SHADE TOLERANCE AND PHOTOSYNTHESIS OF COCOYAM
[Xanthosoma sagittifolium (L.) Schott].

By

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Studies were conducted on cocoyam, Xanthosoma sagittifolium (L.) Schott, an edible aroid grown as a staple food in many tropical areas, to evaluate the effects of different sunlight levels and nitrogen (N) fertilization on gas exchange and growth. Shade-grown plants (30% and 50% full sunlight) had greater foliage dry weights and top:corm ratios, and greater or similar corm dry weights as 100% sunlight-grown plants. Shade plants had a higher leaf area index and crop growth rate (biomass accumulation over time on a whole-plant basis) than sun-grown plants. The underground yield advantage for shade-grown plants was attributed to the greater crop growth rates observed for shade than for 100% sunlight-grown cocoyam. Sun-grown plants had higher net assimilation rates (biomass accumulation over time on a leaf area basis) and specific leaf densities than shade-grown plants. Foliage dry weight, top:corm ratio, and corm fresh weight increased as N level increased from 0 to 475 mg Kg\(^{-1}\).
Equations were developed to predict lamina area through measurements of lamina width, length, and dry weight, and petiole length.

Net CO₂ assimilation (A), and water use efficiency (WUE) were greater for 100% sunlight than for shade-grown plants. Water use efficiency and A increased as N level increased for 100% sunlight plants. Shade plants had greater chlorophyll:N ratios and lamina area:lamina dry weight ratios than 100% sunlight plants, which indicated increased photosynthate and chlorophyll allocation to leaves of shade-grown plants. Increased photosynthate and chlorophyll allocation to the foliage provided for maximization of light interception. Interactions between N and shade during plant development, with respect to gas exchange and growth parameters, indicate that cocoyam response to N is dependent on incident photosynthetic photon flux (PPF) during growth. Thus, cocoyam exhibited a degree of adaptive plasticity, with respect to N allocation within the lamina, in response to PPF and N fertilization during plant development. The results indicate that cocoyam has a unique potential, among terrestrial edible plants, to grow in moderate shade without sacrificing yields. The N fertilization studies indicate that the yield advantages for shade-grown cocoyam should also be evident in tropical agroecosystem polycultures where soil N deficits are common.
CHAPTER 1
INTRODUCTION

In the tropics, where land is increasingly scarce, crop yields may be increased by improving the efficiency of resource (light, water, nutrients) utilization (40). Innovative and ecologically-sound approaches need to be developed to improve efficiency of crop production on a sustainable basis in the tropics (2, 36, 93).

Plants are dependent on solar radiation, for growth and development through the process of photosynthesis. The possibility exists to exploit the genetic diversity in the plant kingdom by identifying edible plants that efficiently utilize solar radiation under particular environmental conditions (3, 4). Also, cultural practices such as planting patterns and densities, and timing of plantings can be manipulated in polycultures to improve light interception and crop productivity (164).

Cocoyam, Xanthosoma sagittifolium (L.) Schott, is a staple in several tropical regions. The edible cormels are used as a source of food calories and cormels have good storage capabilities. Cocoyam is reported to be shade tolerant (22, 105, 143). However, little is known about the mechanisms of its shade tolerance and about its patterns of light interception. An understanding of shade tolerance in cocoyam may help to identify important related factors, such as nutrient utilization or biomass partitioning, which allow the plant to perform well in the shade. This information may help to improve
polyculture system designs (84), where light availability often limits yield potentials of understory crops.

Because nitrogen (N) is an important component of photosynthetic enzymes and of assimilating tissues (60) it is considered an important factor in the acclimation of plants to light. Since N is often deficient in tropical agroecosystems and low N levels limit crop growth, lamina N concentrations may be important in determining the productivity of cocoyam grown in the shade.

To evaluate this hypothesis, experiments were conducted to study the effects of photosynthetic photon flux (PPF) on biomass accumulation, diurnal and seasonal A, stomatal conductance for CO₂ (gₛ), substomatal CO₂ concentration (Cᵢ), transpiration (E), WUE, lamina N and chlorophyll contents, and N utilization patterns for cocoyam.
CHAPTER 2
LITERATURE REVIEW

Crop Description

Cocoyam is an herbaceous, perennial tropical herb, grown for its edible starch-filled corms and cormels. The rhizome-like cormels, the part most often consumed, arise from the base of the corm below the soil surface (110). Cocoyam, a member of the Araceae family, is often grown as an intercrop in tropical areas. Aspects of cocoyam botany, culture and taxonomy have been reviewed by O'Hair and Asokan (110; Also see: 40, 45, and 157).

