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Shade tree management affects fruit abortion, insect pests and pathogens of cacao

Merijn M. Bos *, Ingolf Steffan-Dewenter, Teja Tscharntke

Agroecology, Göttingen University, Waldweg 26, D-37073 Göttingen, Germany

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Abstract

The mortality of cacao fruits caused by early fruit abortion or insect and pathogen attacks was investigated in differently managed agroforestry systems in Central Sulawesi, Indonesia. Nine agroforestry systems shaded by three different types of tree stands were selected, which represented a decrease in structural heterogeneity: forest remnants, diverse planted trees and one or two species of planted leguminose trees. After standardized manual cross-pollination, the development of 600 fruits on 54 trees (6 trees per agroforest) was followed during 18 weeks of fruit development. In total, 432 of all fruits were lost before maturity, which seriously undermined yields. The proportion of harvested fruits per tree (overall average: 27 ± 4%) was not affected by canopy type. Although shade cover did not have a significant effect, losses due to fruit abortion were most likely under forest shade, where nitrogen-fixing leguminose shade trees were absent. Fruit losses due to pathogenic infections and insect attacks increased with the homogenization of the agroforests, supporting the hypothesis that agricultural homogenization increases risks of pest outbreaks. In conclusion, shade management may be improved to increase yields from cacao using highly diversified natural shade agroforestry systems.

Keywords: Flower–fruit ratio; *Helopeltis*; Herbivory; Indonesia; Pollination; *Phytophthora*; Cacao yield

1. Introduction

A common phenomenon in plants is that numbers of flowers exceed final numbers of mature fruits (Stephenson, 1981) and fruit mortality due to internal (e.g., Nichols and Walmsley, 1965; Pías and Guitián, 2006) and external (e.g., Louda, 1982; Arnold et al., 2003) factors can be a major bottleneck in plant reproductive success. Cacao (*Theobroma cacao* L.) is among the most common crops grown in tropical agroforestry systems. Its reproductive system is characterized by high numbers of flowers, of which generally no more than 5% develop into mature fruits (Entwistle, 1972; Young, 1994). The highest ever annual global production of 3.5 million t dry cacao beans was reached in 2004, which equaled a total of 3.7 billion US$ of income to farmers (International Cocoa Organization, 2005). Despite the increasing economic importance of cacao, surprisingly little is known about the mechanisms that determine its yields.

Because productivity of cacao is predicted to decrease under dense shade regimes (Zuidema et al., 2005), recent agricultural intensifications led to large scale landscape homogenization, turning heterogeneous, shaded agroforestry systems into poorly shaded monocultures at local and regional scales (Siebert, 2002). Such intensifications and consequent landscape homogenizations can threaten tropical biodiversity and profitable ecosystem services (e.g., Rice and Greenberg, 2000; Klein et al., 2002) and increase risks of pest outbreaks (Schroth et al., 2000; Wilby and Thomas, 2002; Tscharntke et al., 2005).

Cash crops grown in tropical agroforestry systems depend strongly on ecosystem services provided by naturally occurring species (Schroth et al., 2000; Tylianakis et al., 2005). In cacao, pollination is carried out by small insects such as midges (Entwistle, 1972; Young, 1994) and

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* Corresponding author. Tel.: +49 551 392057.
E-mail address: boommarter@hotmail.com (M.M. Bos).

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some ants are suggested to play important roles in the regulation of insect pests (Entwistle, 1972; See and Khoo, 1996). However, a wide range of herbivorous insects and pathogens attack cacao, and many of them are able to develop high densities, causing severe harvest losses and even regional abandonment of cacao farming (Fowler et al., 1956; Entwistle, 1972; Purdy and Schmidt, 1996; See and Khoo, 1996; Krauss and Soberanis, 2001).

In addition to pest attacks, a major cause of fruit mortality on cacao trees is active abortion, or ‘‘cherelle wilt’’ (Nichols and Walmsley, 1965; Valle et al., 1990; Young, 1994; Falque et al., 1995; Hasenstein and Zavada, 2001). Such losses are regulated by the plant, primarily as a response to pollen incompatibility (Hasenstein and Zavada, 2001) and nutrient limitations that result from low photosynthetic rates or poor soils (Nichols and Walmsley, 1965; Valle et al., 1990).

Here cacao fruit losses in shaded agroforestry systems are investigated, evaluating internal causes (fruit abortion) and external causes (insect attacks and pathogens) of fruit mortality. The question is whether shade density and composition of shade trees in agroforestry systems affect mechanisms of fruit loss. Management recommendations are derived for increasing cacao yields from shaded agroforests.

