Plant and Soil **211:** 207–213, 1999.
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Effects of irrigation on litterfall, fine root biomass and production in a semideciduous lowland forest in Panama

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Received 1 October 1998. Acepted in revised form 31 May 1999

Key words: below ground- productivity, biomass, fine roots, irrigation, litterfall, lowland forest

Abstract

The effects of irrigation on fine root biomass, root production and litterfall were measured at the community level, in a semideciduous lowland forest in Panama. Biomass of roots less than 2 mm in dia. in the first 10 cm of the soil (measured with soil cores), was higher in irrigated (1.80 Mg ha^{-1}) than in non-irrigated plots (1.24 Mg ha^{-1}). During the dry season, productivity of roots (measured with ingrowth cylinders filled with root-free soil), was higher in irrigated (1.6 g m^{-2} day^{-1}) than in control plots (0.3 g m^{-2} day^{-1}). In control plots, root productivity was highly seasonal. Maximum root growth into the root-free soil, occurred during the transitions from dry to wet, and from wet to dry season, possibly as a response to water and/or nutrient pulses. Litterfall was not significantly different between irrigated (3.8 g m^{-2} day^{-1}) and control plots (3.7 g m^{-2} day^{-1}). The results of this study show that root-productivity is limited by the water supply during the dry season, and that water by itself, is not a limiting factor for community-level litter production.

Introduction

Rainfall in many tropical forests is seasonal, with dry seasons varying from a few weeks to several months (Beard, 1944, 1955; Richards, 1952). With increasing drought, forest physiognomy change gradually from lowland rain forest (*sensu stricto*) to evergreen seasonal forest, to semi-evergreen seasonal forest, and to deciduous forest (Beard, 1944, 1955). Along this humidity gradient, the occurrence of deciduous tree species increases and thus the seasonallity in litter production, with leaf fall peaking during the dry seasons (Folster and de las Salas, 1976; Franken et al., 1979; Frankie et al., 1974; Haines and Foster, 1977; Klinge and Rodriguez, 1968; Ogawa, 1978; Schaik, 1986).

Leaf flush often peaks soon after the rains begin (Leigh and Windsor, 1982), and trunk growth is more pronounced during the wet season (Daubenmire, 1972; Raich and Borchert, 1982). On Barro Colorado Island, where the dry season usually begins in December and ends in April or May, leaf fall increases at the beginning of the dry season with maximum rates in January (Dietrich et al., 1982; Wright and Cornejo, 1990b). As the dry season progresses, leaf fall rates decline slowly dropping to a minimum with the onset of rains. Low leaf fall rates are characteristic of the wet season, and may be interrupted by a small increase during the 'veranillo' (shorter dry season) during August and September (Wright and Cornejo, 1990b). The number of deciduous trees producing young leaves peaks in May, while evergreen trees peak during the wet season (September), at the end of the year, and after the onset of rains (Leigh and Windsor, 1982). Furthermore, a survey of saplings of canopy and understory species, showed that leaf production occurs mostly during the transitions from wet to dry and from dry to wet seasons (Aide, 1988).

In contrast to the response of the above-ground biomass to changes in water supply, there is little information on the effects of the dry season on the below-ground ecosystem, particularly on fine-root biomass and production. In spite of the great im-

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portance of fine roots on forest productivity (Persson, 1979; Vogt et al., 1981; Gower et al. 1992), fine root biomass has been measured in only a few tropical forests (i.e. Klinge and Herrera, 1978; Sanford, 1989a,b; Stark and Spratt, 1977), and fine-root productivity in even fewer sites (Cavelier, 1989; Cuevas and Medina, 1983, 1988; Jordan and Escalante, 1980; Sanford, 1985). Responses of roots to tree falls (Sanford, 1990) and mineral nutrient amendments have been studied recently (Cavelier, 1989; Gower and Vitousek, 1989).