Lamina Morphology and Light Interception

The productivity of plants appears to be proportional to the 1) quality and quantity of radiant energy intercepted and 2) efficiency of radiant energy conversion into photosynthates (21). Crop productivity may therefore be improved by learning more about plant strategies for light interception (65).

Plant adaptation to growth in the shade included changes in lamina external (17) and internal (13, 33) morphology. Shade-grown plants exhibited increased assimilate surface area for light interception (13) and a reduced lamina thickness (38). Reduced lamina thickness decreased the intercellular air spaces thus limiting the area available for atmospheric CO₂ to diffuse into the mesophyll cells (107, 108).
In comparison to sun plants, shade-grown plants had higher chlorophyll a:b ratios (8, 13, 32); thinner leaves (6, 10, 13, 25, 53, 58, 66, 68, 101, 107, 108, 167); decreased specific leaf density (SLD; leaf weight divided by leaf area) (6, 10, 25, 68, 162, 167); increased lamina size (6, 53, 61, 81, 132); greater chlorophyll concentrations on a lamina weight basis (13, 162, 167); increased leaf lifespan (51, 80, 102); reduced lamina soluble protein contents (10, 13, 25, 53, 108, 167); reduced starch levels (41); increased stomatal resistance (8, 41, 101), which is probably a result of a decreased stomatal density (13, 53, 58, 101); more stomata per lamina (53); decreased development of the epidermis, vascular system and parenchyma (10, 13); decreased chloroplast number, but increased chloroplast size and chloroplast chlorophyll concentration on a weight basis (13, 66, 162); and thicker and better grana development formed by numerous thylakoids (6, 12, 167). Shade-grown plants also had lower lamina concentrations of the light-harvesting and redox compounds of the thylakoids, including decreased cytochrome b, cytochrome f, plastoquinone, photosystem II reaction centers, and ATP synthetase (33, 113).

Internal lamina modifications for growth in the shade thus reduced the size of the photosynthetic apparatus, and supporting tissues (65), which resulted in decreased A compared to growth at higher PPFs. This may be an adaptation for improved utilization efficiency of the limited available radiant energy. Reduced lamina
starch content, enzyme activity, growth rates (area basis), and respiration rates support the contention that shade-grown leaves can only utilize enough light to support a small energy budget (41, 65). Plant resources for shade-grown plants were allocated toward larger lamina sizes to increase light interception while the size of the photosynthetic apparatus was reduced in proportion to decreased PPFs during growth.

Photosynthate Partitioning

Carbohydrates are partitioned to plant organs for growth, maintenance and respiration (75, 141, 155). The factors which control carbohydrate partitioning are poorly understood and are affected by a number of adaptive, spatial, and temporal environmental parameters (96, 116, 141, 149). Genetic differences in partitioning patterns have been noted for species and cultivars of Dioscorea, (111), Colocasia (115), soybean (104), and Manihot (42, 125).

Photosynthate partitioning patterns are important because they relate to yield improvement of most crops in the form of an increased harvest index (HI) (marketable yield divided by total plant biomass). Improvements in HI are obtained through crop improvement programs (64). For many crops the potential still exists for greater yields through selection for increased HI (7, 104).

The physiological system which controls photosynthetic partitioning is poorly understood for most crops (64). Light quality
may play a physiological role in plant photosynthetic partitioning (3, 85, 171). Several studies revealed that phytochrome is involved in internode elongation (84). Exposure to an increased far red:red light ratio, characteristic of an understory light environment, stimulated increased internode elongation in the dicotyledonous weed *Galium aparine* (5) and in soybean (84).

Lamina morphological adaptations to growth in the shade are accompanied by changes in whole-plant carbohydrate partitioning (10). Corre (38) found similar morphological and growth responses when ten C$_3$ plant species, which ranged from sun- to shade-tolerant, were grown in the shade. In shaded conditions plants had increased specific leaf area (SLA; lamina area divided by lamina weight) and petiole length, and decreased foliage dry weight. In other plants shading increased the shoot:root ratio (1, 14, 37, 51, 58, 77, 83, 112, 133, 136, 137, 138); plant height (1, 38, 77, 112); lamina area (77); and petiole length (22). Shading also resulted in reduced tuber number and yield in potato (136, 137); reduced corm yield in *Colocasia esculenta* (L.) Schott (23); and in delayed initiation of bulking in cassava roots (14, 83, 112). Therefore, plants grown in the shade partitioned photosynthates toward light interception through increased plant height and assimilating area production (10, 13).

