RAIN FOREST PLANT DISEASES: THE CANOPY - UNDERSTORY CONNECTION

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Abstract: Plant diseases are diverse and common in the canopy of tropical rain forests. Many diseases in the canopy are shared by juveniles in the understory, but their relative abundance in the different strata may vary. Ecological effects of the disease may be greater among juveniles than adults. Adult trees may serve as disease incubators, increasing both the amount of pathogen inoculum available and, potentially, the virulence of pathogens.

Keywords: Plant disease, plant pathogens, fungi, canopy access crane, Panama

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Plant diseases are important ecological and evolutionary forces. Plant parasitic fungi, protists, bacteria, viruses, and nematodes cause diseases that can force evolutionary changes in chemical defenses or reproductive strategies, reduce the growth or reproductive output of the host plant, regulate population dynamics, determine the spatial distribution of the host, and maintain high plant community diversity (see reviews in Burdon 1987, Burdon & Leather 1990). Several workers have been drawn to the species-rich tropics to explore the role of plant diseases in this environment. For example, in the seasonal tropical moist forest of Barro Colorado Island (BCI) in Panama, damping-off diseases in young seedlings of several canopy tree species (Augspurger 1990) and a canker disease of juveniles of the lauraceous canopy tree *Ocotea whitei* (Gilbert et al. 1994) lead to greater juvenile mortality close to conspecific adults than farther away, and may be important in host population regulation.

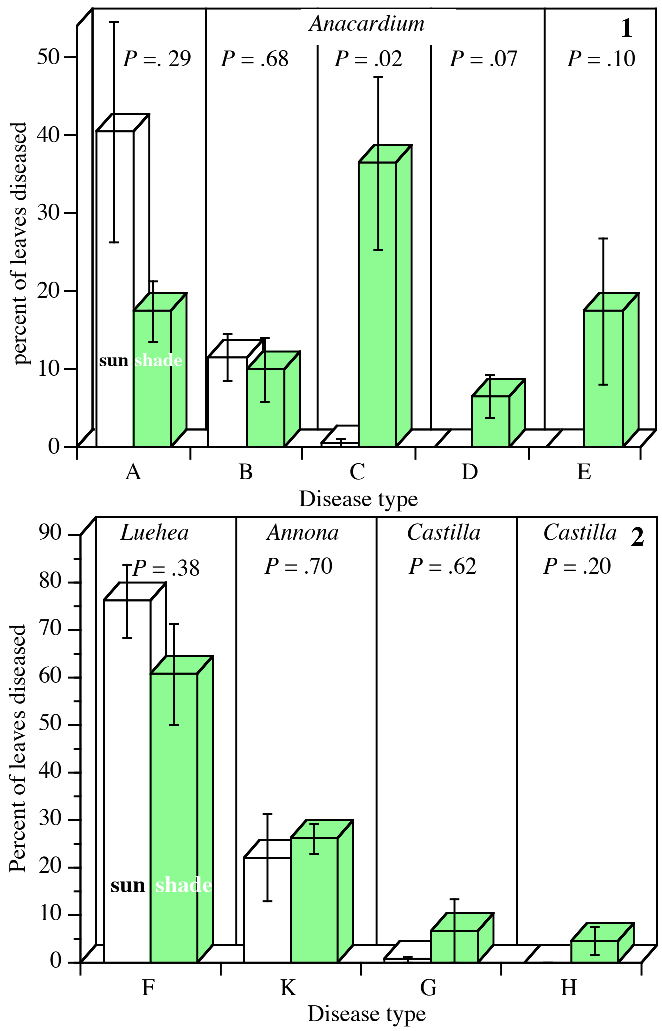
These studies clearly show that plant diseases can be important in rain-forest dynamics, and suggest that adult trees may serve as reservoirs for pathogens. However, the connection between canopy trees as disease reservoirs and mortality of understory juveniles has not been clearly established, since nearly all of the supporting data come from studies in the understory. Additionally, the effects of canopy diseases on adult fitness and survival are largely unknown. Clearly, for us to understand the role of plant diseases in the dynamics of natural plant communities, we must move beyond the readily accessible plants in the forest understory, and include disease processes of the forest canopy above. In this paper, I present some preliminary data which indicate that foliar diseases in the canopy of a tropical forest are common and diverse, and outline several important mechanisms by which diseases in the canopy may be particularly important in forest dynamics, due to links with diseases of understory plants.

