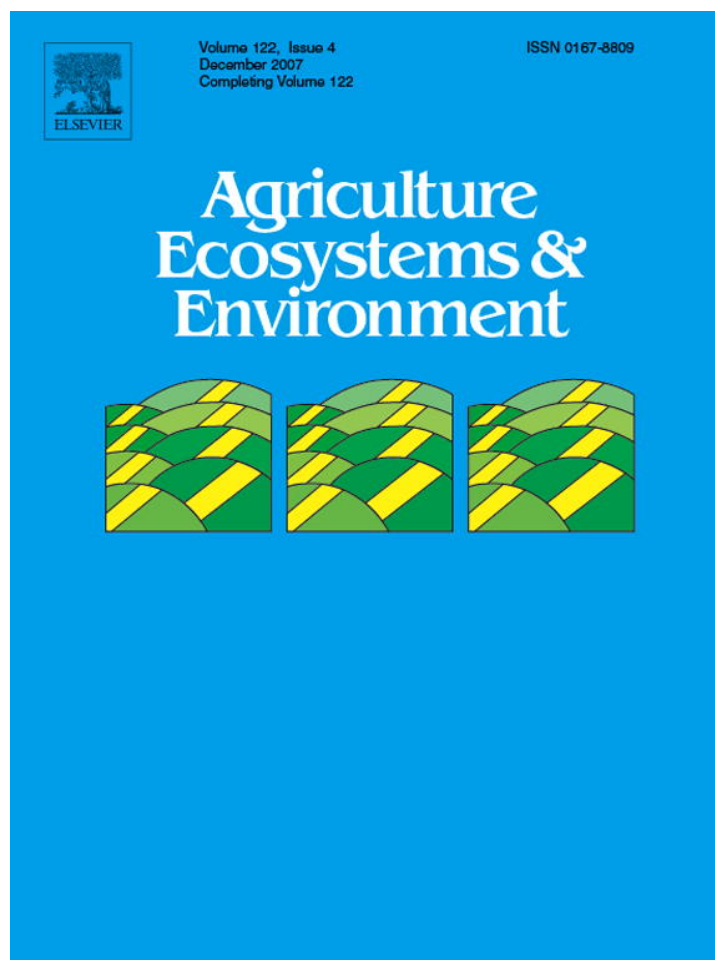


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Short communication

Is productivity of cacao impeded by epiphytes? An experimental approach

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Abstract

The impact of epiphytes on cacao productivity was investigated in agroforests in Central Sulawesi, Indonesia. Effects of epiphyte removal on fruit-set success and eventual yields were studied on 80 trees in an experiment with a balanced full factorial design. The removal treatment had no significant effect on the eventual harvest of the cacao trees. Pollinator availability had the greatest impact on fruit-set success, whereas yields were mainly determined by site-specific factors that mediate fruit-abortion and occurrence of fungal diseases. The results illustrate that epiphytic flora dominated by non-vascular species may have no effects on cacao tree functioning and removal of non-vascular epiphytes is unnecessary for improving the productivity of cacao. Hence, farmers' labour can be reduced and conservation of the rich biodiversity outside natural forests supported.

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1. Introduction

Tropical rainforests harbour a wide range of epiphytic plants (Schimper, 1888; Richards et al., 1996; Nieder et al., 2001). Among these, non-vascular epiphytes such as bryophytes and lichens, are the most diverse and abundant groups, yet they are also one of the least studied (Pócs, 1982; Gradstein et al., 2005). Epiphytic bryophytes play an important role in the stabilization of the abiotic environment in trees (Stuntz et al., 2002) and provide a suitable habitat for various groups of arthropods (Nadkarni and Longino, 1990).

Recent work on non-vascular epiphyte diversity on cacao (*Theobroma cacao* L.) in tropical agroforestry systems has shown that epiphyte assemblages on cacao trees can resemble those of natural tropical rainforest trees (Andersson and Gradstein, 2005). Hence, these agricultural systems may serve as a tool in the conservation of the highly diverse and functionally important, native non-vascular epiphyte flora. In

the case of cacao, however, it is believed that epiphytic layers may constrain the development of the cauliflorous flowers of the host plants, causing decreases in fruit growth and, eventually, losses in harvest. The latter assumption has led to the common management practice of epiphyte removal in cacao plantations (Kautz and Gradstein, 2001; Andersson and Gradstein, 2005; David, 2005). Although dense epiphytic layers can cause damage through breakage of branches (Strong, 1977) and some vascular epiphyte species may have virulent effects on host trees via their symbiotic mycorrhiza ("epiphytosis"; Ruinen, 1953), a negative effect of epiphytes on cacao trees remains essentially unproven.