However, when dealing with crops such as cocoyam, sufficient resources must be partitioned by the plant to achieve storage organ
yields which are marketable. In addition, fast-growing storage organs may provide a "sink strength" to stimulate A (6, 44, 64, 166). Therefore a balance must exist in shade-grown crops between foliage and storage organ biomass accumulation, to maximize assimilating area production without diminishing marketable yields.

Nutrient concentrations may have an effect on plant carbohydrate partitioning (83). Root number and weight for cassava increased with increased potassium and N levels, but N application alone resulted in reduced root biomass (83). Other aspects of plant carbohydrate partitioning, such as the effect of different N sources on biomass accumulation, are poorly understood (98).

Nitrogen Effects on Shade Tolerance

Numerous studies have investigated the effect of N on A since N is a major component of photosynthetic enzymes (48, 135, 147), and because N is a major determinant of plant assimilating area (18, 48, 103, 135, 147), and canopy architecture (28). Increasing A to improve crop yields can only be attained through increased N inputs (16, 20, 96). Nitrogen-stressed leaves had lower lamina N concentrations (162), A (94), SLD, and chlorophyll concentrations (94) than plants receiving optimal N levels. Thus, in areas where plants are grown under N stress, plants with a high N use efficiency (NUE; mg CO₂ fixed per mg lamina N content) may have a competitive advantage over plants with a low NUE.
An interaction between PPF and N has been well documented for several plant species (39). Plants grown in full sunlight utilized more N than shade-grown plants (78) due to the higher growth rates observed for plants grown in full sunlight (10, 65). Corre (39), working with one sun-adapted and two shade-adapted plants, found lower relative growth rates when the plants were grown in high PPF and low N than when the plants were grown in low PPF and low N. The differential utilization of N, depending on incident PPF, may thus play a contributing role in the shade-tolerance of some plants (39).

Lamina N content and A were positively related for several plant species (60) with some exceptions (39, 70, 103). High lamina N concentrations improved stomatal CO₂ (16, 67, 81, 94) and water conductance (43, 67, 103, 134), WUE (16), and A:E ratios (69) for several plants. Under low lamina N concentrations Rubisco was preferentially reduced over other lamina protein sources, which was reflected by reduced A for several plant species (26, 49, 100, 135, 145). In spinach laminas with high N concentrations had greater Rubisco activity:electron transport ratios than N-deficient leaves (49), indicating the greater allocation of N toward Rubisco when N resources were ample.

Nitrogen contributed to the acclimation of plants to high PPFs (57, 114). Shade plants may be less effective in N utilization than sun plants because of an increased investment in lamina compounds other than Rubisco (46, 147, 161). On the other hand, lower
respiratory and maintenance costs for shade plants may increase the NUE at low PPFs. Determinations of A on a lamina weight basis, or N content basis would measure lamina productivity based on plant input costs, which are usually lower (in the form of decreased SLD and N content) for shade- than for sun-grown leaves (65).

Gas Exchange of Sun-adapted Plants Grown in the Shade

Haverkort and Harris (72) found a positive relationship between intercepted PPF and tuber yield in potato. The same relationship between intercepted PPF and sink growth was found for willow tree, until leaf fall occurred (24). Sun-grown soybean leaves had greater A and became light saturated at higher PPF than shade-grown leaves (19). The greater A for sun- than for shade-grown soybean leaves was attributed to greater Rubisco activity and to a greater lamina thickness for the sun leaves (19). Rubisco is considered an important regulator in the photosynthetic activity of plants, based on the strong relationship between Rubisco activity and A (10, 19, 48, 56, 121, 122, 123, 150, 175).

Gas Exchange of Shade-adapted Plants Grown in the Shade

Light saturation for maximum A and CO$_2$ compensation points are lower for shade than for sun-grown plants (15). At limiting PPFs, shade plants had a greater photosynthetic efficiency (moles CO$_2$ fixed per moles of photons absorbed) than sun plants (13, 77). This may
be a consequence of shade-grown plants investing an increased proportion of reserve assimilates toward the maintenance of assimilating tissue (13, 61, 161). Increased quantum yields and low light compensations may be good indicators of shade adaptation (54, 55, 61).

Moderate shading (50% full sunlight) for Amorphophalus (Araceae) resulted in higher A, lower respiration, and higher yields (102) than for full sun-grown plants. Shading greater than 50% sunlight resulted in lower yields than for plants grown in full sunlight. However, the effect of higher shading levels on A was confounded by lamina age. Higher or equal A when grown under lower PPF was also recorded for Colocasia, cocoyam (143), and for other shade species (55, 77, 99). These results indicate that tolerance to grow in the shade may involve adaptations in the photosynthetic activity of shade-adapted plants (51, 102, 143).

