

Root development in simple and complex tropical successional ecosystems

C.W. BERISH¹ and J.J. EWEL

Department of Botany, University of Florida, Gainesville, FL 32611, USA. ¹ Present address: Biology Department, Emory University, Atlanta, GA 30322, USA

Received 20 October 1986. Revised September 1987

Key words: agroecosystems, anedept, nutrient retention, root biomass, root surface area, roots, succession, tropical

Abstract

Fine and coarse root mass and fine root surface area were studied during 5 yr following the felling and burning of a tropical forest near Turrialba, Costa Rica. Five experimental ecosystems were established: 1) natural successional vegetation, 2) successional vegetation enriched by seed applications, 3) imitation of succession (built by substituting investigator-selected species for natural colonizers), 4) monocultures (two maize crops followed by cassava and *Cordia alliodora*), and 5) a bare plot.

Fine roots grew rapidly in all treatments during the first 15 wk, at which time there were 75 g m⁻² in the monoculture and 140 g m⁻² in the enriched and natural successions. Subsequent growth was slower, and fine-root mass decreased during the first dry season. After 5 yr coarse root mass to a depth of 85 cm was about 800, 1370, and 1530 g m⁻² in the succession, enriched succession and imitation of succession, respectively. At the final harvest, the 3.5-yr-old *C. alliodora* plantation had 1000 g m⁻² of coarse-root biomass. Roots < 1 mm in diameter were concentrated in the upper 5 cm of soil and accounted for most fine-root surface area. Total fine-root surface area was greatest in the enriched successional vegetation and usually lowest in the monoculture.

Introduction

Forest felling is often immediately followed by a period of rapid nutrient loss (Edwards and Ross-Todd, 1979; Ewel *et al.*, 1981; Fredriksen, 1971; Johnson and Swank, 1973; Jordan, 1980; Likens *et al.*, 1970). Vegetation removal disrupts nutrient uptake, mineralization, evapotranspiration, and decomposition: processes which, in turn, regulate nutrient retention and cycling patterns (Gorham *et al.*, 1979; Likens *et al.*, 1978; Wells and Jorgensen, 1975). This problem can be especially severe in the humid tropics, where many soils are nutrient-poor and leaching rates can be high.

Rapid nutrient uptake by successional vegetation keeps this problem from being even more severe than it is. Many species grow rapidly on disturbed sites if nutrients are readily available (Boring *et al.*, 1981; Marks and Bormann, 1972;

Vitousek and Reiners, 1975). Because nutrients are absorbed primarily by fine roots, the rapid development of an extensive, fine-root system—in conjunction with nutrient storage in above-ground biomass—can reduce the nutrient losses commonly associated with forest disturbance.

In most ecosystems, fine roots comprise only a small proportion of total root biomass (Santantonio *et al.*, 1977; Vogt *et al.*, 1986), but are associated with many important processes. In addition to nutrient absorption, fine roots absorb water, are associated with mycorrhizal transfer and incorporation of nutrients, especially P (Bowen, 1980; Redhead, 1980; Sanni, 1976), and add organic matter and nutrients to the soil through rapid turnover (Cox *et al.*, 1978; Harris *et al.*, 1977, 1980; Raich, 1980a; Vogt *et al.*, 1986).

Although root systems are still the biggest unknown in our knowledge of plant community struc-

ture, especially in the tropics, several studies of the root systems of tropical plants and whole plant communities have been published in recent years. These studies have dealt with a broad array of topics, including root biomass (Bartholomew *et al.*, 1953; Berish, 1983; Cornforth, 1970; Greenland and Kowal, 1960; Huttel, 1975; Jenik, 1971; Lawson *et al.*, 1970; Murphy and Lugo, 1986; Nye and Greenland, 1960; Raich, 1980b; Singh and Singh, 1981; Stark and Spratt, 1977; Srivastava *et al.*, 1987), root surface area (Berish, 1982; Ewel *et al.*, 1982), root growth and development (Jordan and Escalante, 1980; Sanford, 1987; St. John, 1983; Uhl and Murphy, 1981), and species-specific root system architecture (Jenik, 1978).

This study was part of a long-term agroecosystem investigation designed to explore the possibility of using natural successional vegetation as a model for the design of new tropical agroecosystems. The primary objectives of this part of the research were 1) to describe root development during the early stages of regrowth following the felling and burning of a tropical forest, 2) to characterize the fine-root development of an agricultural ecosystem that physiognomically resembled successional vegetation of the same age, 3) to determine the impact of artificially high species richness on root-system development, and 4) to compare root development in crop monocultures with that of species-rich ecosystems.

Methods

Study site

The study was conducted near Turrialba, Costa Rica, in the Florencia Norte Forest. The site is located at 9°54'N, 83°40'W at an elevation of approximately 650 m. The area is in the Tropical Premontane Wet Forest life zone (Tosi, 1969). Mean annual rainfall is approximately 2700 mm, and the dry season extends from January through March.

The volcanic bedrock of the Turrialba area was formed in the late Tertiary and Quarternary periods (Hardy, 1961) and the basic composition is augite-hypersthene-andesite (Dengo, 1962). The andesite bedrock is composed of white plagioclase feldspar crystals and black pyroxenes, plus small

amounts of magnetite, apatite and pyrites. Quartz is characteristically lacking in the bedrock minerals of the area (Hardy, 1961).

The soil at the study site is an Andept, derived from aged pyroclastic materials of the Irazu-Turrialba volcano complex, and pertains to the Colorado series of Typic Dystrandeps (Alvarado *et al.*, 1981). A typical soil profile has a thin (0 to 6 cm) A11 horizon that has a high organic matter content (*ca.* 15%). The A11 usually grades into an A12 horizon, often extending to 25 cm. Underlying the A horizons is an AB horizon, lower in organic matter content (decreasing with depth from 9 to 3%) and higher in clay and silt content than the A. Below the AB horizon, beginning with a wavy border at about 60 cm, is a highly weathered B horizon; it is characterized by little organic matter (less than 3%) and very high clay and silt contents. The B horizon, a zone of weathered and leached material, usually extends past 6 m (Hardy, 1961). In five soil pits that were deeper than 2 m, saprolite, weathered andesite, was present. This lower part of the B horizon has less than 0.2% weatherable minerals remaining (Dondoli and Torres, 1954).

