Revista Colombiana de Entomología 38 (1): 114-117 (2012)
https://doi.org/10.25100/socolen.v38i1.8967

Atta sexdens (Hymenoptera: Formicidae) nests are located under higher canopy cover in colombian amazon rainforests

Los nidos de *Atta sexdens* se encuentran bajo alta cobertura en la selva amazónica colombiana

HEIKE A. J. A. VAN GILS[1]

Abstract: Leafcutter ants, *Atta* and *Acromyrmex* spp., are dominant herbivores and important ecosystem engineers in the Neotropics. Some rainforest leafcutter ant species seem to be found in higher densities at forest edges or gaps, which in some cases are actively created by themselves. This implies the presence of a lower than average canopy cover which, in addition to several ant activities, may lead to vegetation diversification during and after colony life. This study compared canopy cover at active *Atta sexdens* nests and at random sites in three habitat types in the Colombian Amazon for the years 2008, 2006 and 1992. Canopy cover at nests and random sites was measured with a densiometer in 2008 and estimated by means of satellite images in 2006 and 1992. Contrary to expectation, canopy cover was found consistently higher at *A. sexdens* nests than at random sites. This and other nest aspects differentiate *A. sexdens* from other rainforest *Atta* species. Therefore, it is argued how *A. sexdens* is thought to affect rainforest vegetation differently as well.

Key words: Attini. Ecological impact. Leafcutter ant. Vegetation gap. Satellite image.

Resumen: Se consideran las hormigas arrieras *Atta* y *Acromyrmex* spp. como herbívoros dominantes e ingenieros importantes de ecosistemas en el Neotrópico. Algunas especies de hormiga arriera de la selva lluviosa parecen encontrarse en densidades mayores en los bordes de la selva o en aperturas, las cuales en algunos casos son creadas activamente por ellas mismas. Esto implica la presencia de una cobertura del dosel menor que promedio lo cual, en adición a varias actividades de las hormigas, puede llevar a una diversificación de la vegetación durante y después de la vida de la colonia. Este estudio comparó la cobertura del dosel en los nidos activos de *Atta sexdens* y en sitios escogidos al azar en tres tipos de hábitat en la Amazonía colombiana para los años 2008, 2006 y 1992. La cobertura del dosel en los nidos y en los sitios escogidos al azar se midió con un densiómetro en el 2008 y se la estimó por medio de imágenes satelitales para 2006 y 1992. Contrario a lo esperado, se encontró que la cobertura del dosel fue consistentemente más alta en los nidos de *A. sexdens*. Éste y otros aspectos del nido diferencian *A. sexdens* de las otras especies de *Atta* de la selva lluviosa. Se argumenta cómo, por lo tanto, *Atta sexdens* afecta de manera diferente a la vegetación de la selva lluviosa también.

Palabras clave: Attini. Impacto ecológico. Hormiga arriera. Apertura en la vegetación. Imagen satelital.

Introduction

Leafcutter ants, genera *Atta* and *Acromyrmex*, are considered important ecosystem engineers in the Neotropics (Fowler *et al* 1989; Hölldobler and Wilson 1990). They are also of great relevance as key herbivores during successional processes (Vasconcelos and Cherrett 1997; Vasconcelos 1997) and as pest species in planted forest such as agroforestry and restoration programs, and agricultural land (Della-Lucia 2003). Their nests are heterogeneously distributed (Jaffe and Vilela 1989; Lapointe *et al.* 1998; Schoereder 1998; Meyer *et al.* 2009). For example, *Atta cephalotes* (L., 1758), *Atta laevigata* (F. Smith, 1858) and *Atta colombica* (Guérin-Méneville, 1844) nests in rainforests are more frequently found in vegetation gaps or near edges (Jaffe and Vilela 1989; Farji-Brener and Illes 2000; Peñaloza and Farji-Brener 2003; Wirth *et al.* 2003; Urbas *et al*. 2007;Wirth *et al.* 2007; Meyer *et al.* 2009; Silva *et al.* 2009), which are characterized by pioneer plant species (Turner 2004).