The shade tolerance observed for some plants has been attributed to lower respiratory costs (152); lower structural support costs (10, 65); lower lamina N contents (26, 65); improved light harvesting through modifications of leaf surface areas (92); and greater light interception through increased assimilating surface area (10, 13). In addition, shade-adapted plants may be able to exploit sunflecks (29, 30) (short duration high PPF rays of direct sunlight) to improve net diurnal CO2 assimilation rates under conditions of limited radiant energy (117-120). Shade plants
exploited sunflecks by increasing the speed of stomatal opening and closing in response to sunflecks (30, 31, 35, 80, 81, 120, 148, 174), by maintaining a high-steady state of photosynthetic induction (86, 87, 88, 89), and possibly by controlling A through a light-modulated inhibitor of Rubisco catalysis (146). Several shade-adapted plants were more efficient than sun plants in their ability to increase A in response to sunflecks (61, 80, 108, 147).
INTRODUCTION

Since cocoyam has been identified as a shade tolerant crop (22, 110), the potential exists to utilize it as an understory crop in polyculture or agroforestry production systems (79). Multistory polyculture systems can lead to maximization of light interception and resource utilization. Information on cocoyam growth, ontogeny, phenology, and dry matter partitioning patterns under different photosynthetic photon flux (PPF) levels may assist in designing such systems. Field studies with cocoyam or related edible aroids have demonstrated a steady increase in foliage production during the first 5 months of growth (45, 52, 111, 157). Maximum total biomass production was achieved between 6 and 9 months after planting, followed by a continued accumulation of photosynthates into corms and cormels (45, 111, 156, 157). Depending on environmental conditions, corm and cormel biomass continued to increase until a plateau was reached by 7 to 10 months after planting (45, 111, 156, 157). Positive correlations between lamina area and corm dry weight and also between plant height and corm dry weight have been suggested by some studies (45, 157). Caesar (22) observed an increase in biomass when cocoyam was grown in 20% sunlight (PPF approximately 300 μmol m⁻²
sec\(^{-1}\)), compared to plants grown in 100% sunlight. This was attributed to increased petiole length and lamina area per plant.

The purpose of this study was to conduct a growth analysis of cocoyam under three PPF levels, and to relate several growth parameters to light intensity during plant development.

**Materials and Methods**

In three separate trials, cocoyam cv. South Dade White was grown in 100, 50, or 30% sunlight. Expts. 1 and 2 began 1 June 1988 and Expt. 3 began 28 Dec. 1988. Expts. 1 and 2 were concluded 16 Nov. 1988 and Expt. 3 on 4 July 1989. Shade treatments were provided by 3 x 3 x 1.5-m cages covered with woven polyethylene fabric.

Experiment 1 was designed to compare plant growth in 100% and 30% sunlight. Propagules, approximately 300 g, consisting of the top portion of main corms selected from a recently harvested commercial field, were potted in 1:1 peat-sand (by volume) in 7.5-liter containers. Plants were irrigated daily or every other day to maintain the growing media near container capacity and fertilized twice weekly with 475 ppm N, 104 ppm P, and 192 ppm K, and micronutrients in the irrigation water. Beginning 75 days after planting (DAP), three monthly determinations were made of lamina length along the mid-rib section, maximum lamina width, lamina area [determined with a LI-COR LI-3000 leaf area meter (LI-
COR Inc., Lincoln, Nebraska), petiole length and number, stem diameter at the soil surface, as well as fresh weights of laminas, petioles, and corms. The petioles consisted of the stem tissue which arose from the underground corm and came in contact with the leaf lamina. Each monthly harvest consisted of 16 whole plants (4 plants per replication) for each shade treatment. Determinations at each sampling date were made from all plant parts taken from each separate plant. Only photosynthetically-active green tissue (lamina and petioles) was harvested from the foliage to facilitate growth analysis determinations. Tissue samples were oven-dried at 80°C for 72 hr prior to dry weight determinations.

The following growth parameters were calculated according to Hunt (76): tops:corm (main corm plus cormels) ratio (dry weight basis), specific leaf density (SLD) (lamina dry weight divided by lamina area), specific leaf area (SLA) (the inverse of SLD) (10), leaf area index (LAI), crop growth rate (CGR), net assimilation rate (NAR) (net gain in weight over time per unit lamina area) (76, 172), and leaf area duration (LAD) (leaf area index integrated over time, which is an indication of duration and extent of photosynthetic assimilation area). In previous studies equations were developed for estimating lamina area from measurements of lamina length and width (27, 52, 151, 170). In the present study, we devised a similar equation for the cultivar
investigated to allow future non-destructive lamina area determinations.