The physical structure of the soil is good, stabilized by the large amount of organic matter in the upper horizons and allophane throughout the profile. The soil is strongly aggregated, has a rapid infiltration rate (approximately 30 cm hr⁻¹), and a very high water-holding capacity (over 40% by volume at 15 bars of tension) (Russell and Ewel, 1985). Evidence of extensive pedoturbation from leaf-cutter ant activity was present throughout soil profiles (Alvarado *et al.*, 1981).

At the start of the study the vegetation on the 2.4 ha site was physiognomically typical of second-growth, mid-elevation vegetation in the humid tropics. It consisted of 8- to 9-yr-old second-growth interspersed with scattered individuals of five timber species (*Cordia alliodora*, *Ocotea atirrensis*, *Simarouba amara*, *Swietenia macrophylla*, and *Virola sebifera*) from a forestry planting, plus remnants of an old secondary forest, dominated by *Goethalsia meiantha*, which resulted from abandonment of earlier agriculture, probably coffee. The site included some of the same land where Harcombe (1977a; 1977b) studied the soil-nutrient relationships of early successional vegetation.

Treatments

The vegetation on six 33 by 33 m blocks and a single 14 by 14 m plot was felled during the first week of January, 1979. Border strips of at least 5 m of vegetation were left uncut surrounding each block. In late March, 1979, the slash was burned which left the site covered with a layer of white ash (Ewel *et al.*, 1981). Development of the experimental ecosystems began immediately following the burn.

The single 14 by 14 m plot was maintained free of vegetation by hand weeding and was surrounded by a 0.5-m-deep trench to reduce ingrowth of roots. Each of the six blocks was divided into 16 by 16 m quadrants, each separated by a 1 m wide trail. Thus, we had six blocks, each with four treatments, plus an unreplicated bare plot treatment. These become the plots on which the four kinds of experimental communities, described below, were established in a randomized complete block design.

Succession. The vegetation in this treatment regenerated from naturally occurring seeds and from coppice following the burn. The regrowth was unmanipulated by the investigators.

Imitation of succession. The composition of this community was completely controlled by us, and constituted our attempt to build an ecosystem that resembled the natural second growth of the area structurally and functionally, but not floristically. It was built by replacing naturally occurring species with morphologically analogous ones, both wild species and cultivars, which were not native to the site. Natural colonizers were periodically cut or uprooted and left to decompose *in situ*. The rationale for using natural successional vegetation as a model for agroecosystem design was discussed by Hart (1980) and Ewel (1986).

Enriched succession. The enriched succession contained natural regeneration (equivalent to the succession treatment) that was augmented by the regular addition of a diverse assemblage of propagules (≥ 20 species and $\geq 10\,000$ seeds per plot per month). This treatment was used to determine whether the removal of source constraints to seed input would result in an ecosystem that was even more structurally and functionally complex than the unenriched succession.

Monoculture. The monoculture contained one cultivar at a time, but the species used was changed as the stature of the successional vegetation increased. The monoculture plots were weeded frequently and were generally devoid of live non-crop roots. The first two monocultures were maize (*Zea mays* var. Tuxpeno). The first crop was planted immediately following the burn and was harvested in early July, 1979. The second crop was planted in late July and harvested in November, 1979. Both crops were planted at a spacing of 1 by 0.5 m, two seeds per hole. The third monoculture was cassava (*Manihot esculenta* var. Japonesa), a shrub. Cuttings were planted at a spacing of 1 by 1 m in late November, 1979, and the edible tubers were harvested in September, 1980. After the cassava harvest, seedlings of *Cordia alliodora*, a tree, were planted at a spacing of 2 by 2 m; this species occupied the monoculture plots until the end of the 5-yr study. No insecticides, herbicides, or fertilizers were used on the monocultures, but they were weeded frequently, such that weeds never formed a complete cover nor grew taller than 20 cm. Maize (ears only) and cassava (tubers only) were harvested; crop leaves and stems, as well as weeds, were left to decompose *in situ*.

Root sampling

Roots in the monoculture were initially sampled by randomly selecting one plant per block and harvesting its entire root system by careful excavation. These data were converted to average root mass per unit area by multiplying root mass per plant by plant density, on a block-by-block basis. This sampling technique eventually proved impractical as plants grew and their root systems occupied increasingly greater volumes of soil. Thus, most root harvests in the maize and cassava monocultures were done using the techniques applied in all other treatments, as described below. In the monoculture of *Cordia alliodora* we measured the tap root and principal lateral roots of individual trees by excavating a cylinder of soil 80 cm in diameter and 85 cm deep, centered beneath trees selected for destructive sampling. Tap-root data were related to tree diameter and height, so it was possible to estimate tap-root mass for the whole stand by allometry. The mass of smaller roots in the interstices between the trees was estimated from corings.

Until October, 1980, roots in treatments other than the monoculture were sampled in the center of biomass harvest plots—one in each of the six blocks per treatment—after the above-ground biomass had been carefully removed. Roots were initially sampled at two depths: 0 to 5 cm (including the litter layer) and 5 to 25 cm. The sampling depth was increased to 45 cm after 3 months and to 85 cm after 1 yr. Roots in each sampling interval above 45 cm were sampled by excavating 25 by 25 cm blocks of soil. Deeper roots were sampled with a 4.3-cm-diameter, manually driven corer (Santantonio, 1982). Soil for root samples was initially cored monthly; coring frequency decreased with vegetation age (see Figs. 1 and 3).

After October, 1980, roots at all depths were sampled with the corer. Each sample was a composite of five cores. One core was taken from the center and one from the vicinity of each corner of each biomass-harvest plot, except in the *C. alliodora* monocultures, where the cores were taken from five randomly selected locations throughout the plot. The various root-sampling techniques used over the 5-yr-sample period were not cross-calibrated.

We felt that our corings might have underestimated the mass of large-diameter roots. Therefore, at the time of the final biomass harvest (April, 1984) we supplemented the usual sampling procedures with excavations of all roots > 5 mm in diameter from pits that were 0.5 by 2 by 0.85 m deep. Although the root-pit data did not demonstrate that we had underestimated coarse-root mass by sampling with a small-diameter corer, they did document what our core sampling had indicated: the distribution of coarse roots, tap roots, and tubers was patchy.

Each soil block, core, or composite of cores was soaked in water, then agitated with flowing water. The overflow material, including roots, was collected on a 0.5-mm-mesh sieve. Roots in the smallest size class were rewashed to ensure the removal of external mineral matter.

