Chemical differentiation between leaves of seedlings and spatially close adult trees from the tropical rain-forest species *Nectandra ambigens* (Lauraceae): an alternative test of the Janzen–Connell model

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Summary

1. We tested the hypothesis of Langenheim and Stubblebine that differences in chemical composition between maternal trees and the seedlings under them arise from differential mortality; only seedlings different from the mother survive. Such mortality could explain at least some of the cases where seedlings accumulate under adult conspecifics, contrary to the extreme form of the Janzen–Connell hypothesis.
2. We investigated *Nectandra ambigens* (Lauraceae), an upper-canopy tree at Los Tuxtlas tropical rain forest, Mexico, whose seedlings survive under the canopy of conspecific trees. We analysed chromatographic profiles of leaf terpenoids of 15 groups, each formed by an adult tree and its surrounding seedlings.
3. We predicted that seedlings chemically similar to the adult would be absent under the tree canopy and that they would be present outside that canopy. We also predicted that younger seedlings would be more similar to the adult than the older ones.
4. Chemical similarity analyses showed that most seedlings were significantly different from their closest adult and thus supported the Langenheim and Stubblebine hypothesis. However, we did not find chemical differentiation among seedlings regarding their age or their position inside or outside the tree canopy.

Key-words: Langenheim and Stubblebine hypothesis, seedling survival, terpenoid leaf profile

Functional Ecology (1999) **13,** 725–732

Introduction

Tropical rain forests are well known by their high tree species diversity and the large distances among most conspecific adult trees (Martínez-Ramos 1994). Janzen (1970) and Connell (1971) independently proposed similar hypotheses to explain this pattern. They proposed that seed and seedling predation by specialized herbivores and pathogens greatly reduces the chances of establishment and survival of seedlings under the canopies of their conspecific trees. Thus, spaces will be left under these canopies which may be occupied by seedlings of other species. Greater rates of mortality under conspecific trees have been recorded for a range of species (Clark & Clark 1984) but not for all those tested (Córdova 1979; Martínez-Ramos 1994). In the most comprehensive test, that in the 5 ha plot in Barro Colorado Island, Panama, early analyses suggested that Janzen–Connell effects among saplings (> 1 cm d.b.h.) were rare (Hubbell & Foster 1990; Condit, Hubbell &

Foster 1992) but a recent analysis has suggested that they are all-pervasive (Wills *et al.* 1997).

Langenheim & Stubblebine (1983) found that in various *Hymenaea* spp. from tropical rain forest in Amazonia, seedlings and saplings were abundant under the canopy of conspecific trees. They investigated the sesquiterpene profile of seedlings and their closest conspecific trees finding that seedlings and saplings were chemically different from the trees. They proposed that this chemical differentiation under the tree canopy arose by differential mortality, with only the seedlings that were different from the closest trees surviving. Terpenoid and sesquiterpenoid leaf profiles have been shown to be important in determining differential herbivory in tropical and temperate trees (Stugeon & Mitton 1986; Macedo & Langenheim 1989). Thus, the Langenheim and Stubblebine's hypothesis would be an alternative to the Janzen–Connell hypothesis to explain the cases where seedlings survive under the canopy of conspecific trees.

Nectandra ambigens (Blake) C.K. Allen (Lauraceae) is an upper canopy tropical rain-forest

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tree which has abundant seedlings under conspecific canopies. Moreover, seedling mortality close to conspecific trees can be the same as that found away from conspecifics (Córdova 1979). Less than 15% of the seedlings of the same cohort under the canopy of adult trees survive after 3 years and few saplings may be found under these trees (Martínez-Ramos 1994). However, the seedling bank is renewed with each reproduction episode and, in the event of fall of an adult tree, the most likely replacement would be another *N. ambigens* tree recruited from the seedling bank (Martínez-Ramos 1994). Under conspecific trees, *N. ambigens* is the most abundant seedling species but it is not the dominant species in the sapling community (Martínez-Ramos & Soto-Castro 1993). However, if there is a gap opening, the *N. ambigens* seedlings develop vigorously reaching sapling stages rapidly, which results in a demographic regeneration wave dominated by *N. ambigens* (Córdova 1985). This would explain the mostly clumped distribution of this species in the rain forest, in contrast with the common pattern of widely spaced adult trees for other species (Martínez-Ramos & Álvarez-Buylla 1995). *Nectandra ambigens* is attacked by various foliar pathogens (García-Guzmán 1990) and insects (Dirzo 1984; De la Cruz & Dirzo 1986), however, the leaves have terpenoids which may inhibit foliar fungal pathogens or antagonise insects (Del Amo, Ramírez & Espejo 1986; Langenheim 1994).