For Expts. 2 and 3, cultivar, propagule size, container size, soil mixture, fertilization, and irrigation were similar to that described for Expt. 1. However, in these experiments, plants were grown in 100, 50 or 30% sunlight, and determinations began 60 DAP. In Expts. 2 and 3, monthly non-destructive determinations of petiole length and number, lamina length and width, and stem diameter at the soil surface were made over a 4 month period. Lamina area, in these experiments, was calculated on each sampling date based on the equation developed in Expt. 1. In Expt. 3, plants were harvested at the end of the experimental period and lamina, petiole, and corm fresh and dry weights were determined.

Each experiment was a randomized complete block design with four blocks per shading level. Each block consisted of a shade cage with each cage containing 8 or 12 pots with one plant per pot. Pots were distanced 35 cm from each other to prevent competition for light among plants. In Expts. 2 and 3, data were analyzed by orthogonal contrast analysis (158). Counted data were transformed with the formula $SQT(x + 0.5)$. Results presented are from nontransformed data.
Results

The linear equation: lamina area = 69.27 + 0.87(lamina length x lamina width); \( r = 0.96; N = 233; P<0.01 \), facilitated subsequent nondestructive determinations of lamina area in Expts. 2 and 3. A linear relationship (\( P<0.01 \)) was also found between lamina area and petiole length [\( \log(\text{lamina area}) = 1.03 + 1.01(\log(\text{petiole length})) \); \( r = 0.73; N = 233 \)], and between lamina area and lamina dry weight (LDW) [\( \text{lamina area} = 190.42(\text{LDW}) + 911.11; r = 0.46; N = 96 \)]. Linear relationships (\( P<0.01, r<0.50 \)) were also found between (a) lamina area per plant, foliage fresh weight, and petiole length and (b) corm fresh weight (data not shown).

Cocoyam grown in 30% sunlight had greater foliage dry matter and lamina area than sun-grown (100% sunlight) plants (Tables 3.1 and 3.2). Increased petiole lengths and numbers and stem diameters for shaded plants (Table 3.1) resulted in increased top:corm ratios in Expts. 1 and 3 (Table 3.2). In Expt. 1 top:corm ratios were greater for shade plants than for sun plants beginning 75 DAP (data not shown). Top:corm ratios by 135 DAP were 0.45 and 0.19 for shade and sun plants, respectively. Linear relationships were found between shade level and petiole length 120 DAP; between shade level and petiole number 90 DAP; and between shade level and lamina area per plant 90 DAP (Fig. 3.1).
Shaded plants had greater dry matter per plant than sun plants beginning 105 DAP (Fig. 3.2). In Expt. 3 shade plants (30% and 50% sunlight) also had greater dry matter per plant than sun plants. Dry matter per plant in Expt. 3 by 210 DAP was 143 g and 106 g for shade and sun plants, respectively. Shade plants were more succulent with a water content of 89% versus 86% for sun plants in Expts. 1 and 3.

Shade plants had a greater leaf area index, specific leaf area, crop growth rate, and leaf area duration, than sun plants (Fig. 3.3 and Table 3.3). Specific leaf density in Expts. 1 and 3, was greater (P<0.01) for sun than for shade plants, averaging 4.5 and 3.6 mg cm\(^{-2}\), respectively. Net assimilation rate was also higher for sun plants (Table 3.3).

In Expt. 1, corm fresh weight was similar between treatments 75 DAP (data not shown). Corm fresh weight increased, however, to 490 g for shade plants compared to 465 g for sun plants 135 DAP. No significant difference in corm dry weight was detected between treatments over the length of the experiment (Table 3.2). However, corm dry weight for shade plants in Expt. 1, tended to be greater than for sun plants 135 DAP. Corm dry weight 135 DAP was 73 and 80 g for sun and shade plants, respectively. Corm dry weight in Expt. 3 was greater for shade plants (30% and 50% sunlight) than for sun plants by harvest time (Table 3.2).
Discussion