Roots were separated from all other flotsam. All branch roots were excised, and the segments were separated into six diameter classes: < 1, 1 to < 2, 2 to < 5, 5 to < 10, 10 to < 20, and > 20 mm. Live and dead fine-roots were not distinguished; however, obviously decomposing roots > 2 mm in diameter were discarded. Roots in the bare plot were

regarded as dead. The clean root samples were dried to a constant weight at 70 °C and weighed to 0.5 mg.

During the first several months of sampling, the length (to the nearest mm) of all roots in each of the three smallest diameter classes (< 1, 1 to < 2, and 2 to < 5) was measured for each sample before oven drying. The relationships between root length and root mass were determined. The resulting re-

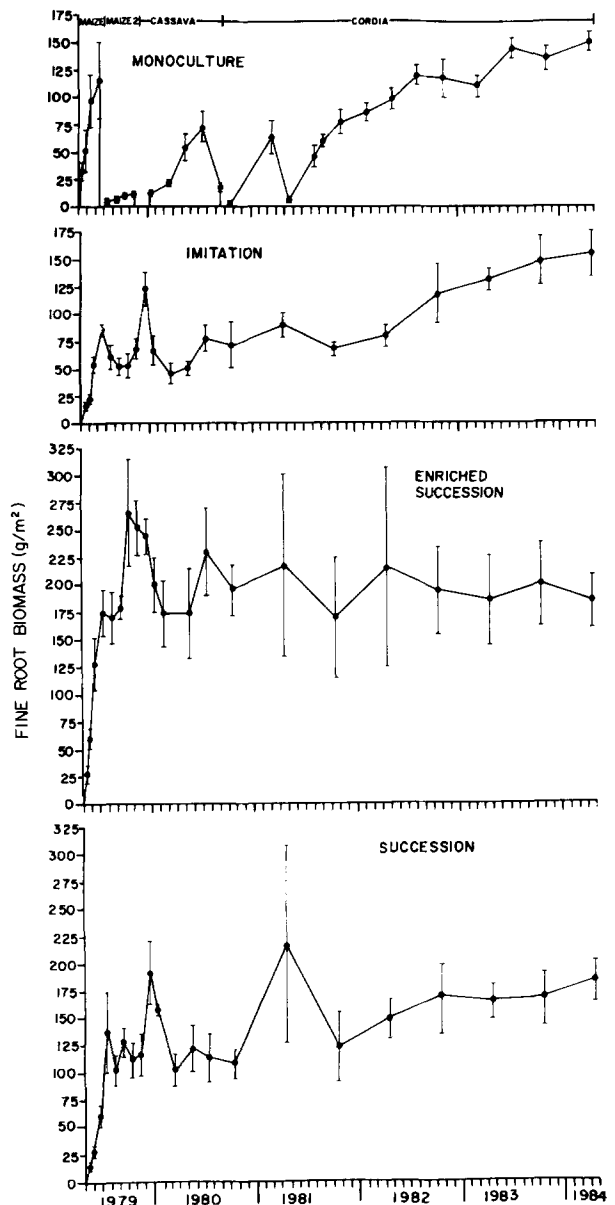


Fig. 1. Fine root (< 2 mm dia.) biomass. Values are means and vertical bars are standard errors.

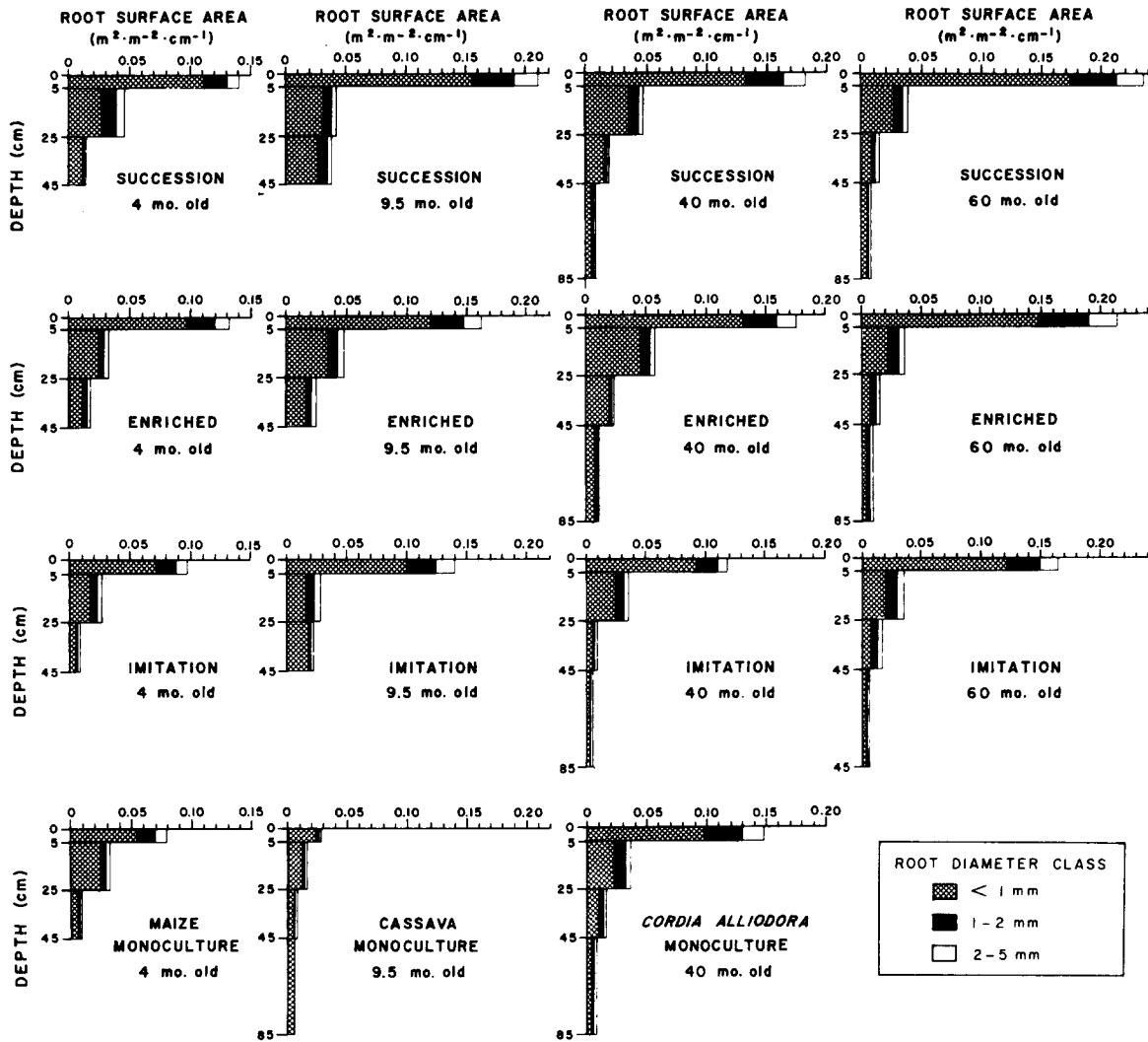


Fig. 2. Surface area of fine roots, by soil depth, in the four experimental ecosystems when they were 4, 9.5, 40 and 60 months old.

gressions (Berish, 1982) were used for all subsequent conversions of root mass to root length.