2. Materials and methods

2.1. Study sites

The study was conducted in nine cacao dominated agroforestry systems in the Toro village, about 100 km southwest of Palu, the capital city of Central Sulawesi, Indonesia. The systems were characterized by three different types of shade tree stands: trees remaining from previous rainforest cover, diverse planted trees (secondarily grown forest trees, fruit and timber trees and leguminose trees) and stands dominated by one or two species of planted trees (dominated by the leguminose *Glyricidia sepium* and *Erythrina subumbrans*). For each of these types of agroforestry, three sites were selected with cacao trees between 8 and 10 years old. The minimum distance between sites was 300 m and agroforestry types were geographically interspersed and not spatially clustered.

In the study area, cacao trees were mainly hybrids (‘‘Trinitario’’ type) between the ‘‘Criollo’’ and ‘‘Forastero’’ varieties. In contrast to cacao growing regions in West Africa and Central America, the usage of genetic varieties of cacao is not controlled in Central Sulawesi, and grown genotypes are not defined.

The percent canopy cover of the shade tree stands was estimated using a Spherical Densiometer$^{©}$; a concave mirror divided into squares (produced by R.E. Lemmon Forest Densiometers, USA). Canopy cover was measured at four locations per site, and means were calculated per site. The cover by the shade tree stands (72.1–90.5%) in the study sites is considered dense agroforestry shade (Zuidema et al., 2005) and did not differ significantly between the three different shade tree types (ANOVA: $F_{(2,6)} = 1.07, p = 0.40$).

2.2. Experimental set-up

In each study site 6 flowering cacao trees of the ‘‘Trinitario’’ type were selected (54 trees in total). Although different genotypes may differ in flowering frequency and rates of fruit abortion (Hasenstein and Zavada, 2001), the experimental set-up with randomized cacao tree selection avoided systematic genetic differences between cacao trees from different sites.

The experiment began in October 2004 and the major harvesting season in the study area lasted from April to June. All fruits from the main stems were removed and each opened flower was manually cross-pollinated until between 8 and 16 flowers were pollinated per tree. All manual pollination took place between 17 and 20 November 2004. Each manually pollinated flower was marked with a number that was attached to the tree’s bark with a needle.

Standardized manual cross-pollination was carried out by rubbing three anthers from flowers of three different trees (from the same plantation) against the selected flower’s stigma. This method maximizes the likelihood of optimal pollination (Falque et al., 1995) and ensures a standardized number of fruits of similar age on each of the experimental trees.

Fruit mortality, fruit abortion (also known as ‘cherelle wilt’, in which fruits stop growing and dry out), insect attacks and pathogens were quantified. The most common pathogen in the study area was black pod disease, which is caused by an oomycete of the genus *Phytophthora* sp., but further pathogens may have also occurred.

Fruits were monitored once every 3 weeks until fruits died or were harvested. The experiment ended in the first half of April 2005 when the remaining fruits were harvested. All fruits were monitored six times at 3 week intervals during the 18 weeks of fruit development.

2.3. Statistical analyses

To investigate the 3-weekly fruit mortality, repeated measures ANOVAs were used on the fruit loss per site as a proportion of the surviving fruits (i.e., fruits of similar age). Mortality differences between habitat types were analyzed per tree using general linear models (GLMs). Using type I hierarchical variance decomposition, habitat type was entered first as a fixed variable, followed by site as a random effect. Because there was one value of canopy cover per site, its effects were tested on a per site level in a GLM with habitat type as fixed factor, canopy cover as a covariate and type I sums of squares. All post hoc tests were carried out using Tukey’s HSD tests.

All analyses were done using Statistica 6.1 ($^{©}$Statsoft Corp.). The response variable for each model was the mortality as a proportion of successfully pollinated flowers, and was therefore arcsine square root transformed before analyses. Moreover, data were transformed where necessary to reach normal distribution of model residuals. Arithmetic means are given ±1 standard error.

3. Results

In total, 600 fruits on 54 trees (average per tree: 11.3 ± 0.58) were monitored. Of the monitored fruits, 432 (72%) were lost before harvest. One-half ($n = 300$) of all fruits were lost due to abortion by the plants themselves. A further 111 fruits (19%) did not reach maturity due to pathogens and 21 fruits (4%) were lost due to insect attacks, which in all cases was due to attacks by *Helopeltis sulawesi* Stonedahl (Hemiptera: Miridae). In total, *H. sulawesi* fed upon 55 fruits, of which 62% still reached the mature stage. Conversely, only 18% of the fruits that were infected with pathogens could eventually be harvested. Ten percent of the fruits lost due to pathogens were also fed upon by insects, although only 3% of the infections were preceded by insect feeding. Fruits that were completely covered by the pathogen were not subsequently fed upon by insects. Two percent of the cases of fruit abortion were preceded by insect feeding.