We decided to investigate whether *N. ambigens* seedlings under and outside the canopy of conspecific trees were chemically different from adult trees as predicted by the Langenheim and Stubblebine hypothesis. We analysed the leaf terpenoid chromatographic profile of seedlings and isolated trees to address our objective. We expected that the seedlings chemically similar to the adult would be absent under the tree canopy and that they could be present outside that canopy. We also explored the patterns of differentiation within seedlings of pairs of neighbouring adult trees. Our expectation was that the seedlings chemically similar to one mature tree would be absent under its canopy but present under the canopy of the neighbouring tree and vice versa. We also expected that the younger seedlings were more similar to the adult than the older ones, if the differential mortality predicted by the hypothesis occurs.

Materials and methods

STUDY SITE

The fieldwork was carried out at the Los Tuxtlas Tropical Field Station, Instituto de Biología, Universidad Nacional Autónoma de México, in the state of Veracruz, south-eastern Mexico (18 ° 36 ′N, 95 ° 07 ′W). The vegetation is tropical rain forest; mean annual rainfall is about 4500 mm and no month has less than 100 mm of rain; mean annual temperature

is 23·7 °C (mean extreme temperatures of 19 and 29 °C; Estrada, Coates-Estrada & Martínez-Ramos 1985). The terrain of the 700 ha reserve is mountainous; medium and steep slopes are common, although flat sites can also be found. More than 200 tree species grow within the station, where the upper canopy attains heights in excess of 30 m (Bongers *et al.* 1988; Ibarra-Manríquez & Sinaca-Colín 1997). This forest has an estimated turnover rate of 50 ± 42 years (Martínez-Ramos *et al.* 1988).

STUDY SPECIES

Nectandra ambigens is found in Mexico, Guatemala and Honduras (Dirzo, Ibarra-Manríquez & Sánchez-Garduño 1997) and it is the most abundant canopy tree (> 20 m height) in the Los Tuxtlas rain forest with about 12 trees (> 10 cm d.b.h.) ha^{-1} (Martínez-Ramos & Álvarez-Buylla 1995). It has a mostly clumped distribution with six to 12 mature trees spaced about 10 m among them; sometimes the trees are solitary or they are completely absent in various hectares. The tree is hermaphrodite and little is known about its pollination, although unidentified bees are frequent visitors to the flowers (Dirzo *et al.* 1997). Seed production in individual trees occurs from September to November every 2 or 3 years, where many mature trees produce seeds simultaneously (Dirzo *et al.* 1997). In a reproductive event an individual may produce hundreds of thousands of drupes 2·5–3·5 cm long and fresh mass 4–7 g (G. Ibarra-Manríquez & M. Martínez-Ramos, unpublished data); 60% of them fall within a distance not larger than twice the radius of the canopy of the parent tree (González-Méndez 1995). Seedling emergence occurs within a month after seed fall, producing a high density seedling carpet (in some places with more than 100 seedlings per square meter) under the canopy of the parent tree (Martínez-Ramos 1991). The cotyledons are hypogeal and one to three postcotyledonary leaves remain attached for more than 1 year while the seedling stays in the seedling bank where it reaches up to 50 cm height (M. Martínez-Ramos, personal observations). Because most *N. ambigens* seeds fall beneath the parent canopy we will assume that seedlings under the canopy of a mature tree are their progeny (Córdova 1979; González-Méndez 1995). This would be more accurate in the case of the isolated trees.