The palatable forage hypothesis argues that leafcutter ants are favored by these pioneer plant species due to their lower chemical and higher nutritional content (Farji-Brener 2001). Many rainforest *Atta* species also actively create gaps by removing all vegetation on and around the nest (Gonçalves 1967). Gap creation, soil perturbation (Alvarado *et al.* 1981; Moutinho *et al.* 2003;Verchot *et al.* 2003) and deposition of organic waste and seeds on the soil surface (Haines 1978; Sternberg *et al.* 2007; Hudson *et al.* 2009), are the most important ingredients of the underlying mechanisms that make these *Atta* colonies key modifiers of rainforest vegetation structure and composition (Garrettson 1998; Hull-Sanders and Howard 2003; Peñaloza and Farji-Brener 2003; Farji-Brener 2005; Meyer 2008; Corrêa *et al.* 2010).

Contrary to site selection of most *Atta* species, *Atta sexdens* (Linneaus, 1758) nests in the Colombian Amazon were observed only in habitat types with high canopy cover (van Gils *et al.* 2010, 2011).This study aimed to evaluate whether nests within these habitat types are located under relatively higher (as seems to be suggested by van Gils *et al.* 2010, 2011) or lower (as is the case for *A. cephalotes*, *A. laevigata* and *A. colombica*) canopy cover. This study contributes to our knowledge of the impact of each leafcutter ant species on different, and especially human-disturbed, ecosystems (Wirth *et al.* 2003; Côrrea *et al.* 2010). *A. sexdens* has rarely been studied for its impact on the vegetation surrounding the nest.

Materials and Methods

Study area. This study was carried out in the community of Palmeras (3°48'40.9"S 70°17'53.3"W) and on the private farm Versalles (3°49'51.2"S 70°14'26.9"W), both located

[1] Ph. D. Facultad de Agronomía, Universidad Nacional de Colombia. Av. Carrera 30 # 45-03, Edificio 500, Bogotá, Colombia. Tel: +57 3102798147. *heike_van_gils@hotmail.com.*

along the Colombian Amazon River. Mean annual rainfall in the study area is 3200 mm. There is a distinct dry season from June to September and a wet season from October to May. Average relative humidity is approximately 86% (Riaño 2003). The study area is part of the hilly sedimentary Amazon plain, which dates from the Tertiary (Riaño 2003). The soil is of marine and continental origin and mostly classified as Typic Hapludult (Ultisol) (Brady and Weil 2002). Natural vegetation cover is tropical rainforest, with Lecythidaceae, Myristicaceae, Violaceae, Moraceae and Fabaceae as abundant plant families (IGAC 1997). Since the beginning of last century, human activity has also created patches of secondary forest, agricultural plots and housing sites in the area (Riaño 2003; Pinilla 2004). Three habitat types were included in this study: OF (old rainforest), AF (secondary rainforest - abandoned agricultural plots) and GF (secondary rainforest - abandoned grassland). In each habitat type, the location of active *A. sexdens* nests was determined directly for the year 2008. The locations were determined indirectly for 2006, 1999 and 1992 and they were mapped on satellite images (as described in van Gils *et al.* 2011). Only the 2006 and 1992 satellite images were considered sufficiently free of cloud formation to be used in the current study.

Canopy cover determination. In 2008, canopy cover was determined with a Robert E. Lemmon densiometer (Model A - Forestry Suppliers) (Englund *et al.* 2000). Measurements were carried out at each active *A. sexdens* nests in OF (N = 26), AF (N = 6) and GF (N = 24) (van Gils *et al.* 2011), and at an equivalent number of random sites in the same habitat types. Four measurements were taken towards the north, east, south and west on the most central nest mound or at each random site. The same procedure was repeated 15 m to the north, east, south and west. This way, a canopy area of approximately 45 x 45 m was covered. Twenty measurements were taken at each nest or random site. The average was multiplied by 1.04 to establish the average percent canopy cover.

To get a relative indication of vegetation cover on active *A. sexdens* nests and random sites without nests in 2006, ASTER satellite image AST_L1B_003_0429200615070_vnir.img was visualized in gray scale *stretched* mode of band ASTER_Band3N in the GIS software program ArcMap (ESRI Inc. 2006). For 1992, LANDSAT satellite image TM004_063_19922808 (ID: 015-784) was visualized in gray scale *stretched* mode of band Layer_5 in the same program. On these two images, all active nests of the respective years were projected. ASTER and LANDSAT satellite images visualized in gray scale *stretched* mode consist of pixels assigned with values according to light reflection. Pixel values, therefore, do not represent actual canopy cover percentages, but give a relative indication: Low canopy cover reflects more light and it causes brighter grey pixels with higher values. In contrast, high canopy cover reflects less light and causes darker grey pixels with lower values. A LANDSAT image pixel measures 45 x 45 m and an ASTER image pixel 15 x 15 m. On the satellite images, it was aimed to determine pixel values of a canopy area similar to that covered by the densiometer method (i.e. approximately 45 x 45 m).