METHODS

I determined the incidence of foliar diseases of sun leaves (fully exposed canopy leaves) and shade leaves (subcanopy leaves) for five tree species using the Canopy Access System crane in the Parque Metropolitano in suburban Panama City, Panama. The forest is seasonally dry, receiving approximately 1,700 mm rain per year. In early September 1994 (rainy season), I counted the number of the 5 terminal leaves per branch that showed disease symptoms, on each of 10 haphazardly selected branches per tree, both in the sun and in the shade (total of 50 leaves per light level, per tree). Sun leaves were observed from the gondola of the crane, as were shade leaves, when possible. In some cases, I repelled down a rope from the gondola to obtain better access to shade leaves in the subcanopy. The five tree species were *Anacardium excelsum* (Anacardiaceae) (n=4), *Luehea seemanii* (Tiliaceae) (n=3), *Annona spraguei* (Annonaceae) (n=3), *Castilla elastica* (Moraceae) (n=3), and *Antirrhoea trichantha* (Rubiaceae) (n=3). Diseases were classified according to symptoms, and causal agents were not identified. Data were analyzed independently for each disease type using a paired *t*-test on proportions of leaves per tree that were symptomatic. Data were arcsin square-root transformed prior to analysis.

RESULTS

The number of recognizable kinds of disease symptoms ranged from none on *Antirrhoea trichantha* to five on *Anacardium excelsum*. *Luehea* and *Annona* each had one type, and *Castilla* two. The incidence of each of the disease types in sun and shade leaves are shown in Figures 1 and 2. Six of nine disease types were present in both the sun leaves and the subcanopy, and none were present exclusively in the sun leaves. *Anacardium*-disease type C was significantly more common in the subcanopy than in the sun leaves (t_3 = 4.78, P = 0.02), and types D (t_3 = 2.74, P = 0.07) and E (t_3 = 2.28, P = 0.10) were exclusively present in the sun. None of the other sun - shade comparisons were statistically significant ($P \geq$ 0.2 for all).



FIGURES 1-2. Proportion of leaves in the sun and in the shade (subcanopy) with disease symptoms, for (1) *Anacardium excelsum*, and (2) *Luehea seemanii*, *Annona spraguei*, and *Castilla elastica*. Bars indicate means ± standard error. *P*-values are for paired *t*-tests as described in the text.

DISCUSSION

Foliar plant diseases are common (more that 75% of leaves in *Luehea*) and diverse (five kinds on *Anacardium* alone) in the tropical forest canopy. Diseases present in the canopy also affect leaves in the shade below, suggesting a potentially important link between diseases of adult trees in the canopy and juveniles in the understory. There are very few other studies of plant diseases in the canopy of natural tropical forests, but those data that are available are similar to those presented here. Garcia-

Guzman and Dirzo (1991) showed that in Los Tuxlas, Mexico, about 45% of leaves of understory plants (from 67 species) and 60% of leaves in the forest canopy (from 30 species) were damaged by fungal pathogens, although they did not indicate whether the diseases were the same in both strata. Barone (1994) showed that on BCI adults of the canopy tree *Quararibea asterolepis* (Bombacaceae) suffer more foliar damage from pathogens than do saplings in the understory (14.4 % and 0.3% of leaf area, respectively). In addition, canker diseases and heart-rot of large branches are common in the canopies of many tropical trees (G. Gilbert, personal observation), and diseases of developing fruits may substantially reduce fruit production in canopy trees (Sánchez-Garduño et al. 1994). To date, we do not know the importance of any of these diseases in the survival or growth of the adult or juvenile hosts.

We are still at the early stages of understanding the complex natural histories of diseases in tropical forests, and in particular the importance of diseases of adult trees in forest dynamics. One critical unexplored question is how (or whether) adult trees serve as reservoirs for plant pathogens. In some cases, they may only indirectly influence the pathogen reservoirs in the soil below their crowns. Regular production of dense carpets of seedlings may maintain a high population of soilborne fungal and oomycete pathogens in the soil in the area of the tree's seed "shadow". Some fungal pathogens can persist as soil saprophytes, but many seedling pathogens produce resting structures that can survive months to years in the soil, germinating on the appearance of a suitable host plant (Agrios 1988, Bruehl 1987). Others may spread from infected to healthy plants through root grafts (Agrios 1988).