LEAF SAMPLING DESIGN

To test our hypothesis leaves were collected from seedlings of unknown age under and outside the canopy (at least 5 m away) of adult trees. A second sampling was made on a different date but with seedlings of known age to find out whether the younger seedlings were more similar to the adult than the older ones.

For the first sampling (collected in October 1993), 12 groups were selected. Each group was formed by one

mature tree and 10 surrounding seedlings. Six of these trees formed three couples with their canopies separated by 1–5 m; we denominated them 'neighbour trees'. According to our hypothesis, we expected that seedlings chemically similar to one tree from the couple would be absent under its canopy but may be present under the canopy of the neighbour. The six remaining groups were formed by trees isolated from any other conspecific tree by at least 45 m; we called these 'isolated trees'. A branch was selected randomly from the lower canopy of each tree collecting the third and the fourth leaves (both mature); from each seedling we collected three mature leaves. We collected 132 leaf samples from trees and seedlings but, because nine samples were lost, only 123 samples were analysed.

For the second sampling (collected in December 1994) we used three trees with cohorts of seedlings that had been marked and followed annually from 1988 to 1994 by one of us (M.M.-R.). Annual seedling mortality at these sites had been 50% and only enough seedlings from 1992, 1993 and 1994 were found. Two leaves from each seedling were collected; all of them were under the canopy of the trees. Although many terpene-producing trees have a uniform chemical profile within the canopy (see Langenheim 1994), we decided to confirm this with *N. ambigens* in the second sampling. Three equidistant branches within the lower canopy of each tree were selected and the third leaf of each one was collected. Nine marked seedlings were sampled under one tree, 14 were sampled under the second one and 16 seedlings were sampled under the third tree.

SAMPLE PROCESSING

For the first sampling, leaves were weighed a few minutes after collection; one leaf was dried for 4 days at 70 °C to obtain dry mass and the other was put in a 75 ml amber flask with 50 ml of hexane. For the second sampling, leaves were transported to Mexico City in ice and within 24 h they were weighed and processed as follows: each leaf was cut in half longitudinally; one part was used to obtain dry mass and the other was put into 75 ml amber flasks with 50 ml of hexane. Leaves remained in hexane for at least 72 h before they were processed for chromatographic analysis: 1 mg of n-tetradecane was delivered in 1 ml of hexane as an internal standard to each flask with leaves. Leaves were ground with chromatographic grade sand and hexane, the extract was dried with magnesium sulphate and concentrated to 0·2 ml under an N_2 current. Of this extract, 1 µl was injected in the chromatograph.

Each sample was injected in a Perkin-Elmer 8410 gas GC equipped with a 30 m long, 0·25 mm ID DB-17 column (J & W Scientific) and a flame ionization detector (FID). Conditions in the GC were as follows: injector at 220 °C, detector at 330 °C, carrier gas Helium, at 1·76 kg cm^{-2} at 0·31 m s^{-1}; initial oven temperature at 50 °C, then increasing at 15 °C min^{-1} to reach 280 °C and maintaining that temperature for 5 min

DATA ANALYSIS

A chromatogram for each sample was obtained and the area under each peak was standardized as mg g^{-1} dry mass relative to the internal standard. The resulting chromatographic profiles were compared among themselves using the peak retention times. All peaks $\geq 1\%$ of the total area of at least one chromatogram were included in the analysis; 105 of these peaks were numbered for mature trees and 112 for seedlings. A matrix with peaks and their concentration for each seedling and their tree was formed; another matrix with only trees was also formed, completing 12 matrices for unknown-age seedlings, and three matrices for known-age seedlings and their mature trees.

In order to position each seedling with respect to the closest mature tree using their chromatographic profile, a varimax Principal Component Analysis (PCA) was performed for each matrix with the program STATISTICA (CSS 1993). Euclidean distances (Ludwig & Reynolds 1988) among the seedlings of a group and between each seedling and its closest mature tree were calculated using the relative concentrations to tetradecane for each peak of their chromatographic profile. Because different compounds have different responses to the FID, the mg g^{-1} obtained for one peak is not comparable to those obtained for peaks with different retention times, nor do they necessarily represent the actual concentration of the compound in the leaf. However, this measurement allows comparison of peaks with the same retention times among chromatograms and therefore the measurement is fit to calculate Euclidean distances.