Cocoyam responded to increased shading (30% and 50% sunlight) with an increased assimilation area, which resulted in greater biomass production and increased crop growth rates. Shade-grown cocoyam also had a greater specific leaf area (Fig. 3.3B), and greater lamina-petiole weight ratios (Table 3.2), the latter determined by the fraction of total plant dry matter allocated to assimilating material (10). Similar changes in specific leaf area have been reported for Malus (6), Fragaria (25), Prunus (173), and several other plant species (10, 154). Decreased lamina thickness with increased shade has been attributed to less developed palisade and spongy mesophyll parenchyma in leaves of Malus (6), Atriplex (101), and other higher plant species (10). Among aroid species, Alocasia exhibited increased specific leaf area with decreased PPF (66), whereas Schaffer and O'Hair (143) found decreased Xanthosoma specific leaf area with decreased PPF. However, their shaded treatment consisted of 60% sunlight, compared to 30% sunlight in the present research. In the present study, lamina area increased spatially and temporally, through increased leaf area index, and through an increased maintenance of lamina area through time, shown by higher leaf area duration. Sun-grown (100% sunlight) plants, conversely, had greater specific leaf densities and net assimilation rates than shade plants, showing a greater photosynthetic productivity on a
leaf area basis than shade plants (10). The greater productivity of photosynthates on a leaf area basis for sun plants is attributable to the greater PPF levels incident on sun than in the shade-grown plants.

Shaded cocoyam partitioned relatively more photosynthates to the foliage than to the storage organs compared to sun-grown plants. Therefore shade plants had a greater shoot:storage organ ratio than sun plants. However, by harvest time, shade plants had a greater whole-plant and storage organ dry weight (yield) than sun plants (Fig. 3.2 and Table 3.2). This was presumably due to the greater assimilation rate on a whole plant basis for shade plants resulting from the greater lamina area.

In Expt. 3, corm dry weight increased with shading treatment (30% and 50% sunlight). Caesar (22) found similar corm dry weights in shaded cocoyam compared to sun plants, and lower cormel dry weights with increased shade. However, in that study, cocoyam was grown in 20% sunlight (PPF = 300 µmol m⁻² sec⁻¹), compared to 30% sunlight (maximum PPF = 650 µmol m⁻² sec⁻¹) in the present study. Likewise, in Amorphophallus, a related edible aroid, greater corm dry weight was obtained for plants grown in 40 and 50% sunlight, with decreased yields in 30% sunlight (102).

Linear relationships between lamina area and lamina linear dimensions, and also between lamina area and lamina dry weight for Xanthosoma (27, 170) and Colocasia (52, 151), were also found in
this study. In addition, a linear relationship was found between lamina area and petiole length. These relationships simplify the estimation of lamina area and allow for the prediction of light interception and transpiration rates under field conditions (151). Earlier measurements for Xanthosoma (45, 157), Amorphophallus (102), and Colocasia (129), suggested a relationship between lamina area and corm dry weight. Our results corroborated these relationships, although our coefficients of determination were low (r<0.50), perhaps attributable to the plant to plant variation and to the small sample size employed in the analysis. The linear relationships observed between foliar growth (petiole length and number and lamina area) and light interception during growth (Fig. 3.1) could facilitate the design of planting patterns in polycultures (21). Planting patterns can be manipulated to help synchronize percentage light interception (or percentage ground cover) with the potential productivity of the agroecosystem (63).

The potential to increase cocoyam productivity in polyculture systems may be exploited through the plant's ability to utilize, with a high degree of efficiency, the lower PPF levels found in typical understory situations. Management and crop improvement techniques could be devised to manipulate cocoyam canopy architecture, leaf production, planting distance, planting pattern, and timing of operations. Such changes should improve
resource utilization (nutrients, light, and water) in tropical agroecosystems by improving light interception.
Table 3.1. Effect of shade on petiole length, petiole number, lamina area per plant, and stem diameter in cocoyam (*Xanthosoma sagittifolium*) in Expts. 1-3.

<table>
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<th>Sunlight level (% daylight)</th>
<th>Petiole length (cm)</th>
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<td>3.4, 2.6</td>
<td>2801, 1523</td>
<td>450, 391</td>
</tr>
</tbody>
</table>

Shade significance

*Mean of 48 measurements taken at 75, 105 and 135 days after planting (DAP).

YPooled mean for 32 and 16 plants per treatment in Expts. 2 and 3 respectively.

**Determinations were made only for plants growing in 30% and 100% daylight.

WSignificance determined by ANOVA's F test (P<0.05).

VSignificance determined by orthogonal contrast analysis (P<0.05).
Table 3.2. Effect of shade on leaf, petiole, and corm dry weight (g), and top:corm ratio (dry wt.) in cocoyam (*Xanthosoma sagittifolium*) in Expts. 1 and 3.