All fruit abortion took place during the first 9 weeks of fruit development and 60% took place during the first 3 weeks. Rates of abortion were highest during the first 3 weeks (repeated measures ANOVA for weeks 3–9: $F_{(3, 18)} = 16.3$, $p < 0.0001$; Fig. 1), and this did not differ between the three habitat types (interaction effect between time and habitat type: $F_{(6, 18)} = 1.33$, $p = 0.38$). Fruits were lost due to pathogens throughout the 18 weeks of fruit development. The proportional loss due to pathogens was highest between weeks 9 and 13 (repeated measures ANOVA: $F_{(5, 30)} = 2.62$, $p = 0.04$; Fig. 1), and this did not differ between the three types of agroforestry (interaction effect between time and habitat type: $F_{(10, 30)} = 1.25$, $p = 0.30$). Fruit loss due to insect attacks began after the first 3 weeks of fruit development and was constant through time (repeated measures ANOVA: $F_{(4, 24)} = 0.62$, $p = 0.65$; Fig. 1).

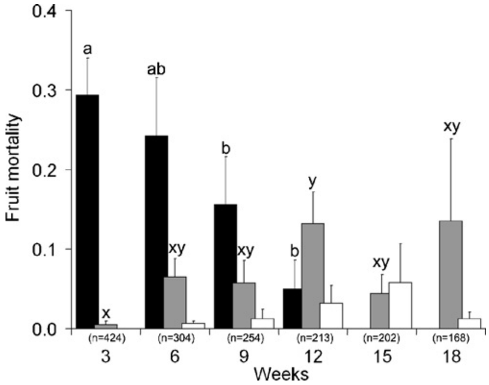

Fig. 1. Overall averaged cacao fruit mortality during six periods of 3 weeks, until harvest of mature fruits. Fruit mortality during each period of 3 weeks is calculated as proportion of fruits that survived after previous monitoring. The amount of surviving fruits (n) is given under the x-axis. Mortality was due to abortion (black), pathogens (grey) and attacks by insects (white). Bars indicate one standard error. Different letters (a and b or x and y) indicate significant differences based on Tukey's HSD post hoc test.

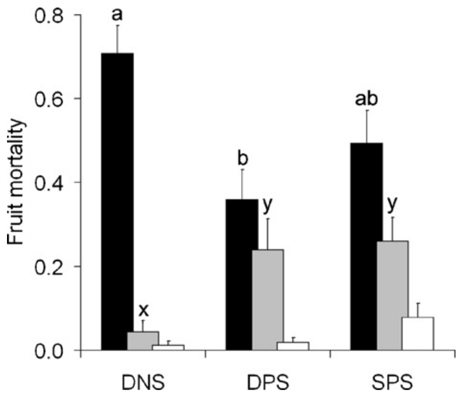

Fig. 2. Cacao fruit mortality per tree due to abortion (black), pathogens (grey) and attacks by insects (white) in agroforestry systems with different types of shade tree stands: diverse natural shade (DNS), diverse planted shade (DPS) and simple planted shade (SPS). Bars indicate one standard error. Values indicated with, respectively, a and b and x and y are significantly different based on Tukey's HSD post hoc test.

The total proportion of fruits lost due to abortion was lowest on trees under diverse planted shade and highest on trees under natural shade (GLM: $F_{(2, 48)} = 6.6$, $p = 0.003$; Fig. 2). The proportions of fruits lost per tree due to pathogens were highest on cacao trees under planted shade and lowest under natural shade (GLM: $F_{(2, 48)} = 6.3$, $p = 0.004$; Fig. 2). There was a trend towards higher fruit loss due to insect attacks under homogeneous shade, however this trend showed only marginal statistical significance (GLM: $F_{(2, 48)} = 2{,}45$, $p = 0.10$; Fig. 2). Hence, the proportion of fruits eventually harvested did not differ between habitat types (overall average per tree: 27 ± 4%; GLM: $F_{(2, 48)} = 2.5$, $p = 0.10$).

After removal of variation due to the type of shade trees, neither fruit abortion (GLM: $F_{(1, 6)} = 1.7$, $p = 0.25$), pest attacks (GLM pathogens: $F_{(1, 6)} = 0.6$, 0.48 and insect attacks: $F_{(1, 6)} = 0.5$, $p = 0.52$), nor harvest ($F_{(1, 6)} = 4.45$, $p = 0.13$) were affected by canopy cover.