Non-parametric Mann–Whitney U and Kruskall-Wallis tests were used to asses statistical differences between the median chemical distance among seedlings and that of seedlings compared with their tree.

Results

Chromatograms of leaves of *N. ambigens* seedlings and mature individuals showed a great number and diversity of leaf chemical compounds. The number of peaks identified in the chromatograms varied between 58 and 99. Although some seedlings have chemical profiles that resembled those of the parental tree, most of them were clearly different from those of the parental trees.

CHEMICAL SIMILARITY BETWEEN PARENT TREES AND UNKNOWN-AGE SEEDLINGS

Principal component analysis segregated most seedlings from clumped or isolated parental trees. In

all analyses performed, the three first components explained more than 67·4% of total variance. In one of the six cases where mature trees were neighbours, two seedlings, very similar to one of the neighbours, were growing outside the canopy of the other neighbour (Fig. 1a). In another case, a single seedling was chemically close to the parental tree (Fig. 1b), located on the edge of the two neighbouring mature canopies. In two of the six cases where mature trees were isolated, only one or two seedlings were chemically close to the parental tree (Fig. 1c,d) and these seedlings were located outside the parental tree canopy. All other seedlings, in these and other groups, were chemically very different to their closest mature tree (Fig. 1e). In 11 of 12 groups, most seedlings were clumped away from the adult in one to three clusters (e.g. Fig. 1).
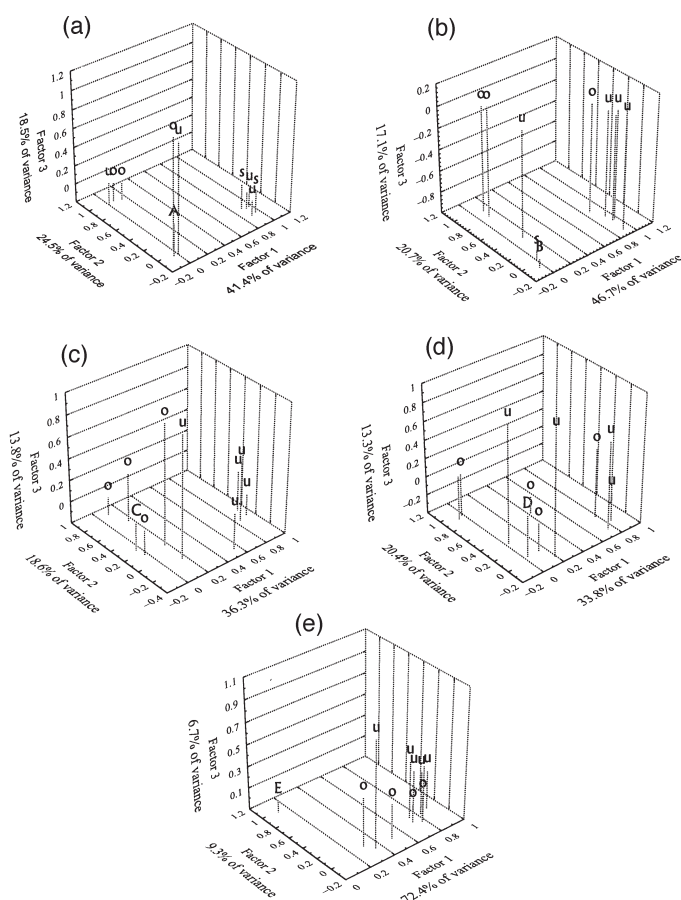

Fig. 2. Arrangement according PCA based on chemical profiles of two neighbour trees (**A,Q**) with their 19 seedlings (letters in lower case). The PCA explains 75·9% of the variance with three factors. Two seedlings (**z**) that were collected away from the canopy of the mature tree **Q**, were chemically close to the other mature tree **A**: seedlings (**a**) were collected under the canopy of tree **A**; seedlings (**x**) were collected far away from tree **A**; seedlings (**r**) were collected under the canopy of tree **B**; seedlings (**s**) were located on the edge of the two neighbouring mature canopies.