The present study is an experimental approach into the impact of epiphytes on cacao productivity in Indonesian cacao systems. Indonesia, the third most important cacao producing country in the world (International Cacao Organization, 2005), is a hotspot in terms of both biodiversity (Myers et al., 2000) and deforestation (Achard et al., 2002). We tested two hypotheses on the effects of epiphytic layers on cacao production: (1) epiphytic layers have direct effects on cacao productivity in that flowering and fruit development is

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inhibited and (2) epiphytic layers have indirect effects by promoting pests that depend on the availability of moist habitats provided by the layers density. The cacao pest Black Pod Disease (*Phytophthora* sp., BPD) was common in the study region (Bos et al., 2007) and is known to depend on moist habitats (Thorold, 1952; David, 2005).

2. Materials and methods

The study took place in cacao-dominated agroforestry systems around Toro Village in the Kulawi Valley, Central Sulawesi, Indonesia. The village is situated at ca. 800 m a.s.l. along the western border of the 231,000 ha. Lore Lindu National Park. Four agroforestry systems owned by farmers who did not practice removal of epiphytic layers were selected. The sites had similar shade tree stands, consisting of diverse species such as *Durio zibethinus* Murr., *Nephelium lappaceum* L., *Syzygium aromaticum* (L.) Merr. & Perry, *Erythrina subumbrans* Hassk., *Aleurites moluccana* Wild., *Calamus zollingerii* Becc., *Lansium domesticum* Corr., *Persea americana* Mill. and *Myristica fragrans* Houtt.

To study the direct and indirect effects of epiphytic layers on cacao productivity, a balanced full factorial design repeated in four blocks was used. In each of the four agroforestry systems (blocks) 20 cacao trees (i.e., a total of 80 trees) were selected randomly. The epiphytic layers were removed from half of these trees before the start of the experiment. Per site, trees were divided into four treatment groups: (1) 5 trees with removed epiphytic layers and with emerging flowers being manually cross-pollinated until development of a minimum of 16 fruits, (2) 5 trees with emerging flowers being manually cross-pollinated, but with epiphytic layers left intact, (3) 5 trees with removed epiphytic layers and emerging flowers left for natural pollination, and (4) 5 control trees (epiphytic layers intact, emerging flowers left for natural pollination). Epiphyte removal was done very carefully, avoiding damage to the flowers and bark.

Cacao flowers are generally self incompatible and under natural circumstances mainly pollinated by midges of the family Ceratopogonidae (e.g., Entwistle, 1972; Young, 1994). Manual standardization of cross pollination was achieved by transferring pollen from flowers of three other trees to the stigma of the target flower.

The experiment started in December 2004. Fruits were monitored and measured regularly until growth was terminated due to harvest or other causes (see also Bos et al., 2007). The number of wilted fruits was noted as well, serving as an indicator of physiological constraints on fruit development (Valle et al., 1990). All measurements were carried out on the tree's main stem, where most flowering and fruiting takes place (Entwistle, 1972). The experiment ended with the harvest of the last fruits in June 2005.

The effects of the treatments were statistically tested in general linear models (GLMs) with study site as random

factor and treatments (pollination and removal of epiphytic layers) as fixed factors, using Type III decomposition of variance. Interaction effects were included in the model to identify treatment- and site-specific effects of both treatments on the tested variables. Effects were tested on fruit-set success, amount of fruit-wilt, amount of fruits infected with BPD and numbers of fruits harvested. All variables were calculated as percentages of initial amounts of flowers per tree.

Initial fruit-set, subsequent fruit wilt and incidence of BPD, and harvested fruit data, were proportional and therefore arcsine square-root transformed before analyses. Additionally, data were square-root transformed where necessary to achieve normal distribution of model residuals. All analyses were conducted using Statistica 7.0 (Statsoft Inc., 1984–2004).

3. Results

In total, 3077 flowers on 80 trees were studied. About half of the flowers (1534) were successfully pollinated. Of these, a total of 182 resulted in mature fruits.

Removal of the epiphytic layers had no significant effect on fruit-set (Table 1a). Instead, a non-significant, positive effect ($p = 0.07$) of the presence of epiphytic layers on fruit-set was found (Table 1a).

The pollination treatment had the strongest impact on fruit-set success (Table 1a), with hand-pollination resulting in a much more successful fruit-set ($75 \pm 3\%$) than natural pollination ($43 \pm 5\%$). Natural pollination differed significantly between sites; in one site natural fruit-set success even equalled that resulting from hand-pollination. Incidence of the BPD was not affected by the treatments, although the effect of moss removal differed between sites (Table 1c). The proportion of wilted fruits was significantly higher after hand pollination than after natural pollination (Table 1b). Finally, the percentage of flowers that resulted in mature fruits (overall average $7 \pm 1\%$) did not seem to depend on either epiphyte removal or on the pollination treatment (Table 1d).

4. Discussion and conclusions

The results of this study show that epiphyte removal had no significant effect on the productivity of the cacao trees. Neither initial proportions of fruit-set success, subsequent levels of fruit-wilt and BPD-infections, nor final proportions of fruits harvested were significantly altered by the removal of the epiphytic layers. In fact, natural fruit-set was even slightly lower ($p = 0.07$) on trees with epiphyte layers removed.