Root lengths were then converted to surface area by assuming that all roots were cylinders having diameters equal to the midpoint of their diameter class. Since root surface area calculations were based on the midpoint of diameter classes, the precision of our estimates decreased with increasing root diameter. We report the surface area of fine roots, rather than length or mass, because surface area is more directly related to absorptive potential, just as leaf area is a more direct measure of photosynthetic potential than is leaf mass. Mass to length and mass to surface area relationships for crops plants such as maize have been shown to vary

with plant age and soil strength (Allmaras *et al.*, 1975; Smika and Klute, 1982). We felt, however, that because we had a substantial sample size ($n > 118$, see Berish, 1983) taken from successional vegetation of various ages and physiological conditions from a very small area (< 3 ha) on a single soil type, the relationship between fine-root mass and fine-root length we developed was valid for our site.

Results

After the March, 1979 burn, there were approximately 38 g m^{-2} of fine roots (*i.e.*, those

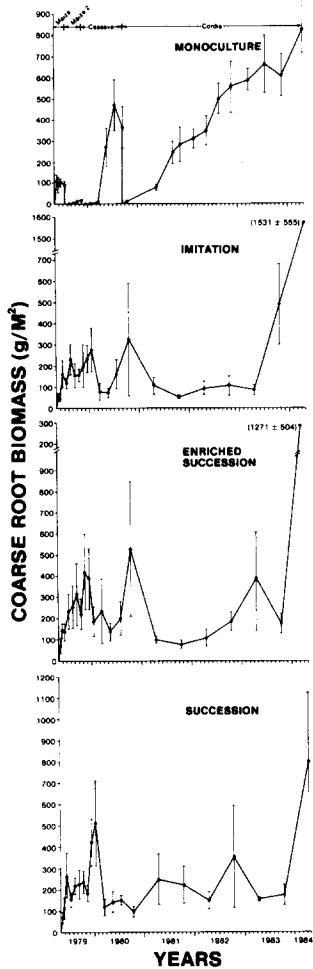


Fig. 3. Coarse root (> 2 mm dia.) biomass. Values are means and vertical bars are standard errors.

< 2 mm dia.) to a depth of 25 cm on all plots. These residual roots were readily distinguished from the white, fleshy roots of maize in the monoculture and from maize plus other cultivars in the imitation of succession treatment. In these two ecosystems residual roots were excluded from root mass determinations. In the succession and enriched-succession communities, however, where sprouts were not removed, all non-decomposing roots were included in root mass determinations. These presumably included many roots that had been present before the burn.

Dead roots were measured on the bare plot to estimate the disappearance rate of roots remaining from the pre-clearing forest. Total dead-root mass in this plot decreased from 185 g m^{-2} in May, 1979,

to 42 g m^{-2} in April, 1984. The mass of dead, fine roots (*i.e.*, those < 2 mm in diameter), however, was 23 g m^{-2} in May, 1979, and 32 g m^{-2} in April, 1984. Two factors complicated the measurement of the mass of dead, fine roots. One factor was their spatial patchiness, which may have increased with time. Most of the roots still present after five years, for example, were concentrated near decomposing stumps. A second factor was that, as larger roots decayed they probably shrank, so they might have been measured as part of the next smaller root size class.

Variances of the root mass data were not homogeneous but were generally proportional to the square of the means, so the values were logarithmically transformed (Steel and Torrie, 1960). Statistical analyses (SAS, General Linear Model) followed by Duncan's Multiple Range Test when significant differences were detected (SAS, 1979) were performed on the transformed data. However, means and standard deviations (or standard errors) are reported for untransformed data.

Fine and coarse roots were separately analyzed in one-way (treatment) analyses of variance by horizon and sample date. The root mass data from all four ecosystems were usually included in each analysis. However, when no living root mass was present in the monoculture, only the three equal-aged successional vegetations were included, because all monoculture vegetation planted after the harvest of the first maize crop (in July, 1979) was younger than the vegetation in the other three treatments.

Fine roots

Biomass. Fine roots grew rapidly in all four communities during the first 15 wk. By early July, 1979, fine-root mass ranged from approximately 75 g m^{-2} in the monoculture to about 140 g m^{-2} in the succession and enriched succession communities (Fig. 1). The rate of increase of fine-root biomass slowed on all three diverse communities after the first year.

At the end of the first rainy season the fine-root mass of the successional vegetation—then 9 months old—reached approximately 190 g m^{-2} . During the subsequent dry season, however, it decreased about 40% (Fig. 1). The other two diverse communities also experienced dry-season declines

in fine roots, although less markedly so in the enriched succession than in the other diverse vegetations, perhaps because it contained drought-tolerant species introduced by us.

The dry-season decrease in mass of fine roots that was evident during the first year in the three diverse communities was not apparent during the next 4 yr. This may have been an artifact of the timing and frequency of our sampling, or it may reflect increased robustness of the root systems of older vegetation. More fine roots in the older vegetation were woody and presumably would have been less likely to break down during harsh conditions than the non-suberized roots that characterized the younger vegetation.

Fine roots developed more slowly in the imitation of succession than in the succession and enriched succession. The short dry season of July, 1979, coincided with the maturation of the maize it contained, resulting in the loss of approximately 70% of its fine-root mass. From July, 1979, until October, 1981, there was approximately 40% less fine-root mass in the imitation vegetation than in the successional vegetation, primarily because species turnover was rapid and we were unable to build the imitation at the same speed at which the natural communities developed. During the last three years, however, the imitation of succession began to approach the stature of the successional vegetation and its root mass increased steadily. After 5 yr the total fine-root mass in the imitation of succession was approximately 150 g m^{-2} , nearly the same as that of the natural and enriched successions.