4. Discussion

The results of this study show the enormous influence that fruit mortality had on potential yields of cacao: 72% of the pollinated flowers did not develop into mature fruits. The majority of fruit mortality was driven by within-tree factors (i.e., abortion), over one-half of which took place during the first 3 weeks of fruit development. The recorded fruit mortality is within the range of reported estimates in poorly shaded, intensive cacao plantations in Brazil

(79%; Hasenstein and Zavada, 2001), Costa Rica (62%; Young, 1982) and Ivory Coast (29%; Falque et al., 1995).

In this study we also showed for the first time that the composition of shade tree stands had a strong effect on the mechanisms that drive fruit losses on cacao trees. Losses due to early fruit abortion were highest under natural shade, whereas losses due to pathogens generally increased under planted shade, so that the overall proportion of fruits reaching the mature stage did not differ. In contrast to expectations, yields of cacao trees were not affected by canopy cover (in the range of 72.1–90.5%), implying that light intensity was not limiting fruit production.

The agroforestry systems shaded by forest remnants had a shorter history of agroforestry use and harbored no planted leguminose trees. Planting leguminose shade trees is a common measure to relieve agroforestry crops from nutrient deficiencies (Beer et al., 1998), which most likely explains the increased fruit abortion on cacao under shade tree stands that remained from the previous rainforest cover. In the study region, leguminose trees have been reported to enrich agroforestry with 70 kg/ha nitrogen (Dechert et al., 2005). However, under the simple shade of planted leguminose trees, fruit abortion was intermediate, which indicates that nitrogen was not the only limiting factor, but may have been complemented by external factors that were not visible in the field, such as early pathogen infections. Sites with diverse, planted shade tree stands performed best in relieving cacao trees from pressures that drive trees to fruit abortion.

In contrast to fruit abortion, the proportion of fruits lost due to external causes increased under simple planted shade, which supports the hypothesis that homogenized agricultural systems increase the risk of pest outbreaks (Schroth et al., 2000; Wilby and Thomas, 2002; Tscharntke et al., 2005). In this study, pathogens (mainly *Phytophthora* sp.) were, after fruit abortion, the most common cause of fruit mortality. This was in part because the farmers in the study area did not know of management practices that reduce risks of pathogenic infections. Successful disease management includes frequent removal of diseased fruits and sustainable shade management (e.g., Krauss and Soberanis, 2001). The highly diversified fungal cacao endophytes, which may be particularly important in high-diversity natural shade agroforestry, are known to be important antagonists of *Phytophthora* sp. (Arnold et al., 2003).

Mortality due to insect attacks (4% of all fruits) was of less importance than pathogen attacks (19% of all fruits). Nearly all fruits attacked by insects were attacked by the mirid bug *H. sulawesi*. However, the majority of those fruits (62%) still reached maturity. In this study only a minority of fruit loss due to pathogens was preceded by insect attacks, although fruit damage by mirids in particular may increase subsequent vulnerability to pathogens (Muhamad and Way, 1995).

Fruit losses due to internal and external causes were largely separated in time. After the initial 'mass fruit-wilt' during the first 6 weeks of fruit development, the risk of fruit loss due to insect and pathogenic infections peaked between the 9th and 13th week of fruit development. Therefore, differences in the number of fruits lost due to pest attacks are likely because of the initial differences in rates of fruit wilt. Hence, achieving a decrease in fruit wilt only may not lead to increased yields.

5. Conclusions

Fruit mortality is an important bottleneck in the reproductive success of flowering plants. The results of this study show that mechanisms of cacao's fruit mortality within well-shaded agroforestry systems may differ greatly among shade management types. The distinction between fruit abortion and insect and pathogen attacks as causes of fruit mortality revealed an as yet unexploited management potential for realizing higher yields from cacao in shaded agroforestry systems. Natural shade was associated with reduced black pod disease, possibly because of more endophytic antagonists (see Arnold et al., 2003), but higher fruit abortion than planted shade, which may be due to nitrogen limitation. Hence, an enrichment of natural shade agroforestry with planted leguminose trees appears to be a promising management option to improve cacao yields and keep complex agroforestry systems with their high functional biodiversity (see Rice and Greenberg, 2000). Management practices aimed at decreasing pest pressures were largely unknown among farmers in the study area, which underlines the importance of educational programmes in the conservation of shaded agroforestry systems.

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References

Arnold, A.E., Mejía, L.C., Kyllo, D., Rojas, E.I., Maynard, Z., Robbins, N., Herre, E.A., 2003. Fungal endophytes limit pathogen damage in a tropical tree. Proc. Natl. Acad. Sci. U.S.A. 100, 15649–15654.