In this paper we present the results of an irrigation experiment in a semideciduous lowland forest in central Panama. We investigate whether seasonal changes in soil water content affect productivity at the community level and whether there are effects on the patterns of allocation of resources above- and belowground. If water is a limiting factor, as suggested by seasonal differences in rainfall and soil water potential, irrigation should have a direct and positive effect on the biomass and productivity of fine roots, and indirectly on fine litterfall through higher water and/or nutrient consumption by the roots.

Methods

Study site

Soil irrigation was carried out in a semideciduous lowland forest at an altitude of 60m on Barro Colorado Island (BCI). This forest is composed of a mixture of deciduous and evergreen species (Croat, 1978; Foster and Brokaw, 1982). The number of deciduous trees bearing young leaves peak in May and June and is lowest from October to February. Canopy evergreen trees show a continuous change in foliage, with a minimum during the leaf flush of deciduous canopy trees (Leigh and Windsor, 1982). In all, the canopy is never entirely deciduous. This forest experiences a marked seasonal variation in water supply. The annual rainfall on BCI averages 2612 mm (1925–1986; Windsor, 1990) with a median length of the dry season of 17 weeks between mid December–early January and late April-early May. During this part of the year, panevaporation exceeds rainfall and soils become dry and hard. Surface soil moisture content declines to 27% (wet weight) during the dry season, in contrast to 45% during the wet season (Windsor, 1990). This forest has remained without human intervention for more than 500 years (Piperno, 1990). Detailed description of the flora, structure and ecology of this forest can be found in Croat (1978), Leigh et al. (1982) and Windsor (1990).

Experimental design

Four 2.25-ha plots were located in Poacher's Peninsula. The distance between plots averaged over 50 m. Two of these plots were irrigated and two served as controls. Water was added to the irrigated plots by 160 sprinklers placed 1.8 m above the ground at 15.3 m intervals in an hexagonal array. Thus, each point in the forest would receive water from three or more sources, except plot borders and where water was intercepted by vegetation. During a typical week in the dry season, each irrigated plot received 135 metric tons of water during 1.5 h of irrigation between 11:00 and 14:00 h on each of five days. This is equivalent to a daily rainfall at the forest floor of 6 mm. Mean soil water potential was maintained at or slightly above field capacity (-0.04 MPa) throughout the dry seasons of 1986-1990.

Water availability

Rainfall was measured daily at the site with a metric rain gauge (All Weather Rain Gauge). Soil water content was measured at eight randomly located stations in the interior of each plot (> 15 m from edge). Tensiometers (Soil Moisture Equipment Corp., 2725A), soil psychrometers (Wescor PCT55) and a hydroprobe (Campbell Nuclear Pacific, Model 503) were used to monitor soil water content as described elsewhere (Wright and Cornejo, 1990a).

Root measurements

Standing root biomass was measured with ten soil cores per plot on 14–15 December 1988 at the end of the rainy season, and on 29–30 March 1989 at the end of the dry season. Root biomass was sampled by driving into the soil a sharp-edge steel corer with an internal diameter at the hardened cutting edge of 5.6 cm. The corer had an internal PVC pipe, 7.5 cm in diameter, divided longitudinally in two halves to allow the cores to be removed (Ford and Deans, 1977). The soil corer was driven to a depth of −10 cm. Each soil core was placed in a plastic bag, labeled and stored at 3 °C until soil washing could take place, usually within 30 days. The samples were rinsed with tap water over a 500μm sieve to loosen the soil and facilitate root sorting. Root fragments which were mixed with organic

matter (and not easily identifiable as roots), were not collected. Roots were sorted by diameter (Very Fine Roots, VFR=<1 mm; Fine Roots, FR=1-2 mm and Medium Roots, MR=2-5 mm). After sorting, roots were dried at 60 °C for 48 h, weighed to the nearest 0.0001 g.