The mean (± SD) chemical Euclidean distance among seedlings (3·0 ± 1·9, $n = 461$) was significantly smaller than the distance among mature trees and seedlings (4·8 ± 2·6, $n = 111$; $U = 13175·5$, $P < 0·00001$). There was no difference between the mean distance among the mature tree and the seedlings under its canopy (4·8 ± 2·6, $n = 48$) and the mean distance among the tree and the seedlings outside of its canopy (4·8 ± 2·8, $n = 53$; $U = 1245·0$, $P = 0·854$).

We expected that in neighbour trees the seedlings chemically similar to one mature tree would be absent under its canopy but present under the canopy of the neighbour tree and vice versa. This case only occurred partially with one pair of neighbour trees (Fig. 2) where two seedlings similar to one adult were growing under the canopy of the other adult. In the other two groups of neighbours, most seedlings were distant from both adult trees.

Using the PCA results, the determinant chromatographic peaks in the grouping of seedlings and their mature trees were selected. Considering only these peaks, the chemical profile of the mature tree is clearly different from those of their seedlings (e.g. Fig. 3). In most cases the typical compounds of the adult were absent or in different proportions to those typical in their seedlings (Fig. 3a,b), although in some cases the chemical profiles of one or few seedlings were very similar to that of their adult (Fig. 3c).

CHEMICAL SIMILARITY BETWEEN PARENT TREES
AND SEEDLINGS OF KNOWN AGE

Seedlings of known age showed a similar chemical

Fig. 1. Arrangement according to PCA based on chemical profiles of *Nectandra ambigens* trees and their seedlings. Trees in uppercase and seedlings in lowercase: u, under the canopy; o, outside the canopy; s, in between two canopies. In many cases the symbols for seedlings do not appear because they overlap with others: (a) neighbour tree **A** with its seedlings, the PCA explained 84·5% of the variance with three factors; (b) neighbour tree **B** with its seedlings, the PCA explained 84·5% of the variance with three factors [only one seedling (**s**, behind **B**) was chemically close to the parent tree **B**]; (c) isolated tree **C** with its seedlings, the PCA explains 68·7% of the variance with three factors [two seedlings (**o**) were chemically close to the parent tree **C**]; (d) isolated tree **D** with its seedlings, the PCA explains 67·4% of the variance with three factors [two seedlings (**o**) were chemically close to the parent tree **D**]; (e) isolated tree **E** with its seedlings, the PCA explains 87·5% of the variance with three factors.
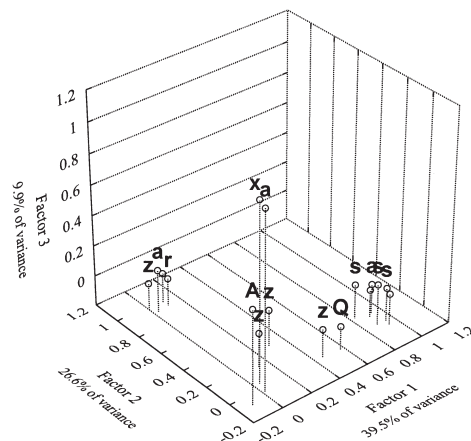
differentiation pattern as that found in unknown-age seedlings (Fig. 4). Besides being chemically away from the mature trees, seedling age did not increase systematically along with the chemical distance to the adult. As predicted by the differential mortality hypothesis, the mean distance ($\pm$ SD) of the seedling from the mature tree was not statistically different between seedlings of less than 1 year old ($28 \cdot 5 \pm 6 \cdot 1$, $n = 4$) and those of 2–3 years old ($27 \cdot 6 \pm 24 \cdot 4$, $n = 14$), while the seedlings of 1–2 years old ($19 \cdot 2 \pm 4 \cdot 96$, $n = 20$) were closer to the mature tree than the other two categories (Kuskall–Wallis test, $H = 5 \cdot 94_{2,38}$, $P = 0 \cdot 051$). The leaves sampled within a single mature tree canopy were almost identical (Fig. 4).