On the LANDSAT image of 1992, the values were determined for only those pixels on which more than 50% of each nest symbol was located (N = 34 in OF; N = 13 in AF; N = 34 in GF – van Gils *et al.* 2011). In the same image, the values of an equal number of randomly located pixels in each habitat type were also determined. For the ASTER image of 2006, the values were determined of the pixel on which more than 50% of each nest symbol was located (N = 59 in OF; N = 24 in AF; N = 35 in GF – van Gils *et al.*2011), plus the values of all eight surrounding pixels. This way, a canopy area of 45 x 45 m was covered. Then, the average of these nine pixels was calculated to obtain one value per nest. In the same image, the average values of an equal number of randomly located groups of such nine pixels in each habitat type were also determined.

Statistical analysis. Canopy cover percentages of 2008 and average pixel values of 2006 and 1992 were compared per habitat type and for all habitat types together with Kolmogorov-Smirnov tests carried out in statistics software program SPSS 15.0.1 (SPSS Inc. 2006).

Results

In 2008 the percent canopy cover in OF, GF and all habitat types together was higher at *A. sexdens* nests than at random sites; only in AF the difference was not significant (Table 1). In 2006 and 1992, nest pixel values were significantly lower in OF, GF and all habitat types together (Table 1). In AF, nest pixel values showed the same trend, but differences were not significant.

Discussion

Contrary to the nests of other common rainforest *Atta* species, this study showed that *A. sexdens* nests were consistently located under higher than average canopy cover in old rainforest (OF), abandoned grassland secondary forest (GF) and in general. The lack of a clear pattern and significant differences in abandoned agricultural plot secondary forest (AF) may be due to a relatively large variability in canopy cover in this habitat or to the low sample number. It seems unlikely that the higher canopy cover at nests was caused only by non-removal of vegetation from *A. sexdens* nest mounds (Gonçalves 1967). Although *A. sexdens* founding queens seem to prefer open spaces for nest establishment (Vasconcelos 1990), there may be some advantages to being located at more shaded micro-sites: Nests, young ones in particular, may be less conspicuous to natural enemies, and micro-climatic conditions may be more favorable (van Gils 2011). *Atta* worker ants frequently travel as far as 200 m to reach suitable forage (Eidmann 1932; Cherrett 1968). Therefore, high canopy cover micro-sites should not limit the access of ants to palatable pioneer plants.

Nests of other common rainforest leafcutter ant species, such as *A. colombica* and *A. cephalotes*, receive significantly more light due to the gaps they create overhead by removing vegetation from nest mounds and surroundings up to canopy level (Garrettson *et al.* 1998; Farji-Brener and Illes 2000; Hull-Sanders and Howard 2003; Wirth *et al.* 2003; Farji-Brener 2005; Meyer 2008; Côrrea *et al.* 2010). Partly due to this activity, both species strongly affect the surrounding vegetation structure and composition (Garrettson *et al.* 1998; Hull-Sanders and Howard 2003; Wirth *et al.* 2003; Farji-Brener 2005; Meyer 2008; Côrrea *et al.* 2010). However, colonization patterns and fine plant root growth of plants growing near nest mounds differ between nests of these two leafcutter ant species due to the above vs. underground lo-

Table 1. Average percent canopy cover for 2008 and average pixel values (+s.e.) for 2006 and 1992 at *A. sexdens* nests and random sites in old rainforest (OF), abandoned agricultural plot secondary rainforest (AF), abandoned grassland secondary rainforest (GF), and in all habitat types together.