Root growth was measured by means of ingrowth cylinders (Cuevas and Medina, 1983, 1988; Lund et al., 1970; Persson, 1979). Each ingrowth cylinder (IC) was made with 30 mm^2 plastic mesh, 9 cm in diameter and 25 cm tall. The cylinders were placed in holes created with a Dutch auger. The holes were placed in random positions, at least 15 m from the plot edges and each point at least 10 m from all others. Each hole was filled with root free soil. This soil was obtained by drying (60 °C for 48 h), crushing and removing the roots with forceps, from soil collected at the site. IC were collected by carefully cutting the roots that had penetrated the cylinder, and then lifting out the column. Four series of 5 ingrowth cylinders were inserted in each plot, and the location of all 20 IC within the plot, was selected at random. The first series (dry season) was installed on 11 February and collected on 10 April 1988. The second series (transition dry-wet season) was installed on 5 May and collected 5 July 1988. The third series (wet season) was installed 22 September and collected 23 November 1988. The fourth series (transition wet-dry season) was installed on 7 December and collected on 14 February 1989. The contents of the cylinder were processed as described for the soil cores.

Leaf fall

Leaf fall was measured with 15 litter traps, located in random positions in each plot. The surface area of each trap was 0.25 m^2. Traps were constructed with PVC tubing and plastic screening (1.2 mm mesh), and mounted 40 cm above the soil. Traps were emptied every seven days. Plant material was dried to a constant weight at 60 °C and weighed to the nearest 0.1 g. In this paper we present total weekly litterfall from 7 December 1987 through 29 May 1989.

Calculations and statistical analysis

Two-way ANOVAs were performed for standing root biomass and root ingrowth. Treatment and seasons were fixed main effects. Plots were a random factor nested within treatment. Levels of treatment were irrigated and control. For the analysis of standing root biomass, levels of season were December 1988 (end of wet season) and March 1989 (late dry season). For standing root biomass, analyses were performed separately for untransformed biomass of VFR (<1 mm) and FR (1-2 mm). For root ingrowth, analyses were performed for logarithmically transformed biomass of roots < 2 mm in diameter. The transformation was necessary to achieve homoscedastic residuals.

Annual root production was estimated using rates of root ingrowth. Because the IC were in the field for less than 12 months, the productivity measured during the four seasons (dry season = 60 days, dry-wet season transition = 61, wet season = 61 and wet–dry season transition = 68 days) were extrapolated assuming that the seasons were 81, 61, 155, and 68 days in duration, respectively.

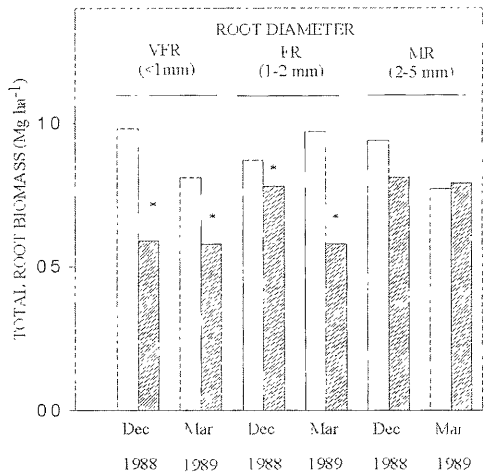

Figure 1. Standing root biomass for very-fine (<1 mm in diameter), fine (1–2 mm) and medium roots (2–5 mm) at the end of the wet season of 1988 (December) and at the end of the dry season of 1989 (March). (▧) = root biomass in control plots and (□) = root biomass in the irrigated plots. (*) represent significant differences ($p<0.05$) between treatments.