The development of fine roots in the monocultures was far different from that in the other communities, partly because the other ecosystems contained far more species, but primarily because the monocultures were periodically set back by harvests. The development of fine roots in the first maize planting kept pace with the three diverse communities. The second maize crop, however, developed only about one-sixth of fine-root mass of the first planting. Its plants were stunted and many of them lodged; grain yield was extremely low. The poor development of the second maize crop was due primarily to high, but unquantified, levels of root herbivory by coleopteran larvae. When the second maize crop was replaced by cassava, fine roots once again developed rapidly. Mass of fine roots in the cassava peaked at approximately

65 g m^{-2} when the tubers approached maturation. Fine roots of the fourth monoculture, the *C. alliodora* plantation, developed rapidly. After approximately 3 yr, the fine-root mass in the *C. alliodora* stand was about the same as that of the successional vegetation.

Surface area. Very fine roots (*i.e.*, those $< 1 \text{ mm}$ in diameter) accounted for most root surface area in all four communities throughout the investigation. Like fine-root biomass, root surface increased rapidly in all four communities from May through early July, 1979. At approximately 4 months, the root area index (RAI), or m^2 of root surface area m^{-2} ground, was 1.9, 1.6, 1.2, and 1.0 in the enriched succession, succession, imitation of succession, and maize monoculture, respectively (Fig. 2). Subsequent increases in fine-root surface area, line biomass, were slower. Decreases in root surface area in all treatments were associated with periods of low precipitation.

Over time, all four of the communities tended to have an increasingly greater proportion of their small, nutrient-absorbing roots in the surface-soil horizon. This concentration of fine roots in the surface soil was accompanied by canopy closure and litter accumulation. Presumably, as community structure built up, within-community recycling of nutrients increased. Fine roots would then develop preferentially near the soil surface, where nutrients were relatively concentrated because of litter inputs.

Coarse roots

After approximately 5 yr of growth, the mean mass of coarse roots (*i.e.*, those $> 2 \text{ mm}$ in diameter) to a depth of 85 cm was about 800, 1370, and 1530 g m^{-2} (or nearly 2000 g m^{-2} if yam tubers included) in the succession, enriched succession, and imitation of succession, respectively (Fig. 3). However, because of spatial variability, few statistically significant differences were detected among treatments. This was true even at the time of the final harvest, when roots were excavated from large pits. In the imitation of succession, for example, most coarse roots were from large-rooted cultivars such as plantains, yams, and cassava. As only a few individuals of each were present in each block,

large variances in mass were associated with the scattered locations of those species.

Many of the coarse roots in the succession and enriched succession communities developed from sprouts, an important source of regeneration in the successional vegetation.

At the time of the final harvest the monoculture was a 3.5-yr-old tree plantation. Its coarse root biomass was surprisingly high: 800 g m^{-2} , which was about the same as that of the 5-yr-old, species-rich successional vegetation.

Discussion

Numerous studies indicate that a steady state of fine root biomass is reached at the time of canopy closure (McQueen, 1968; Moir and Bachelard, 1969; Nemath, 1973; Vogt *et al.*, 1981) which occurs often after 20 yr in many temperate-zone forests. At our tropical site, where canopy closure occurs much sooner, the steady state of fine roots will be reached in fewer than 20 yr. Within the first growing season the successional vegetation we studied had about 40% of the amount of fine roots of an adjacent, 75-yr-old forest (Berish, 1982). After 5 yr the mass of fine roots in the three diverse communities we studied were only slightly lower than values reported for mature tropical forests in Costa Rica (range 290 to 350 g m^{-2}) (Berish, 1982; Raich, 1980b), a tropical deciduous forest in India (276 g m^{-2}) (Singh and Singh, 1981) and a 4-yr-old hardwood forest in North Carolina (732 g m^{-2}) (Boring *et al.*, 1984), but much lower than values from forests in Ghana (Lawson *et al.*, 1970) and the Brazilian Amazon (range 528 to 1089 g m^{-2}) (Klinge, 1973). Rapid growth of fine roots has been reported for other tropical forests (Jordan and Escalante, 1980; Jordan, 1985; Raich, 1980b; Sanford, 1987) and a warm temperate forest where resprouting was common (Boring *et al.*, 1981).

Soil fertility may be inversely related to rate of root-mass recovery. For example, 1 yr after deforestation of a nutrient-impooverished soil in the Venezuelan Amazon, total plant biomass was less than 70 g m^{-2} (Uhl *et al.*, 1981). In contrast, less than 8 wk after we deforested our relatively fertile site, there was more than 100 g m^{-2} of root biomass alone.

The slower rate of fine root mass increase after

the first growing season at our site may have been due to decreased root growth, perhaps because photosynthate was preferentially allocated to larger roots (Atkinson, 1983) or to aboveground tissues (Tyron and Chapin, 1983). This explanation fits with regeneration that is primarily by seed, as on our site, where an early balance is established between above- and below-ground biomass. Regeneration by sprouting, however, is different in that early aboveground vegetative growth is not necessarily new net production, but may be a reallocation of stored photosynthate from root tissues (Schier and Zasada, 1973; Tew, 1970). Alternatively, the decline in net growth rate may have been due to accelerated root turnover, which can increase independently of biomass (Nadelhoffer *et al.*, 1985). A third possibility is that annual variation in fine-root production is so large that it masks small annual biomass increments. Large annual variations of fine-root growth have been reported for many species and investigations (Atkinson, 1973; Santantonio and Herman, 1985; Singh *et al.*, 1984).

Functional inferences of root development patterns

The rapid accumulation of biomass during succession means that substantial amounts of nutrients are removed from the soil, where they are potentially susceptible to leaching or chemical fixation, and stored in plant tissues (Boring *et al.*, 1981; Marks and Bormann, 1972; Vitousek and Reiners, 1975). Although the early development of a fine-root system is essential for this uptake and sequestering of nutrients in biomass to occur, this is not a period when vast amounts of photosynthate are allocated to large, supportive roots (Ewel, 1971). Studies of temperate coniferous forests (Coutts, 1983; Coutts and Lewis, 1983; Deans, 1981; Fraser, 1962) indicate that the formation of large roots is a long process and occurs primarily after the development of a fine-root system. This same trend was observed at our site.