	Habitat type			
	OF	**AF**	**GF**	**All**
Average percent canopy cover 2008	*N* = 26	*N* = 6	*N* = 24	*N* = 56
A. sexdens nests	94.3 + 0.20	92.7 + 0.78	90.1 + 1.58	92.3 + 0.73
Random sites	92.9 + 0.40	92.4 + 0.49	86.8 + 1.01	90.3 + 0.62
Z ; P	1.664 ; < 0.05	0.577 ; 0.893	1.588 ; < 0.05	2.268 ; < 0.001
Average pixel value 2006	*N* = 34	*N* = 13	*N* = 34	*N* = 81
A. sexdens nests	95.75 + 0.57	111.7 + 2.04	107.8 + 1.17	103.05 + 0.99
Random sites	99.05 + 0.65	109.7 + 1.91	112.6 + 0.87	106.43 + 0.89
Z ; P	2.183; < 0.001	0.784; 0.570	1.698; < 0.05	1.807; < 0.05
Average pixel value 1992	*N* = 59	*N* = 24	*N* = 35	*N* = 118
A. sexdens nests	41.4 + 0.75	50.0 + 0.57	46.0 + 1.01	44.5 + 0,58
Random sites	44.3 + 0.50	52.8 + 0.76	51.1 + 1.07	48.05 + 0.56
Z ; P	1.657 ; < 0.05	1.155 ; 0.139	1.673 ; < 0.05	1.758 ; < 0.05

cation of their organic waste dumps (Farji-Brener and Medina 2000). Another study on *A. sexdens* nests in cerrado vegetation (Schoereder and Howse 1998) found that there they had no observable effect at all on vegetation structure. These studies clearly illustrate how the overall impact of each *Atta* species on the surrounding rainforest ecosystem is defined differently according to their particular behavior and nest-building characteristics (Fowler *et al.* 1989; Fowler and Claver 1991; Farji-Brener 2005; Côrrea *et al.* 2010). Contrary to *A. colombica* and *A. cephalotes* nests, those of *A. sexdens* were located under higher than average canopy cover. This implies that less light reaches the forest floor at nest locations, even after colony death. Furthermore, *A. sexdens* does not accumulate organic waste or seeds on the soil surface but in deep underground chambers and does not remove all vegetation from the nest mounds and surroundings (Eidmann 1932; Gonçalves 1967).

Conclusion

Increased light and nutrient availability and a bare forest floor are the principal ingredients for vegetation diversification and growth, especially for shade-intolerant plant species (Côrrea *et al.* 2010). However, none of these are attributes of *A. sexdens* nests, during or after colony demise. It seems that *A. sexdens* nests in human-disturbed rainforests do not provide a suitable niche at all for light-demanding, nutrient-limited, and small-seeded litter-gap demanding plant species (Côrrea *et al.* 2010). Therefore, general seedling germination and plant growth may even be reduced on and around these nests. The influence of *A. sexdens* on vegetation structure and composition is likely to differ from the influence of other rainforest *Atta* species. Further studies should elucidate the extent of *A. sexdens* engineering role in rainforest and other ecosystems.

Acknowledgements

I thank the community of Palmeras and the Barbosa family for allowing access to their lands. I am greatly indebted with Andreas Gaigl and Cas Vanderwoude for comments made on an earlier version of the manuscript. This research was financially supported with grants from the Vice Dean of Investigation and the Faculty of Agronomy of the National University of Colombia, Bogotá. Logistic assistance was provided by the Amazon Institute of Scientific Research – SINCHI in Leticia, Amazonas, Colombia.

Literature cited

ALVARADO, A.; BERISH, C.W.; PERALTA, F. 1981. Leaf-cutter ant (*Atta cephalotes*) influence on the morphology of Andepts in Costa Rica. Soil Science Society of America Journal 45: 790-794.

BRADY, N.C.;WEIL, R.R. 2002. The nature and properties of soils. 13th Edition. Pearson Education, U.S.A. 936 p.

CHERRETT, J.M. 1968. Some aspects of the distribution of pest species of the leaf-cutting ants in the Caribbean. Proceedings of the American Society of Horticultural Science of Tropical Regions 12: 295-310.

CORRÊA, M.M.; SILVA, P.S.D.; WIRTH, R.; TABARELLI, M.; LEAL, I.R.2010. How leaf-cutting ants impact forests: drastic nest effects on light environment and plant assemblages. Oecologia 162: 103-115.

DELLA-LUCIA, T.M.C. 2003. Hormigas de importancia económica en la región Neotropical. pp. 337-349. En: Fernández, F. (Ed.). Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander Von Humboldt, Bogota, Colombia. 424 p.

EIDMANN, H. 1932. Beiträge zur Kenntnis der Biologie, insbesondere des Nestbaues der Blattschneiderameise *Atta sexdens* L. Zeitschrift für Morphologie und Oekologie der Tiere 25:154-183.

ENGLUND, S. R.; O´BRIEN, J. J.; CLARK, D. B. 2000. Evaluation of digital and film hemispherical photography and spherical densiometry for measuring forest light environments. Canadian Journal of Forest Research 30: 1999-2005.

