O	F_{is}	F_{st}
Big Scrub	4	17	16	3.25	0.58	0.52	0.10	0.13
Northern Ranges	2	16	17	3.00	0.48	0.29	0.53	0.05
Southern Coast	1	15	14	4.67	0.75	0.44	0.42	na
Overall	8	48	19	3.67	0.63	0.52	0.27	0.13

This preliminary genetic investigation in the population dynamics of these two native vine species produced some interesting trends — differences in overall species diversity, and the role of the Big Scrub in providing a continuum between southern and northern rainforest populations. Future research should involve more extensive study areas, larger populations, direct measures of gene flow and a greater number of SSR loci. Such an approach would provide more suitable information about the consequences of rainforest fragmentation on the gene flow of two vines that rely on similar dispersal mechanisms but occupy slightly different ecological niches.

Conclusion

Ecological and vegetation dynamic studies on two *Cissus* species uncovered differences across the Big Scrub remnants. What essentially unites these sites is that they share similar altitude, which is midway between that of the Northern Ranges and the Southern Coast. Genetic analysis confirmed an intermediary role for the Big Scrub, as it appears to have provided a continuum for gene flow across these otherwise disjunct rainforest areas. However, despite the similarity in fruit dispersal mechanisms, there is no clear indication that consistent levels of gene flow are persisting in the currently fragmented habitat.

Some tangible distinctions were detected between the two vines. *Cissus hypoglauca* appears to have the greatest ecological amplitude, including resilience to disturbance and somewhat drier environmental conditions. Land clearing is likely to have reduced overall genetic variability within Big Scrub populations of this species, yet it still exhibits a marginally broader genetic spectrum than *C. sterculiifolia*. Wide range of habitat preference, efficacious vegetative growth, efficient predisposition for dispersal and a broader genetic spectrum make *C. hypoglauca* less susceptible to the detrimental effects of rainforest fragmentation.

Cissus sterculiifolia is restricted to more humid rainforest habitats. In northern NSW, and in particular within the Big Scrub area, undisturbed rainforest is increasingly uncommon. Since edge effect decreases humidity, fragmentation is having a greater effect on the long-term survival of this species than for *C. hypoglauca*. Rarity and a narrow genetic spectrum in *C. sterculiifolia* suggest the possible occurrence of past bottlenecks throughout northern NSW. As most of the remaining *C. sterculiifolia* individuals appear to be large and old, it is possible that in most areas they embody senescent populations or relics of a better past. Because of its specific ecological requirements, this species is more likely to disappear in the current fragmented and extensively disturbed conditions.

This preliminary study was not intended to develop a full understanding of population ecology and genetics of these two vine species. Rather it was intended to provide new insights on how two closely related vine species respond to rainforest fragmentation. What has emerged is an account of two species occupying fairly distinct ecological niches, and consequently being differently affected by current environmental disturbances. In the long term, *C. sterculiifolia* is likely to be more extensively affected by rainforest degradation and fragmentation.

Acknowledgements

The authors would like to acknowledge the assistance provided by K. Scott and J. McNally. This project was partly funded by the Swiss National Foundation for Scientific Research and Southern Cross University.