A general pattern evident during succession is that internal recycling of nutrients increases with time and plants become less dependent upon acquisition of new supplies from the mineral soil (Odum, 1969; Vitousek and Reiners, 1975). This switch from abiotic to biotic nutrient sources is accompanied by an increasingly greater concentra-

tion of fine roots near the surface, where they have ready access to nutrients returned to the soil as detritus, canopy leachate, and stemflow. This trend was apparent at our site and has also been reported for temperate forests (Grier *et al.*, 1981; Vogt *et al.*, 1981). The total mass of fine roots increased throughout the profile during succession, but the fraction of fine roots in the surface 5 cm increased from about 35% at 4 months to 55% of the total in five years.

The large roots that develop later in succession not only provide support for the woody plants that soon dominate successional vegetation in the humid tropics, but they also penetrate deep into the soil where they are connected to a network of finer roots that extract nutrients. This mining of nutrients from deep soil is an important aspect of the restoration of fertility by fallow vegetation (Nye and Greenland, 1960). At our site monospecific patches of an exotic grass, *Panicum maximum*, were dispersed among the predominantly woody successional vegetation. Roots were dense beneath these grass patches, but they tended to be concentrated near the soil surface, so nutrients that filtered below them were lost, perhaps irretrievably. Shallow roots may be one of the main reasons why long-term occupation by grasses, such as the notorious *Imperata cylindrica* of southeast Asia, may lead to site degradation (Charley, 1983).

Implications for tropical agroecosystem design

Roots are a very significant source of soil organic matter. In many forests, for example, the inputs of organic matter to the soil from roots and mycorrhizae are two to five times greater than the inputs from leaves and small branches (Fogel, 1983; Fogel and Hunt, 1983; Gholz *et al.*, 1986; Vogt *et al.*, 1982, 1986). One of the agronomically important features of perennial plants is that the organic matter they produce is delivered to the soil more or less continuously. This contrasts with annual crops, in which most organic matter is returned to the soil all at once, at the time of harvest. If residues are decomposed and nutrients are mineralized at a time of reduced plant growth, nutrients can be leached or eroded away.

These differences in life span and their relationship to soil organic matter inputs are illustrated by

the crops we planted in our monocultures. Our first maize crop developed an extensive network of fine roots, which became part of the soil organic matter at harvest, only about 90 days after planting. The second maize crop, an agronomic failure, contributed little organic matter to the soil. Our third crop, cassava (a shrub of intermediate longevity), developed a fine-root system that persisted more than 6 months and diminished only after tuber maturation. Our fourth crop, *Cordia alliodora*, slowly developed a more permanent root system, and at 2.5 yr its root mass was approximately equal to that of the diverse 5-yr-old communities. Permanence may be a more important factor than diversity in determining the ability of the vegetation to contribute organic matter to—and to exploit—the soil.

Diversity is not irrelevant, however, especially in the early stages of stand development. One result of increasing the species richness of the successional vegetation was that during the first year fine roots developed more rapidly in the enriched successional vegetation than in the unenriched vegetation. Another result was that the mass of fine roots decreased less during the 1980 dry season in the enriched vegetation than in either the unenriched successional vegetation or in the monoculture.

An important question for agroecosystem design was, did the imitation of successional vegetation have the same structural and functional attributes as the diverse, naturally occurring successional vegetation? In general, yes. One difference between the two communities was caused by the time lag that inevitably preceded development of the mimic. We had to determine what the course of succession was before we could replace naturally occurring species with species of our choice. Because of this delay, the development of root surface area in the imitation lagged behind that of the natural successional vegetation. After 4 yr of growth, however, fine-root surface area was very similar in the native vegetation and its mimic. This indicates that one can achieve similar structure—and possibly similar ecosystem function—with a mix of species having no elements in common with the native plant community.

Because the imitation of successional vegetation was comprised of many species, it offers the advantage of permanent site occupancy that is missing in all except the longest-lived monocultures. If in-

dividual species had been harvested, dozens of other cohabitants would have been available to take up nutrients and protect the soil. Tropical soils are especially vulnerable when they are bare, and extreme exposure usually accompanies harvests.

Agroecosystems that incorporate features of natural regrowth, such as extensive fine-root systems and permanent aboveground structure, will reduce nutrient losses by storing large quantities of nutrients in biomass, by augmenting soil organic matter, and by protecting the soil. Such features might usefully be incorporated into the design of agroecosystems appropriate for the humid tropics, where potential nutrient loss rates through leaching and erosion are high.

Acknowledgements

This research was conducted as part of a cooperative investigation between the University of Florida and the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) and was supported by National Science Foundation grants DEB 78-10721 and DEB 80-11136. We thank Norman Price and Donald Hazlett for assistance with field and laboratory work and W Cropper, H Gholz and C Jordan for reviewing drafts of the manuscript. This paper is journal series number 7448 from the Institute of Food and Agricultural Studies, University of Florida, Gainesville, Florida, 32611.