However, spores produced by fungi on the leaves or branches of adult trees may be equally important when they are dispersed by rainfall, air movement, and in some cases, insect vectors to juveniles in the understory below. A foliar disease, or even a pathogen infecting twigs and branches, may have little effect on the short-term survival of the adult tree. A branch killed by a fungus can easily be discarded and the trunk chemically or physically walled off from further invasion. Large trees may have enough reserves to rebound from even serious epidemics of foliar diseases. But, the same diseases may quickly kill seedlings or saplings with only one to a few branches, few leaves, and limited reserves. For example, the cankers on *Ocotea whitei* are common on living branches of adults, but may kill understory juveniles (Gilbert et al. 1994, G. Gilbert, unpublished data). This differential response means the adult trees would act as "incubators" for pathogens that then attack the more susceptible progeny, forging a strong link between diseases in the forest canopy and the processes that determine the structure and composition of the forest itself.

Furthermore, the canopy - understory connection may lead to even more virulent pathogens attacking progeny of individual canopy trees than might otherwise occur. Repeated passage of a single strain of fungal pathogen through a particular host will often select for strains more virulent on that host species or genotype (Rufty et al. 1981, Kolmer 1990). The long-lived nature of the canopy of a large tree (with respect to the life cycle of most pathogens) may provide opportunities for multiple infection - sporulation - reinfection cycles in the canopy of the same tree. Should increased genotype- or species-specific virulence arise in a pathogen in the canopy of a parent tree, its effects on that tree's progeny below are likely to be much more severe than if disease inoculum arrived from random sources throughout the forest.

Plant diseases in the canopy have potential for ecological influence that reaches far beyond their effects on plant parts high above the forest floor. Spores produced high in the canopy may have a dispersal advantage, making them more likely to spread to neighboring plants than would a similar infection in the understory. The "incubator" effect of adult trees for diseases that also affect juveniles may be important both in production of disease inoculum and for selecting more virulent strains of pathogens. Long-term studies to evaluate the role of disease in the canopy and the extent and nature of this canopy - understory connection is important for understanding basic forest dynamics.

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LITERATURE CITED

AGRIOS G. N. 1988. Plant Pathology, 3rd edition. Academic Press, New York. 803 pp.

AUGSPURGER C. 1990. Spatial patterns of damping-off disease during seedling recruitment in tropical forests. Pp. 131-144 *in* J. J. BURDON and S. R. LEATHER (eds.), Pests, Pathogens and Plant Communities. Oxford, Blackwell Scientific.

BARONE J. A. 1994. Herbivores and herbivory in the canopy and understory on Barro Colorado Island, Panama. P. 64 *in* Forest Canopies: Ecology, Biodiversity and Conservation, 1st International Canopy Conference, Marie Selby Botanical Gardens, Sarasota, FL, November 1994.

BRUEHL G. W. 1987. Soilborne Plant Pathogens. Macmillan Publishing Company, New York. 368 pp.

BURDON J. J. 1987. Diseases and Plant Population Biology. Cambridge University Press, Cambridge. 208 pp.

_________ and S. R. LEATHER (eds.). 1990. Pests, Pathogens and Plant Communities. Blackwell Scientific, Oxford. 333 pp.

GARCIA-GUZMAN G. and R. DIRZO. 1991. Plant - pathogen - animal interactions in a tropical rainforest. Association for Tropical Biology Annual Meeting, San Antonio, Texas. 4-8 August 1991.

GILBERT G. S., S. P. HUBBELL, AND R. B. FOSTER. 1994. Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. Oecologia 98: 100-108.

KOLMER J. A. 1990. Selection of virulence phenotypes in a heterogeneous, asexual population of *Puccinia recondita* f. sp. *tritici*. Phytopathology 80: 1377-1381.

RUFTY R. C., T. T. HEBERT, AND C. F. MURPHY. 1981. Variation in virulence in isolates of *Septoria nodorum*. Phytopathology 71: 593-596.

SÁNCHEZ-GURDUÑO, C., S. J. WRIGHT, AND C. POTVIN. 1994. 99.96% of the buds produced by *Anacardium excelsum* are lost before becoming mature seeds. P. 70 *in* Forest Canopies: Ecology, Biodiversity and Conservation, 1st International Canopy Conference, Marie Selby Botanical Gardens, Sarasota, FL, November 1994.