Results

Standing root biomass and root ingrowth

Biomass (measured with soil cores) of VFR and FR was significantly higher in irrigated than in control plots (Figure 1). Neither season nor the season–treatment interaction were significant for either VFR (F=0.81, α = 0.05; F = 0.65, α = 0.05, respect-

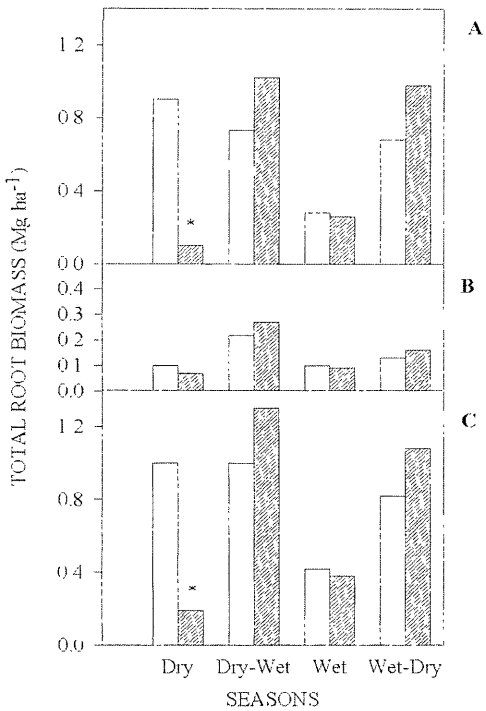

Figure 2. Root biomass in the ingrowth cylinders at the end of a 60 day period during the dry, dry–wet, wet and wet–dry seasons of 1988 and 1989. In the upper panel (A) is the biomass of roots less than 1 mm in diameter, in the second panel (B) is the biomass of roots 1-2 mm in diameter, and in the third panel (C) is the biomass of all roots inside the cylinders. (□) = Irrigated plots and (▧) = control plots. (*) represent significant differences ($p<0.05$) between treatments.

ively) or FR (F=0.31, α = 0.05; F = 0.92, α = 0.05, respectively).

There was a season × treatment interaction in the productivity of VFR (measured with IC) during the dry season (Figure 2). During the wet season and seasonal transitions, root productivity was not significantly different between irrigated and control plots ($p>0.20$). Annual root production (of roots <2 mm), estimated from root ingrowth, was not significantly different between irrigated (4.32 Mg ha^{-1} year^{-1}) and control plots (3.52 Mg ha^{-1} year^{-1}). Thus, statistically significant dry-season increase under irrigation is offset by non-significant treatment differences in the opposite direction in the wet season and in the transitions between seasons. As a result, year-long estimates of productivity do not show a treatment effect.

Litterfall

Between 7 December 1987 and 29 May 1989, mean daily litterfall was not significantly different between irrigated (3.8 g m^{-2} day^{-1}) and control plots (3.7 g m^{-2} day^{-1}) as shown in Figure 3. Litterfall increased during the dry season (7.7 g m^{-2} day^{-1} in January 1988) and later decreased to a minimum in mid October (about 2.0 g m^{-2} day^{-1}) in both treatments.

Discussion

Treatment effects

The large treatment difference for VFR and FR standing biomass in December 1988 and March 1989, is probably the result of small cumulative increments in biomass under irrigation during the three previous dry seasons. This conclusion is supported by the results of the ingrowth cylinder experiments, where fine-root productivity was significantly higher in irrigated plots only during the dry season.

Fine-root production, measured with ingrowth cylinders, was significantly higher in irrigated than in control plots only during the dry season (Figure 2). Roots grew more in irrigated cylinders, as a response to higher water availability (a direct effect of irrigation), and probably also as a response to softer soils. Soil strength, measured with a soil penetrometer, decreased from 3.5 kg cm^{-2} (+/−0.30; n=15) in dry soils (27% water content at the end of the 1992 dry season), to 1.8 kg cm^{-2} (+/−0.13; n=15) in saturated soils (45% water content). Because soils are very hard during the dry season, fine-root elongation and exploration are likely to be reduced. Furthermore, soils crack as a result of low water content (around 27% on a percentage wet weight; Windsor, 1990) and high clay content (Cavelier, 1992), probably killing some of the fine-roots and making it difficult for other roots to grow. These cracks usually open at the beginning of the dry season and deepen and widen as the dry season progresses (Cavelier, 1992).