Discussion

The clear differentiation between chemical profiles of seedling and adult leaves agrees with Langenheim and Stubblebine's hypothesis. Because the chemical phenotype for terpenoid-producing trees has an strong genetic control (Langenheim 1994), our results could indicate that this pattern of chemical differentiation enhances genetic variability within the *N. ambigens*

(a)

Fig. 3. (a) Legend on next page.

population. The difference in seedling–mature tree chemical distance among age categories, although marginally significant, could suggest that there is an increasing distance to the mature tree from young to old seedlings. However, the fact that the < 1 year-old seedling group and the 2–3 year-old category were equidistant to the mature tree is at odds with this suggestion. We believe that the very small sample size in the youngest category ($n = 4$) precludes a definitive conclusion; the four seedlings we could find might not have been an unbiased sample of that age category.

The lack of differentiation among seedlings with different spatial positions could mean that our sample size was not big enough. However, the chemical distance between trees and their seedlings was clear with the same sample sizes. This indicates that chemical differentiation among seedlings may exist but with a magnitude much smaller than that of the tree and its seedlings. An indication against this possibility is that seedlings very similar to one neighbour tree survived outside its canopy or under the canopy of the other neighbour tree (Figs 1a, 2). Whether chemical differentiation among seedlings occurs at tree–seedling distances larger than those used in our sampling design still needs to be demonstrated experimentally. If our sampling size and design were correct, this would mean that differential mortality among seedlings occurs during the first year of their life and that the seedlings most similar to the adult die quickly. This would imply a minimum chemical distance to ensure seedling survival under the canopy of the parental tree. The chemical differentiation between seedlings and their closest adult tree might have alternative explanations to differential mortality that could be grouped in genetic, ontogenetic and environmental causes.

GENETIC VS ENVIRONMENTAL SOURCES

There is a possibility that the adult canopy leaves vary chemically among themselves and thus the seedlings are not really different from their closest adult, because they only reflect the natural variation of the canopy. An argument against this possibility is that our results show that leaves from three equidistant points of the lower canopy are almost identical (Fig. 4) and that many seedlings are very similar (e.g. Fig. 2) suggesting that they were full siblings. The uniformity of the chemical profile, or chemotype, within a canopy has been demonstrated for other temperate and tropical trees (Hanover 1966; Langenheim 1994), implying a strong genetic control of the chemical phenotype.