ESRI INC. 2006. ArcMap versión 9.2. www.esri.com.

FARJI-BRENER, A. G. 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. Oikos 92: 169-177.

FARJI-BRENER, A. G. 2005. The effect of abandoned leaf-cutting ant nests on plant assemblage composition in a tropical rainforest of Costa Rica. Écoscience12 (5): 554-560.
FARJI-BRENER, A. G.; ILLES, A. E. 2000. Do leaf-cutting ants make "bottom-up" gaps in neotropical forests?: a critical review of the evidence. Ecology Letters 3: 219-227.
FARJI-BRENER, A. G.; MEDINA, C. A. 2000. The importance of where to dump the refuse: Seed banks and fine roots in nests of the leaf-cutting ants *Atta cephalotes* and *Atta colombica*. Biotropica 32: 120-126.
FOWLER, H. G.; CLAVER, S. 1991. Leaf-cutter ant assemblies: effects of latitude, vegetation and behaviors. pp. 51-59. En: Huxley C. R.; Cutler D. F. Ant plant interactions Oxford University Press, Oxford, UK. 601 p.
FOWLER, H. G.; PAGANI, M. I.; SILVA, O. A.; FORTI, L. C.; SILVA, V. P.; VASCONCELOS, H. L. 1989. A pest is a pest is a pest? The dilemma of Neotropical leaf-cutting ants: Keystone taxa of natural ecosystems. Environmental Management 13: 671-675.
GARRETTSON, M.; STETZEL, J. F.; HALPERN, B. S.; ERAN, D. J.; LUCEY, B. T.; MCKONE, M. J. 1998. Diversity and abundance of understorey plants on active and abandoned nests of leaf-cutting ants (*Atta cephalotes*) in a Costa Rican rain forest. Journal of Tropical Ecology 14: 17-26.
GONÇALVES, C. R. 1967. As formigas cortadeiras da Amazônia, dos generos "*Atta*" Fabr. e "*Acromyrmex*" Mayr (Hym., Formicidae). Atas Simposio Biota Amazônica 5 (Zoologia): 181-202.
HAINES, B. L. 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. Biotropica 10: 270-277.
HÖLLDOBLER, B.; WILSON, E. O. 1990. The ants. Cambridge: Harvard University. 732 p.
HUDSON, T. M.; TURNER, B. J.; HERZ, H.; ROBINSON, J. S. 2009. Temporal patterns of nutrient availability around nests of leaf-cutting ants (*Atta colombica*) in secondary moist tropical forest. Soil Biology and Biochemistry 41: 1088-1093.
HULL-SANDERS, H. M.; HOWARD J. J. 2003. Impact of *Atta colombica* colonies on understory vegetation and light availability in a Neotropical forest. Biotropica 35: 441-445.
INSTITUTO GEOGRÁFICO AGUSTÍN CODAZZI (IGAC). 1997. Zonificación ambiental para el plan modelo Colombo-Brasilero. (Eje Apaporis-Tabatinga: PAT). Linotipia Bolívar, Santafé de Bogotá, Colombia. 410 p.
JAFFE, K.; VILELA, E. 1989. On nest densities of the leaf-cutting ant *Atta cephalotes* in tropical primary forest. Biotropica 21: 234-236.
LAPOINTE, S. L.; SERRANO, M. S.; JONES, P. G. 1998. Microgeographic and vertical distribution of *Acromyrmex landolti* (Hymenoptera: Formicidae) nests in a Neotropical savanna. Environmental Entomology 27: 636-641.
MEYER, S.T. 2008. Ecosystem engineering in fragmented forests: edge mediated hyper abundance of leaf-cutting ants and resulting impacts on forest structure, microclimate and regeneration. Ph. D. dissertation, University of Kaiserslautern, Kaiserslautern, Germany. 159 p.
MEYER, S. T.; LEAL, I. R.; WIRTH, R. 2009. Persisting hyperabundance of keystone herbivores (*Atta* spp.) at the edge of an old Brazilian Atlantic forest fragment. Biotropica 41 (6): 711-716.
MOUTINHO, P. R.; NEPSTAD, D. C.; DAVIDSON, E. A. 2003. Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. Ecology 84 (5): 1265-1276.
PEÑALOZA, C.; FARJI-BRENER, A. G. 2003.The importance of treefall gaps as foraging sites for leaf-cutting ants depends on forest age. Journal of Tropical Ecology 19: 603-605.