<table>
<thead>
<tr>
<th>Sunlight level (%) daylight</th>
<th>Leaf</th>
<th>Petiole</th>
<th>Corm</th>
<th>Top:corm ratio^2</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td><em>γ</em></td>
<td><em>γ</em></td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>50</td>
<td><em>γ</em></td>
<td><em>γ</em></td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>30</td>
<td>10.8</td>
<td>6.2</td>
<td>16.2</td>
<td>17.4</td>
</tr>
<tr>
<td>Shade significance</td>
<td><strong>v</strong></td>
<td><strong>u</strong></td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Shade linear</td>
<td>--</td>
<td><strong>u</strong></td>
<td>--</td>
<td>**</td>
</tr>
<tr>
<td>Shade quadratic</td>
<td>--</td>
<td>NS</td>
<td>--</td>
<td>NS</td>
</tr>
</tbody>
</table>

^2Main corm plus cormels.
γMean of 48 measurements taken at 75, 105 and 135 days after planting (DAP).
XMean measurement of eight plants per treatment 210 days after planting.
Determinations were made only for plants growing in 30% and 100% daylight.
VSignificance determined by ANOVA's F test (P<0.05).
USignificance determined by orthogonal contrast analysis (P<0.05).
Table 3.3. Effect of shade on growth of cocoyam (*Xanthosoma sagittifolium*) in Expt. 1.

<table>
<thead>
<tr>
<th>Sunlight level (% daylight)</th>
<th>Crop growth rate (g m(^{-2}) day(^{-1}))</th>
<th>Net assimilation rate (mg m(^{-2}) day(^{-1}))</th>
<th>Leaf area duration (m(^2) day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>1.4(^{\text{y}})</td>
<td>62.3</td>
<td>342</td>
</tr>
<tr>
<td>30</td>
<td>2.1</td>
<td>37.4</td>
<td>867</td>
</tr>
</tbody>
</table>

Significance:
Shade

\(^{\text{y}}\)Means of 32 measurements taken at 105 and 135 DAP.
\(^{\text{x}}\), **, significant at 10% and 5% level, respectively.
Figure 3.1. Mean effect of shade on petiole length 120 days after planting (DAP) (A); petiole number 90 DAP (B); and lamina area per plant 90 DAP (C) of cocoyam (Xanthosoma sagittifolium) (Expt. 2). Each point represents the mean of 40 determinations. Vertical bars represent ±SE, n=40. In all cases SE bars were smaller than the symbols. Lines were fit by regression (N=120).
\[ Y = 80.5 - 51.5X \quad r = 0.76 \quad P < 0.01 \]

\[ Y = 2.1 - 0.6X \quad r = 0.41 \quad P < 0.01 \]

\[ Y = 2.63 - 2.03X \quad r = 0.67 \quad P < 0.01 \]
Figure 3.2. Effect of shade on total plant dry matter of cocoyam (*Xanthosoma sagittifolium*) (Expt. 1). Each point represents the mean of 16 determinations. Vertical bars represent ±SE, n=16. In most cases SE bars were smaller than the symbols. The lines were fit by regression (N=48) using the following equations: 100% daylight: \( Y = 7.0X - 10.9 \), \( r = 0.77 \); 30% daylight: \( Y = 1.1X - 34.7 \), \( r = 0.72 \).
120
100% DAYLIGHT

30% DAYLIGHT

90
60
30

135
105
75

DAYS AFTER PLANTING

TOTAL BIOMASS (g)
Figure 3.3. Effect of shade on leaf area index (LAI) (A); and specific leaf area (SLA) (B) of cocoyam (*Xanthosoma sagittifolium*) (Expt. 1). Each point represents the mean of 16 determinations, calculated at 75, 105 and 135 days after planting (DAP). Vertical bars represent ±SE, n=4. In most cases SE bars were smaller than the symbols. Lines were fit by regression (N=48) using the following equations: LAI, sun: $Y = 4.5^{-1}(DAP) - 2.2^{-3}(DAP)^2 - 20.9$, $r = 0.82$; LAI, shade: $Y = 1.1(DAP) - 5.2^{-3}(DAP)^2 - 48.2$, $r = 0.81$; SLA, sun: $Y = 49.2 - 2.8^{-1}(DAP)$, $r = 0.92$; SLA, shade: $Y = 120.4 - 7.3^{-1}(DAP)$, $r = 0.92$. 
CHAPTER 4
DEVELOPMENTAL LIGHT ENVIRONMENT ON NET GAS EXCHANGE OF COCOYAM