Another possibile explanation to the chemical differentiation between the tree and its seedlings is that *N. ambigens* adults cannot produce their own chemical phenotype because all seeds arise from outcrossing. This possibility does not seem to occur in our study system because some seedlings closely resembled
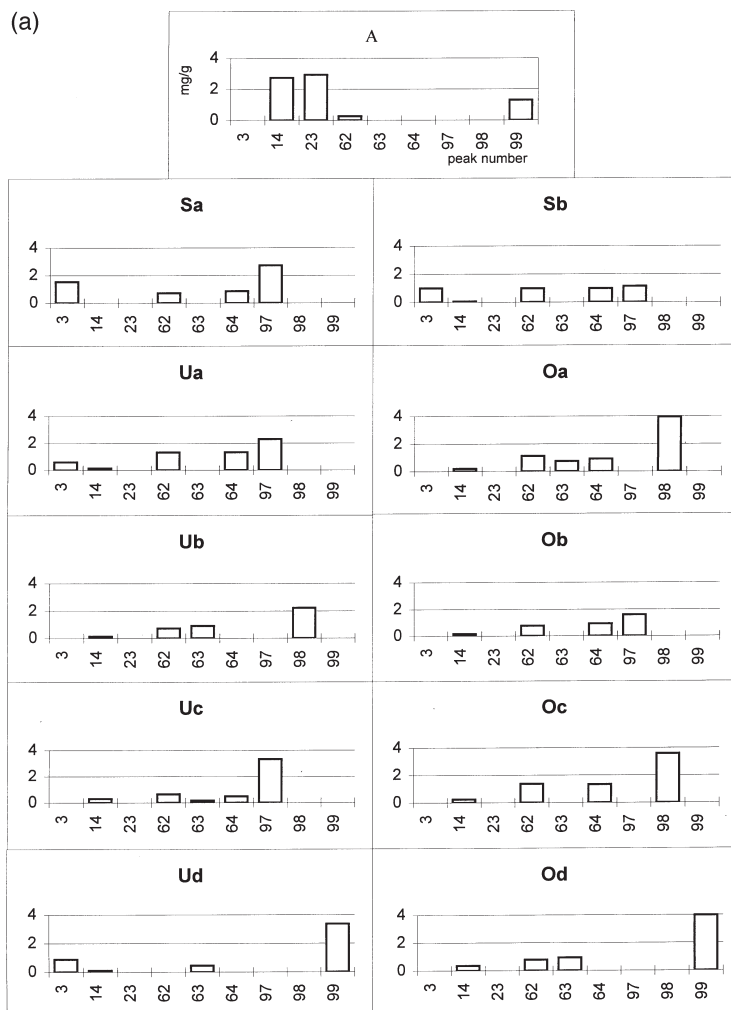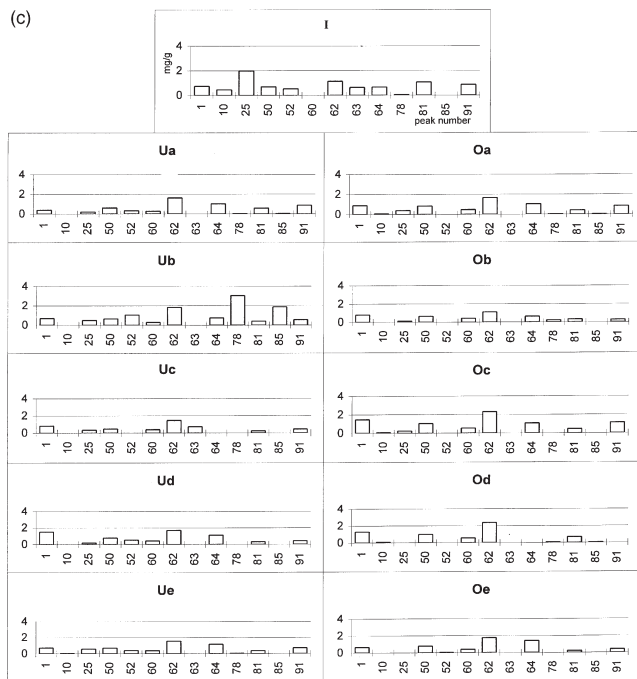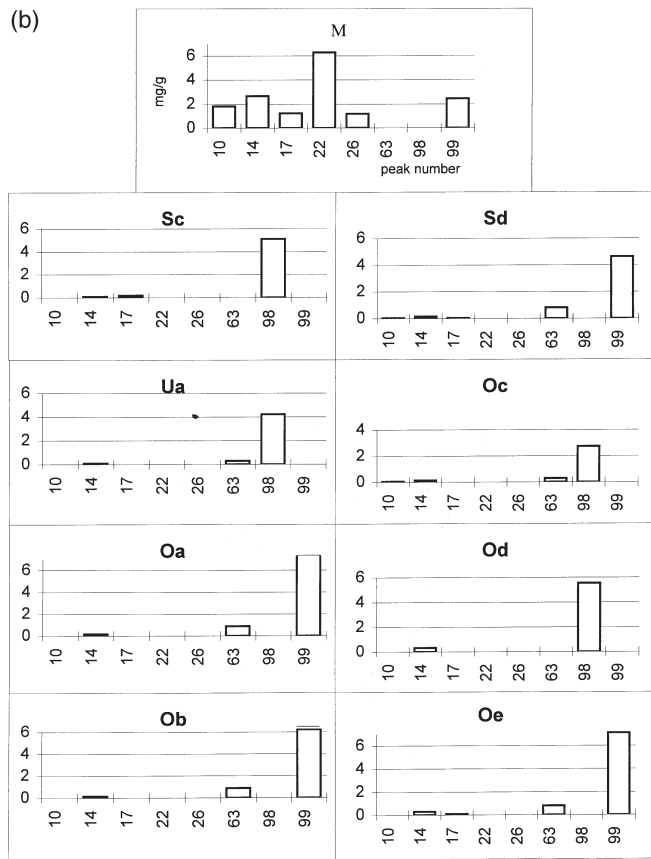
(b)