In irrigation and fertilization experiments in temperate conifer forests (*Pseudostuga menziesii* var. *glauca*), fine root production (< 2 mm) decreased in comparison with control plots (Gower et al. 1992). While fertilization with N + P in a nearby semideciduous forest at Gigante península in Panama also resulted in reduction in fine root biomass and production (Cavelier, 1989), irrigation at Poacher's Península on Barro Colorado Island, resulted in only a seasonal

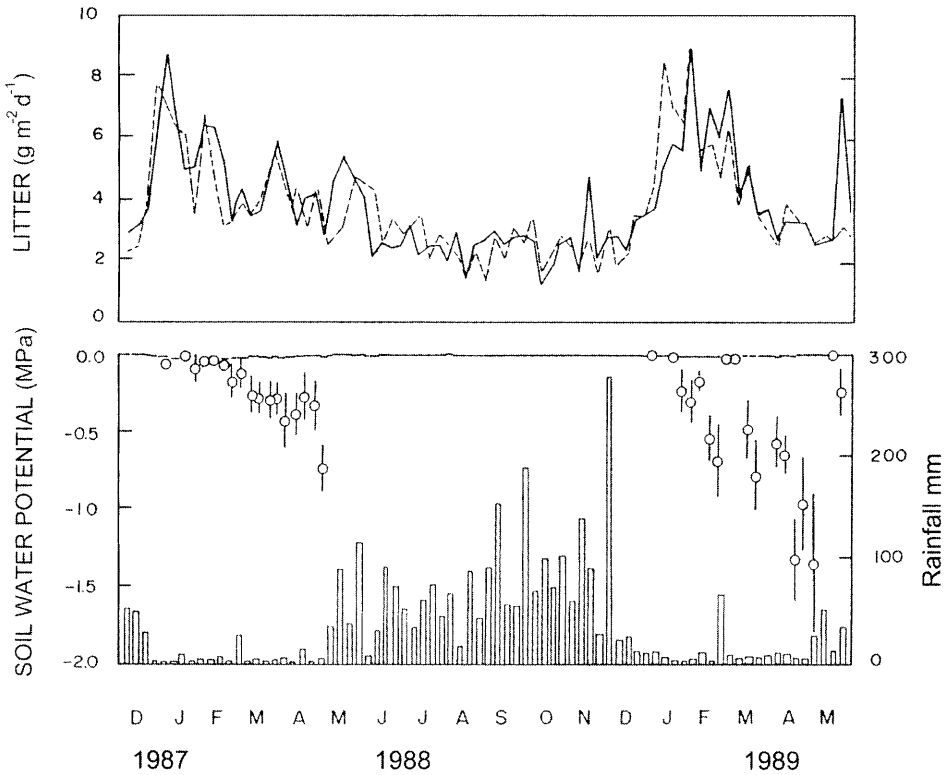

Figure 3. Rainfall (mm), soil water potential (MPa) and fine litter fall (g m^{-2} day^{-1}) between December 1988 and March 1989. In the bottom panel, weekly rainfall is presented by the histogram, mean soil water potential in irrigated plots is represented by the solid line at the top of the panel (above −0.04 MPa), and mean soil water potential and standard errors for control plots are represented by the closed circles and error bars (n = 16). Soil water potentials are at 25 cm depths. In the top panel, weekly mean fine litter fall for irrigated and control plots is represented by the solid and broken lines, respectively.

(i.e. dry season) increase in both very fine root biomass (< 1 mm) and production. The increase in fine root biomass and production in irrigated plots during the dry season, may be the response to the amelioration of a seasonal limiting factor (water availability), that drives most of the phenological responses in this forest type. Fine root biomass and production, are likely to *decrease* year round, in non-seasonal ecosystems with relatively low water availability. Suppression of the dry season at the soil level, had no effect on litterfall, an important component of the above-ground productivity (see also Wright, 1991; Wright and Cornejo, 1990a,b). This result contrasts with the increases in new twigs and foliage in irrigated plots of *Pseudostuga menziesii* var. *glauca* (Gower et al. 1992). It is possible that irrigation during the dry season had a positive effect on other components of forest productivity not measured in this study, like small branches and total height of trees.