Epiphytic bryophyte layers are an indicator of abiotic environmental variables, especially of humidity (van Reenen and Gradstein, 1983; Frahm and Gradstein,

Table 1
Impact of site, pollination, and epiphyte removal on fruit-set success, fruit wilt, occurrence of Black Pod Disease (BPD) and cacao harvest, using general linear models (GLMs) with type III decomposition of variance

	MS	d.f.	F	p
(a) Fruit-set				
Site	0.33	3, 1.9	2.09	0.345
Pollination	4.07	1, 3	20.73	0.020
Epiphyte removal	0.13	1, 3	7.27	0.074
Pollination × epiphyte removal	0.02	1, 67	0.41	0.525
Site × pollination	0.20	3, 67	3.48	0.021
Site × epiphyte removal	0.02	3, 67	0.33	0.806
Error	0.06			
(b) Wilt				
Site	0.08	3, 1.3	1.70	0.457
Pollination	0.91	1, 3	13.49	0.035
Epiphyte removal	0.05	1, 3	4.57	0.122
Pollination × epiphyte removal	0.00	1, 67	0.02	0.899
Site × pollination	0.07	3, 67	1.99	0.124
Site × epiphyte removal	0.01	3, 67	0.35	0.791
Error	0.03			
(c) BPD ^a				
Site	0.05	3, 2.3	0.25	0.854
Pollination	0.06	1, 3	3.05	0.179
Epiphyte removal	0.01	1, 3	0.03	0.881
Pollination × epiphyte removal	0.00	1, 67	0.03	0.854
Site × pollination	0.02	3, 67	0.43	0.734
Site × epiphyte removal	0.23	3, 67	4.74	0.005
Error	0.05			
(d) Harvest ^a				
Site	0.26	3, 1.4	3.38	0.301
Pollination	0.05	1, 3	0.71	0.461
Epiphyte removal	0.00	1, 3	0.03	0.884
Pollination × epiphyte removal	0.18	1, 67	2.27	0.136
Site × pollination	0.07	3, 67	0.94	0.425
Site × epiphyte removal	0.08	3, 67	1.03	0.385
Error	0.08			

Site entered as random factor (values 1–4), epiphyte removal and pollination type as fixed variables (1, 0). MS: means of squares and d.f.: degrees of freedom. Significant relationships are highlighted in bold.

^a Analyses after square root transformation of the data to reach normal distribution of model residuals.

1991). It has been shown that moist environments also promote fungal cacao diseases such as BPD (Thorold, 1952). However, these results indicate that the association between non-vascular epiphytes and fungal cacao diseases might be merely correlative instead of causal. No impact of epiphytic layers on BPD infection rates could be found. These results imply that removal of epiphytic layers eliminates the indicators, not the underlying causes of increased chances of BPD-infections in the research area.

Importantly, epiphytic assemblages on cacao in the study area consisted almost exclusively of lichen and bryophyte species while vascular epiphytes were rare (S.G. Sporn, unpublished data). Future studies in other regions should take into account the possible impact vascular epiphytes may have on cacao production. Moreover, epiphytic layers may have long-term deteriorative effects on their hosts (Ruinen, 1953), which were not studied in this experiment.

A strikingly low percentage of flowers produced mature fruits, which for cacao is not unusual (Valle et al., 1990) and may be explained by the relatively unspecialized natural pollination system of the cacao trees (Young, 1994). Fruit-set success significantly increased with hand pollination, indicating a significant pollination deficiency in the agroforestry systems, which was independent of the removal of epiphytic layers. Furthermore, natural pollination differed significantly between sites, suggesting that there are important site specific factors other than epiphyte removal, that influence cacao pollination. The increase in fruit-set after hand-pollination, however, was followed by an increase in harvest loss due to fruit-wilt. Fruit-wilt is a form of abortion when the number of fruits produced exceeds the load that trees can physiologically support (Valle et al., 1990). Therefore, our results demonstrate that increased pollination does not necessarily lead to increases in cacao's yields, as long as other environmental factors remain limiting. The potential fruit load of a cacao tree is restricted by factors such as available nutrients and local shade conditions (Entwistle, 1972; Bos et al., 2007).

In conclusion, epiphyte removal is not necessary for improving the productivity of cacao in the study region. We therefore strongly recommend abandoning this practice when such layers predominantly consist of non-vascular epiphytes. In contrast, this study revealed a slightly negative effect of epiphyte removal on the natural pollination of cacao. This may be explained by damage on the cacao tree caused by the practice of epiphyte removal, or even by the possible importance of the epiphyte layers as a substrate for pollinator populations (Fish and Soria, 1978). Pollinator availability had the greatest impact on fruit-set success, although total harvest was presumably mainly determined by site-specific factors, which are yet to be studied. In short, this study shows that if farmers consider epiphytic layers on cacao trees as irrelevant in terms of productivity, they may reduce their labour, and, at the same time, enhance the biodiversity supported by these agroforestry systems.

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