(c)

Fig. 3. Chromatographic profiles using selected peaks for a groups of seedlings and their closest conspecific tree. The peaks were selected because of their high factor score in the PCA. (a) Neighbour tree **A** and its seedlings collected under the canopy (**Ua, Ub, Uc** and **Ud**) and away from the canopy (**Oa, Ob, Oc,** and **Od**); seedlings in between the canopies of **A** and its neighbour (**Sa** and **Sb**). (b) Neighbour tree **M** and its seedlings collected under the canopy (**Ua**) and away from the canopy (**Oa, Ob, Oc, Od** and **Oe**); seedlings in between the canopies of **M** and its neighbour (**Sc** and **Sd**). (c) Isolated tree **I** and its seedlings collected under the canopy (**Ua, Ub, Uc, Ud** and **Ue**) and away from the canopy (**Oa, Ob, Oc** and **Od**).
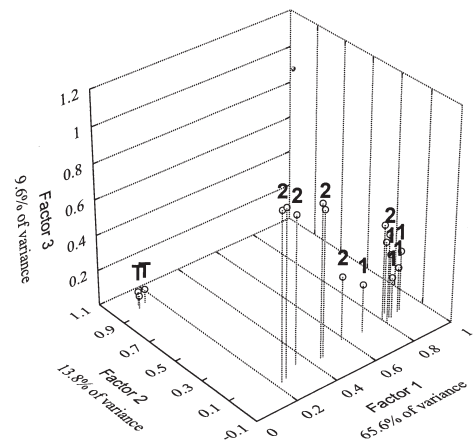

Fig. 4. Arrangement according PCA based on chemical profiles of an isolated tree, with three foliar samples indicated by letter **T** (two samples were indentical) and 16 seedlings with 1 year-old (**1**) and 2 year-old seedlings (**2**). The PCA explains 89% of the variance with three factors.

the chemical phenotype of their presumed parental trees (Fig. 1b–d). Langenheim & Stubblebine (1983) found that their *Hymenaea* trees were able to reproduce their own chemotype, although none of these chemotypes were found surviving under their parental trees.

ONTOGENETIC CAUSES

In some terpene-producing trees, such as *Umbellularia californica*, leaves from sprouts have a different chemical profile from that of leaves from the sprouting tree (Goralka & Langenheim 1996). Once that the sprouts reach a certain height, the leaf chemical profile becomes similar to that of the sprouting tree. This may suggest that seedlings in *N. ambigens* could have a similar chemical ontogenetic variation and thus we did not detect differentiation owing to differential mortality among seedlings. The fact that some of our seedlings closely resembled the chemical phenotype of their presumed parental trees argues against this possibility.

Conclusion

Our results suggest that the cause of chemical differentiation between seedlings and their closest adult tree is differential mortality among seedlings as a result of biological agents, much in the way as Langenheim & Stubblebine (1983) proposed. We detected dozens of compounds in the individual chromatograms but few of them were the determinants in chemically separating seedlings from their closest adult. Although we did not identify any compound from the chromatograms, we do know that *N. ambigens* leaves have terpenoids and phenylpropanoids (Del Amo *et al.* 1986) which are well known for their antagonistic activity against insects and fungal pathogens (see

Langenheim 1994). Of course, experiments are required to demonstrate that the compounds that differentiated seedlings from their closest adult have antagonistic function against plant enemies that attack *N. ambigens*. The ultimate test of the differential mortality according to the chemical phenotype hypothesis will need of the chemical phenotypes of seedlings before they are placed and followed in time under and away from the canopy of the parental tree.

We agree with D. H. Janzen's assertion (personal communication) that herbivores or pathogens do not eat Latin binomials. Our study with *N. ambigens* seems to agree with this. This insight applied to the Janzen–Connell hypothesis may help to explain cases where its predictions have been rejected.

Acknowledgements

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