References

- Alvarado A, Berish C and Paralta F 1981 Leaf-cutter ant (*Atta cephalotes*) influence on the morphology of Andepts in Costa Rica. *Soil Sci. Soc. Am. J.* 45, 790-794.
- Atkinson D 1973 Seasonal changes in the length of white un-suberized root on raspberry plants grown under irrigated conditions. *J. Hort. Sci.* 48, 413-419.
- Atkinson D 1983 The growth, activity and distribution of the fruit tree root system. *Plant and Soil* 71, 23-25.
- Bartholomew W J, Meyer J and Landelout H 1953 Mineral nutrient immobilization under forest and grass fallow in the Yangambi (Belgian Congo) Region. *Publ. Inst. Natn. Etude agron. Congo Belge, Ser. Sci. No.* 57.
- Berish C W 1982 Root biomass and surface area in three successional tropical forests. *Can. J. For. Res.* 12, 699-704.
- Berish C W 1983 Roots, Soil, Litter and Nutrient Changes in Simple and Diverse Tropical Successional Ecosystems. PhD. Dissertation, University of Florida, Gainesville, FL.
- Blanton C M and Ewel J J 1985 Leaf-cutting ant herbivory in successional and agricultural tropical ecosystems. *Ecology* 66, 861-869.
- Boring L R, Monk C D and Swank W T 1981 Early regeneration of a clearcut southern Appalachian watershed. *Ecology* 62, 1244-1253.
- Boring L R and Swank W T 1984 The role of black locust (*Robinia pseudo-acacia*) in forest succession. *J. Ecol.* 62, 1244-1253.
- Bowen G D 1980 Mycorrhizal roles in tropical plants and ecosystems. *In Tropical Mycorrhizae Research*. Ed. P M Kola. pp 165-190. Oxford University Press, New York, New York.
- Charley J L 1983 Tropical highland agricultural development in a monsoonal climate, the utilization of Imperata grassland in northern Thailand. *In Natural Resource Development and Environmental Stability in the Highlands of Northern Thailand*. pp. 389-396. Chiang Mai University and United Nations University, Thailand.
- Cornforth I S 1970 Reafforestation and nutrient reserves in the humid tropics. *J. Appl. Ecol.* 7, 609-615.
- Coutts M P 1983 Root architecture and tree stability. *Plant and Soil* 71, 171-188.
- Coutts M P and Lewis G L 1983 When is the structural root system determined in Sitka spruce? *Plant and Soil* 71, 155-160.
- Cox T L, Harris W F, Ausmus B S and Edwards N T 1978 The role of roots in biogeochemical cycles in an eastern deciduous forest. *Pedobiologia* 18, 264-271.
- Deans J D 1981 Dynamics of coarse root production in a young plantation of *Picea sitchensis*. *Forestry* 54, 139-154.
- Dengo G 1962 Tectonic-igneous sequence in Costa Rica. *In Petrologic Studies: a Volume to Honor A F Buddington*. pp 133-161. *Spec. Pub. Geol. Soc. Amer.*
- Dondoli C and Torres J A 1954 Estudio geoagronómico de la region oriental de la Meseta Central. *Ministerio de Agricultura y Industrias, San Jose, Costa Rica.*
- Edwards N T and Ross-Todd B M 1979 The effects of stem girdling on biogeochemical cycles with a mixed deciduous forest in eastern Tennessee. I. Soil solution chemistry, soil respiration, litterfall, and root biomass studies. *Oecologia* 40, 247-257.
- Ewel J 1971 Biomass changes in early tropical succession. *Turrialba* 21, 110-112.
- Ewel J 1986 Designing agricultural ecosystems for the humid tropics. *Annu. Rev. Ecol. Syst.* 17, 245-272.
- Ewel J, Berish C, Brown B, Price N and Raich J 1981 Slash and burn impacts on a Costa Rican wet forest site. *Ecology* 62, 816-829.
- Ewel J, Gliessman S, Amador M, Benedict F, Berish C, Bermudez R, Brown B, Martinez M, Miranda R and Price N 1982 Leaf area, light transmission, roots and leaf damage in nine tropical plant communities. *Agro-Ecosystems* 7, 305-326.
- Fogel R 1983 Root turnover and productivity of coniferous forests. *Plant and Soil* 71, 75-85.
- Fogel R and Hunt G 1983 Contribution of mycorrhizae and soil fungi to nutrient cycling in a Douglas-fir ecosystem. *Can. J. For. Res.* 13, 219-232.
- Fraser A I 1962 The soil and roots as factors in tree stability.

- Forestry 35, 117–127.
- Fredriksen R L 1971 Comparative chemical quality—natural and disturbed streams—following logging and slash burning. *In* Proceedings of Symp. effects of forest land use and stream environment. pp 125–137. Oregon State University Press, Corvallis, Oregon.
- Gholz H L, Hendry L C and Cropper W P Jr 1986 Organic matter dynamics of fine roots in plantations of slash pine (*Pinus elliottii*) in north Florida. *Can. J. For. Res.* 16, 529–538.
- Gorham E, Vitousek P M and Reiners W A 1979 The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annu. Rev. Ecol. Syst.* 10, 53–84.
- Greenland D and Kowal J 1960 Nutrient content of the moist tropical forest of Ghana. *Plant and Soil* 12, 154–174.
- Grier C G, Vogt K A, Keyes M R and Edmonds R L 1981 Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Can. J. For. Res.* 11, 155–167.
- Harcombe P A 1977a The influence of fertilization on some aspects of succession in a humid tropical forest. *Ecology* 58, 1375–1383.
- Harcombe P A 1977b Nutrient accumulation by vegetation during the first year of recovery of a tropical forest ecosystem. *In* Recovery and Restoration of Damaged Ecosystems. Eds. J Cairns, Jr, K L Dickson, and E E Herricks. pp 347–378. Univ. Press of Virginia, Charlottesville, Virginia.
- Hardy F 1961 The soils of the IAIAS area. Mimeo, Instituto Interamericano de Ciencias Agrícolas, (IICA). Available through Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE) library, Turrialba, Costa Rica.
- Harris W F, Kinerson R S Jr and Edwards N T 1977 Comparison of belowground biomass of natural deciduous forests and loblolly pine plantations. *In* The Belowground Ecosystem: a Synthesis of Plant Associated Processes. Ed. J K Marshall. *Colo. Ran. Sci. Pub.* 26, 29–37.
- Harris W F, Santantonio D and McGinty D 1980 The dynamic belowground ecosystem. *In* Forests: Fresh Perspectives from Ecosystem Analysis. Ed. R H Waring. pp 118–129. Oregon State University Press, Corvallis, Oregon.
- Hart R D 1980 A natural ecosystem analog approach to the design of a successional crop system for tropical forest environments. *Biotropica* 12(suppl.), 73–82.
- Huttel C 1975 Root distribution and biomass in three Ivory Coast rain forest plots. *In* Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research. Eds. F B Golley and E Medina. pp 123–130. Springer-Verlag, New York, New York.
- Jenik J 1971 Root structure and underground biomass in equatorial forests. *In* Productivity of Forest Ecosystems. pp 323–331. UNESCO.
- Jenik J 1978 Roots and root systems of tropical trees: morphologic and ecologic aspects. *In* Tropical Trees as Living Systems. Eds. P Tomlinson and M Zimmerman. pp 323–349. Cambridge University Press, London.
- Johnson P L and Swank W T 1973 Studies of cation budgets in the southern Appalachians on four experimental watersheds with contrasting vegetation. *Ecology* 54, 70–80.
- Jordan C F 1980 Nutrient leaching from agro-ecosystems in the Amazon basin, and implications for recovery of the forest. *In* Tropical Ecology and Development. Ed. J I Furtado. pp 553–559. International Society of Tropical Ecology, Faridabad, India.
- Jordan C F 1985 Nutrient Cycling in Tropical Forest Ecosystems. John Wiley and Sons, Ltd, pp 190.
- Jordan C F and Escalante G 1980 Root productivity in an Amazonian rain forest. *Ecology* 61, 14–18.
- Klinge H 1973 Root mass estimation in lowland tropical rainforests on central Amazonia, Brazil. I. Fine root masses of a pale-yellow latosol and giant humus podzol. *Trop. Ecol.* 14, 29–38.
- Lawson G W, Armstrong-Mensah K O and Hall J B 1970 A catena in tropical moist semi-deciduous forest near Kade, Ghana. *J. Ecol.* 58, 371–398.
- Likens G E, Bormann F H, Johnson N M, Fisher D W and Pierce R S 1970 Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecol. Mono.* 40, 23–47.
- Likens G E, Bormann F H, Pierce R S and Reiners W A 1978 Recovery of a deforested ecosystem. *Science* 199, 492–496.
- Marks P L and Bormann F H 1972 Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. *Science* 176, 914–915.
- McQueen D R 1968 The quantitative distribution of absorbing roots of *Pinus sylvestris* and *Fagus sylvatica* in a forest succession. *Oecol. Plant* 3, 83–89.
- Moir W H and Bachelard E P 1969 Distribution of fine roots in three *Pinus radiata* plantations near Canberra, Australia. *Ecology* 50, 658–662.
- Murphy P G and Lugo A E 1986 Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica* 18, 89–96.
- Nadelhoffer K J, Aber J D and Melillo J M 1985 Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. *Ecology* 66, 1377–1390.
- Nemath J C 1973 Dry matter production in young loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* engelm.) plantations. *Ecol. Monogr.* 43, 21–41.
- Nye P H and Greenland D J 1960 Changes in the soil after clearing a tropical forest. *Plant and Soil* 21, 101–112.
- Odum E P 1969 The strategy of ecosystem development. *Science* 164, 262–270.
- Raich J W 1980a Carbon Budget of a Tropical Soil under Mature Wet Forest and Young Vegetation. Master's Thesis, University of Florida, Gainesville, Florida.
- Raich J W 1980b Roots regrow after forest felling. *Biotropica* 12, 231–232.
- Redhead J F 1980 Mycorrhiza in natural tropical forests. *In* Tropical Mycorrhiza Research. Ed. P M Kola. pp 127–142. Oxford University Press, New York, New York.
- Russell A E and Ewel J J 1985 Leaching from a tropical Andepit during big storms: a comparison of three methods. *Soil Sci.* 139, 181–189.
- Sanford R L Jr 1987 Apogeotropic roots in an Amazonian rain forest. *Science* 235, 1062–1064.
- Sanni S O 1976 Vesicular-arbuscular mycorrhiza in some Nigerian soils: the effect of *Gigaspora gigantea* on the growth of rice. *New Phytol.* 7, 763–774.
- Santantonio D 1982 Production and Turnover of Fine Roots of Mature Douglas-fir in Relation to Site. Ph.D. Dissertation. Oregon State University, Corvallis, Oregon.