Beer, J., Muschler, R., Kass, D., Somarriba, E., 1998. Shade management in coffee and cacao plantations. Agroforest. Syst. 38, 139–164.

Dechert, G., Veldkamp, E., Brumme, R., 2005. Are partial nutrient balances suitable to evaluate nutrient sutainability of land use systems? Results from a case study in Central Sulawesi, Indonesia. Nutr. Cycl. Agroecosyst. 72, 201–212.

Entwistle, P.F., 1972. Pests of Cocoa, first ed. Longman, London.

Falque, M., Vincent, A., Vaissiere, B.E., Eskes, A.B., 1995. Effect of pollination intensity on fruit and seed set in cacao (*Theobroma cacao* L.). Sex. Plant Reprod. 8, 354–360.

Fowler, R.L., Dessosiers, R., Hoff, H., 1956. Evaluation of certain factors affecting the yield of cacao in Ecuador. Ecology 37, 75–81.

Hasenstein, K.H., Zavada, M.S., 2001. Auxin modification of the incompatibility response in *Theobroma cacao*. Physiol. Plantarum 112, 113–118.

International Cocoa Organization, 2005. Annual Report for 2003/2004. The International Cocoa Organization (ICCO), London.

Klein, A.-M., Steffan-Dewenter, I., Buchori, D., Tscharntke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conserv. Biol. 16, 1003–1014.

Krauss, U., Soberanis, W., 2001. Rehabilitation of diseased cacao fields in Peru through shade regulation and timing of biocontrol measures. Agroforest. Syst. 53, 179–184.

Louda, S.M., 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. Ecol. Monogr. 52, 25–41.

Muhamad, R., Way, M.J., 1995. Damage and crop loss relationships of *Helopeltis theivora*, Hemiptera, Miridae and cocoa in Malaysia. Crop Prot. 14, 117–121.

Nichols, R., Walmsley, D., 1965. Translocation of phosphorus-32 into wilting and healthy fruits of cacao (*Theobroma cacao*). Plant Soil 23, 149–160.

Pías, B., Guitián, P., 2006. Breeding system and pollen limitation in the masting tree *Sorbus aucuparia* L. (Rosaceae) in the NW Iberian Peninsula. Acta Oecol. 29, 97–103.

Purdy, L.H., Schmidt, R.A., 1996. Status of cacao Witches' broom: biology, epidemiology, and management. Annu. Rev. Phytopathol. 34, 573–594.

Rice, R.A., Greenberg, R., 2000. Cacao cultivation and the conservation of biological diversity. Ambio 29, 167–172.

Schroth, G., Krauss, U., Gasparotto, L., Duarte Aguilar, J.A., Vohland, K., 2000. Pests and diseases in agroforestry systems of the humid tropics. Agroforest. Syst. 50, 199–241.

See, Y.A., Khoo, K.C., 1996. Influence of *Dolichoderus thoracicus* (Hymenoptera: Formicidae) on cocoa pod damage by *Conopomorpha cramerella* (Lepidoptera: Gracillariidae) in Malaysia. Bull Entomol. Res. 86, 467–474.

Siebert, S.F., 2002. From shade- to sun-grown perennial crops in Sulawesi, Indonesia: implications for biodiversity conservation and soil fertility. Biodivers. Conserv. 11, 1889–1902.

Stephenson, A.G., 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annu. Rev. Ecol. Syst. 12, 253–279.

Tscharntke, T., Klein, A.-M., Kreuss, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. Ecol. Lett. 8, 857–874.

Tylianakis, J.M., Klein, A.-M., Tscharntke, T., 2005. Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. Ecology 86, 3296–3302.

Valle, R.R., de Almeida, A.A.F., Leite, R.M.D.O., 1990. Energy costs of flowering, fruiting and cherelle wilt in cacao. Tree Physiol. 6, 329–336.

Wilby, A., Thomas, M.B., 2002. Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. Ecol. Lett. 5, 353–360.

Young, A.M., 1982. Effects of shade cover and availability of midge breeding sites on pollinating midge populations and fruit set in two cocoa farms. J. Appl. Ecol. 19, 47–63.

Young, A.M., 1994. The Chocolate Tree. Smithsonian Institution Press, Washington.

Zuidema, P.A., Leffelaar, P.A., Gerritsma, W., Mommer, L., Anten, N.P.R., 2005. A physiological production model for cocoa (*Theobroma cacao*): model presentation, validation and application. Agric. Syst. 84, 195–225.