In contrast to the lack of effect of irrigation on litterfall of trees and lianas, irrigation had a weak effect on the phenology of some shrubs (Mulkey et al., 1991; Wright, 1991) and strong effects on photosynthesis, growth and survivorship of herbs and seedlings (Fisher et al., 1991; Mulkey et al., 1991). Changes in relative humidity, and thus in vapour pressure deficits, are probably the cause for changes in stomatal conductance of plants close to the ground but not in the canopy (Sternberg et al., 1989). Indeed, carbon isotopic ratios of leaves from control and irrigated plots were different for understory saplings but not for canopy trees of the same species (Sternberg et al., 1989).

Seasonal variations in root biomass

Strong seasonal variation was measured in fine-root production. In control plots, productivity was high during seasonal transitions and low both during the dry and wet seasons (Figure 2). The peak in root biomass

in the transition from dry to wet season, was marked by heavy rains (140 mm in May in contrast to 10 mm in April 1988) and the largest amount of leaf litter on the forest (Leigh and Windsor, 1982). This peak in fine-root biomass can be suppressed by the addition of a N+P fertilizer (Cavelier, 1989). Indeed, at a site 1 km from this study, the dry-wet season transition peak in fine-root growth was suppressed by the addition, in three doses, of 300 Kg N ha^{-1} y^{-1} and 100 Kg P ha^{-1} y^{-1} (Cavelier, 1989). Thus, this peak was probably a response to increasing nutrient availability, rather than to water.

The high productivity during the transition from wet to dry season is more difficult to explain because there are no peaks in N or P availability (Yavitt and Wright, 1996). It is likely that the roots responded to the increase in aeration that results from the decreasing soil water content, or to the build up in exchangeable cations such as K, Ca and Mg (Yavitt and Wright 1996). This peak in root biomass was not observed during the fertilization experiment at Gigante Peninsula (Cavelier, 1989).

While the low root production during the dry season is probably related to low soil water content and hard soils, low wet season productivity is probably related to very high soil water content and a lack of nutrient pulses. A second and smaller peak in fine-root biomass was detected in the same forest type (Gigante Peninsula, part of Barro Colorado Natural Monument), several weeks before the wet season series of ingrowth cylinders was placed at Poacher's Peninsula (Cavelier, 1989). This second peak in fine-root biomass, apparently missed by the ingrowth cylinders of the present study, coincides with the peak in leaf flush of evergreen trees (Leigh and Windsor, 1982).

Thus, seasonality of fine-root production is related to water and mineral pulses and also to the growth of the above-ground biomass. Relationships between fine-root productivity and environmental and biological variables, is also known in temperate forests. For instance, in a 23-y old *Abies amabilis* forest in the north-west USA, conifer fine root biomass peaks in spring and autumn. The spring peak correlates well with the onset of water percolating into the soil from the snow pack (Grier et al., 1981; Vogt et al., 1981).

The experimental results presented here show that water supplementation has a positive effect on one of the below-ground components of productivity, but not on litterfall. In the long term, increases in below-ground biomass should have a positive effect on the water and nutrient balance of the trees, that should be reflected in the above-ground biomass and production. Apparently, four years of irrigation and a marginal increase in root biomass and productivity are not enough to stimulate growth that can be measured at the community level. Further research is needed at the species level to study the timing of events in the root and shoot biomass, and the effect of the addition of water and mineral nutrients.

Acknowledgements

We wish to thank David Rodriguez, Helena and Manuel Sedeño for assistance in the field. This research was possible thanks to a Smithsonian Tropical Research Institute predoctoral Fellowship and a Smithsonian Institution predoctoral fellowship to JC. Special thanks to J.L. Machado and all STRI faculty and personnel, for support during the field work at BCI.

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Section editor: H Lambers