- Santantonio D and Hermann R K 1985 Standing crop, production, and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. *Ann. Sci. For.* 42, 113–142.
- Santantonio D, Hermann R K and Overton W S 1977 Root biomass studies in forest ecosystems. *Pediobiologia*, Bd 17, 1–31.
- Schier G A and Zasada J C 1973 Role of carbohydrate reserves in the development of root suckers of *Populus tremuloides*. *Can. J. For. Res.* 3, 243–250.
- Singh K P, Lauenroth W K, Hunt H W and Swift D M 1984 Bias and random errors in estimators of net root production: a simulation approach. *Ecology* 65, 1760–1764.
- Singh K P and Singh R P 1981 Seasonal variation in biomass and energy of small roots in tropical dry deciduous forest, Varanasi, India. *Oikos* 37, 88–92.
- Srivastava S K, Singh K P and Upadhyay R S (1986) Fine root growth dynamics in Teak (*Tectono grandis* Linn. F.). *Can. J. For. Res.* 16, 1360–1364.
- St John T V 1983 Response of tree roots to decomposing organic matter in two lowland Amazonian rain forests. *Can. J. For. Res.* 13, 346–349.
- Stark N and Spratt M 1977 Root biomass and nutrient storage in rain forest Oxisols near San Carlos de Rio Negro. *Trop. Ecol.* 18, 1–9.
- Statistical Analysis System Institute (SAS) 1979 A user's guide to SAS. SAS Institute, Raleigh, North Carolina.
- Steel R G and Torrie J H 1960 Principles and Procedures of Statistics. McGraw-Hill, New York, New York.
- Tew R K 1970 Root carbohydrate reserves in vegetative reproduction of Aspen. *For. Sci.* 16, 318–320.
- Tosi J A 1969 Mapa ecologia de Costa Rica. Centro Cientifico Tropica, San Jose, Costa Rica.
- Tyron P R and Chapin F S III 1983 Temperature control over root growth and root biomass in taiga forests. *Can. J. For. Res.* 10, 523–529.
- Uhl C and Murphy P 1981 A comparison of productivities and energy values between slash and burn agriculture and secondary succession in the upper Rio Negro region of the Amazon Basin. *Agro-Ecosystems* 7, 63–83.
- Uhl C, Clark K, Clark H and Murphy P 1981 Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon Basin. *J. Ecol.* 69, 631–649.
- Vitousek P M and Reiners W A 1975 Ecosystem succession and nutrient retention: a hypothesis. *Bioscience* 25, 376–381.
- Vogt K A, Edmonds R L and Grier C C 1981 Seasonal changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifer roots in 23- and 180-year-old sub-alpine (*Abies amabilis*) stands. *Can. J. For. Res.* 11, 223–229.
- Vogt K A, Grier C C, Meier C E and Redmonds R L 1982 Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. *Ecology* 63, 370–380.
- Vogt K A, Grier C C and Vogt D J 1986 Production, turnover and nutrient dynamics of above- and below-ground detritus of world forests. *Adv. Ecol. Rev.* 15, 303–377.
- Wells C G and Jorgensen J R 1975 Source-sink relations and the partition of assimilates in the plant. *In* Symposium on the Impact of Intensive Harvesting on Forest Nutrient Cycling. pp 212–230. State University of New York, Syracuse, New York.