PINILLA, M. C. 2004. Uso del paisaje en el sector sur del Parque Natural Nacional Amacayacu. Cuadernos de Desarrollo Rural 53: 133-156.
RIAÑO, E. 2003. Organizando su espacio, construyendo su territorio. Transformaciones de los asentamientos Ticuna en la ribera del Amazonas colombiano. Unibiblos, Bogotá D.C., Colombia. 236 p.
SCHOEREDER, J. H. 1998. Nest density of leaf-cutting ants in natural ecosystems. Revista Brasileira de Entomología 41: 233-234.
SCHOEREDER, J. H.; HOWSE, P. E. 1998. Do trees benefit from nutrient-rich patches created by leaf-cutting ants? Studies on Neotropical Fauna and Environment 33: 111-115.
SILVA, P. S. D.; BIEBER, A. G. D.; LEAL, I. R.; WIRTH, R.; TABARELLI, M. 2009. Decreasing abundance of leaf-cutting ants across a chrono sequence of advancing Atlantic forest regeneration. Journal of Tropical Ecology 25: 223-227.
SPSS INC. 2006. SPSS version 15.0.1. Chicago, IL, U.S.A.
STERNBERG, L.; PINZÓN, M. C.; MOREIRA, M. Z.; MOUTINHO, P.; ROJAS, E. I.; HERRE, E. A. 2007. Plants use macronutrients accumulated in leaf-cutting ant nests. Proceedings of the Royal Society Biological Sciences Series B 274: 315-321.
TURNER, I. M. 2004. The ecology of trees in the tropical rainforest. Cambridge Tropical Biology Series, Cambridge University Press, UK. 298 p.
URBAS, P.; ARAÚJO JR., M. V.; LEAL, I. R.; WIRTH, R. 2007. Cutting more from cut forests: Edge effects on foraging and herbivory of leaf-cutting ants in Brazil. Biotropica 39: 489-495.
VAN GILS, H. A. J. A. 2011. Los factores ambientales en relación con la hormiga arriera (*Atta sexdens*) en el sur del trapecio amazónico, Colombia. Ph.D. dissertation, Facultad de Agronomía, Universidad Nacional de Colombia, Colombia. 236 p.
VAN GILS, H. A. J. A.; GAIGL, A.; GÓMEZ, L. E. 2010. The relationship between soil variables and leafcutter ant (*Atta sexdens*) nest distribution in the Colombian Amazon. Insectes Sociaux 57: 487-494.
VAN GILS, H. A. J. A.; GÓMEZ, L. E.; GAIGL, A. 2011. Leafcutter ant (*Atta sexdens* L.) (Hymenoptera: Formicidae) Demography in the Colombian Amazon: An Evaluation of the Palatable Forage Hypothesis. Environmental Entomology 40 (4): 770-776.
VASCONCELOS, H. L. 1990. Habitat selection by the queens of the leaf-cutting ant *Atta sexdens* L. in Brazil. Journal of Tropical Ecology 6: 249-252.
VASCONCELOS, H. L. 1997. Foraging activity of an Amazonian leaf-cutting ant: responses to changes in the availability of woody plants and to previous plant damage. Oecologia 112: 370-378.
VASCONCELOS, H. L.; CHERRETT, J. M. 1997. Leaf-cutting ants and early forest regeneration in central Amazonia: Effects of herbivory on tree seedling establishment. Journal of Tropical Ecology 13: 357-370.
VERCHOT, L. V.; MOUTINHO, P. R.; DAVIDSON, E. A. 2003. Leaf-cutting (*Atta sexdens*) and nutrient cycling: deep soil inorganic nitrogen stocks, mineralization, and nitrification in Eastern Amazonia. Soil Biology and Biochemistry 35: 1219-1222.
WIRTH, R.; BEYSCHLAG, W.; RYEL, R.; HERZ, H.; HÖLLDOBLER, B. 2003. Herbivory of leaf-cutting ants: a case study on *Atta colombica* in the tropical rainforest of Panama. Springer-Verlag, Berlin, Heidelberg, Germany. 233 p.
WIRTH, R.; MEYER, S. T.; ALMEIDA, W. R.; ARAÚJO, M. V.; BARBOSA, V. S.; LEAL, I. R. 2007. Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest. Journal of Tropical Ecology 23: 501-505.

Received: 28-jun-2011 • Accepted: 9-feb-2012