References

Adam, P. (1992) *Australian rainforests* (Oxford University Press: Oxford).
Arnold, C. (1999) *Ecologie de la vigne sauvage (Vitis vinifera subsp. sylvestris Gmelin Hegi) dans les forêts alluviales et colluviales d'Europe*. Ph. D. Thesis, University of Neuchâtel, Switzerland.
Arnold, C., Rossetto, M., McNally, J. & Henry, R. J. (2002) The application of SSRs characterised for grape (*Vitis vinifera*) to conservation studies in Vitaceae. *American Journal of Botany* 89: 22–28.
Avalos, G. & Mulkey, S. S. (1999) Photosynthetic acclimation of the liana *Stigmaphyllon lindenianum* to light changes in a tropical dry forest canopy. *Oecologia* 120: 475–484.
Benson, D. & McDougall, L. (2001) Ecology of Sydney plants species Part 8: Dicotyledon families Rutaceae to Zygophyllaceae. *Cunninghamia* 7: 241–462.
Bungard, R. A., Morton, J. D., L., M. D. & Daly, G. T. (1998) Effects of irradiance and nitrogen on *Clematis vitalba* establishment in a New Zealand lowland forest remnant. *New Zealand Journal of Botany* 36: 661–670.
Connelly, S. & Specht, A. (1988) *Big Scrub Conservation Strategy* (NSW National Parks and Wildlife Service: Sydney).
Hartl, D.L. & Clark, A.G. (1997) *Principles of population genetics, 3rd edit.* (Sinauer Associates: Canada).
Hegarty, E. E. (1988) *Canopy dynamics of lianes and trees in subtropical rainforest.*, Ph. D. Thesis, University of Queensland, Brisbane.
Hegarty, E. E. (1990) Leaf life-span and leafing phenology of lianes and associated trees during a rainforest succession. *Journal of Ecology* 78: 300–312.
Jackes, B. R. (1988) Revision of the Australian Vitaceae, 3. *Cissus* L. *Austrobaileya* 2: 481–505.
Legendre, P. & Legendre, L. (1998) *Numerical Ecology, 2nd English Edition* (Elsevier: Amsterdam).
Lewis, P. & Zaykin, D. (2002) *Genetic Data Analysis*. http://alleyn.eeb.uconn.edu/gda/
Lott, R.H. & Duggin, J.A. (1993) *Conservation significance and long term viability of subtropical rainforest remnants of the big scrub, north-eastern New South Wales* (Department of Ecosystem Management, University of New England: Armidale).
Mesquita, R. C. G., Delamônica, P. & Laurance, W. F. (1999) Effect of surrounding vegetation on edge-related tree mortality in Amazoninan forest fragments. *Biological Conservation* 91: 129–134.
Putz, F. E. & Chai, P. (1987) Ecological studies of lianes in Lambir National Park, Sarawak, Malaysia. *Journal of Ecology* 75: 523–531.
Putz, F. E. & Mooney, H. A. (1991) *The biology of vines* (Cambridge University Press: Cambridge).
Roldan, A. I. & Varela, R. O. (1999) Seasonal changes in liana cover in the upper canopy of a Neotropical dry forest. *Biotropica* 31: 186–192.
Rossetto, M., Harriss, F.C.L., Mclauchlan, A., Henry, R.J., Baverstock, P.R. & Lee, L.S. (2000) Interspecific amplification of tea tree (*Melaleuca alternifolia* — Myrtaceae) microsatellite loci — potential implications for conservation studies. *Australian Journal of Botany* 48: 367–373.
Rossetto, M. (2001) Sourcing SSR markers from related plant species. Chapter 14 pp. 211–224 in R.J. Henry ed. *Plant genotyping: the DNA fingerprinting of plants* (CABI: Wallingford).
Rossetto, M., Jackes, B., Scott, K.D & Henry, R.J. (2001) Intergeneric relationship in the Australian Vitaceae: new evidence from cpDNA analysis. *Genetic Resources and Crop Evolution* 48: 307-314.
Rossetto, M., Jackes, B., Scott K.D. & Henry, R.J. (2002) Is the genus *Cissus* (Vitaceae) monophyletic: evidence from plastid and nuclear ribosomal DNA. *Systematic Botany* 27: 522–533.
Schnitzer, S. A. & Carson, W. P. (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82: 913.
Schnitzer, S. A. & Bongers, F. (2002) The ecology of lianas and their role in forests. *TRENDS in Ecology and Evolution* 17: 223–230.
Scott, K.D., Eggler, P., Seaton, G., Rossetto, M., Ablett, E.M., Lee, L.S. & Henry, R.J. (2000) Analysis of SSRs derived from grape ESTs. *Theoretical and Applied Genetics* 100: 723–726.
Sizer, N. & Tanner, E. V. J. (1999) Response of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biological Conservation* 91: 135–142.
Specht, R. L. & Specht, A. (1999) *Australian plant communities: dynamics of structure, growth and biodiversity* (Oxford University Press: Melbourne).
Ter Braak, C. J. F. (1991) *CANOCO version 3.12*. Agricultural Mathematics Group, DLO, Wageningen.
Wiens, J. A., Crawford, C. S. & Gosz, J. R. (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45: 421–427.
Winter, J.W., Bell F.C., Pahl L.I., & Atherton R.G. (1984) *The specific habitats of selected northeastern Australian rainforest mammals*. Report to the World Wildlife Fund, Australia.

Manuscript accepted 21 January 2003