Introduction

Cocoyam has been identified as shade tolerant (22, 143). Therefore, the potential exists for utilization of this corm-producing species as an understory crop in polyculture systems. The effect of shading on photosynthetic activity of cocoyam needs to be elucidated to identify optimal photosynthetic photon fluxes (PPF) for maximum yields of this crop. Other aroids species grown in moderate shade have equal (102), greater (143), or lower (152) net CO₂ assimilation (A) rates than sun-grown plants. Schaffer and O'Hair (143) observed that 60% sunlight-grown cocoyam had greater A than 100% sunlight-grown plants. However, their study focused on gas exchange of cocoyam grown at PPFs above the light saturation point for A (>750 μmol m⁻² s⁻¹). Diurnal and seasonal gas exchange data are lacking for cocoyam growing at PPFs below the light saturation point.

Lamina nitrogen (N) and chlorophyll concentrations can affect A (59). Chlorophyll is important for light harvesting while N is an important component of several photosynthetic enzymes (47, 59). To our knowledge no information exists which evaluates the role of lamina chlorophyll and N on shade acclimation of cocoyam.
Previous studies have shown that biomass accumulation and yield of cocoyam is greater for shade- than sun-grown plants (168). The purpose of this study was to determine if the shade-tolerance of cocoyam is related to gas exchange characteristics and to lamina N and chlorophyll contents of this crop species.

**Materials and Methods**

In four separate experiments, ‘South Dade White’ cocoyam was grown in 100%, 50%, or 30% sunlight (maximum PPF as determined on a cloudless day at 1300 hr with a LI-COR 190SA quantum sensor was 2200, 1100, and 650 μmol m⁻² s⁻¹, respectively). Mean integrated daily PPFs for the 100% sunlight treatments were 35.0 mol m⁻² day⁻¹ for Expts. 1 and 2, and 37.4 mol m⁻² day⁻¹ for Expts. 3 and 4 as determined with a pyranometer (Model PSP, Eppley Laboratory, Inc., Newport, Rhode Island). Shade treatments were provided by covering 3 x 3 x 1.5-m cages with neutral woven polyethylene fabric of different mesh sizes.

Propagules consisting of the top portion of main corms were potted in 1:1 peat:sand (v:v) in 7.5-liter containers. Plants were irrigated daily or every other day, as required, and fertilized twice weekly with 475 ppm N, 104 ppm P, and 192 ppm K, and micronutrients in the irrigation solution. Plants for Expt. 1 were grown in 100% or 30% sunlight and plants for Expts. 2-4, were
grown in 100%, 50%, or 30% sunlight. The first two experiments began in June 1988 and the last two began in late Dec. 1988.

Net CO₂ assimilation, transpiration (E), stomatal conductance for CO₂ (gₛ), and substomatal CO₂ concentration (Cᵢ) were determined in the field by enclosing a portion of the lamina in a Parkinson leaf chamber, connected to a portable CO₂ and water vapor exchange analyser (LCA-2, Analytical Development Co., Hoddesdon, Herts, U.K.), as described by Schaffer and O'Hair (143). Outside air containing 340 ± 10 μmol CO₂ mol⁻¹ and dried to a constant 20% RH, was pumped into the chamber at a rate of 0.375 liters min⁻¹. A preliminary analysis of light response for A of mature leaves showed that the saturating PPF for maximum A of cocoyam was >750 μmol m⁻² s⁻¹ (143). Therefore, all measurements were made at PPFs > 800 μmol m⁻² s⁻¹ using sunlight as the source. All measurements were made on cloudless days between 0930 hr and 1130 hr to minimize diurnal effects on gas exchange. The experimental design was a randomized complete block with four shade cages (replications) per treatment and four single-plant samples per replication. Gas exchange was determined on the youngest fully expanded leaf of plants in each treatment. Data were analyzed by ANOVA and by orthogonal contrast analysis. Gas exchange determinations within and between experiments were tested for homogeneity of slopes and intercepts. Gas exchange
determinations from all experiments were pooled for statistical analysis if slopes and intercepts were homogeneous.

Diurnal patterns of $A$, $g_s$, $Ci$, $E$, WUE, and lamina temperature were determined in the field 95 and 130 days after planting (DAP) for plants grown in 100% and 30% sunlight in Expt. 4. Diurnal gas exchange determination dates were separated by about one month to identify effects of phenological changes (vegetative stage 95 DAP and cormel initiation 130 DAP) on patterns of diurnal gas exchange. Shade-grown plants were removed from the shade and allowed to equilibrate to ambient light for five minutes prior to gas exchange determinations. A stepwise regression analysis was performed to evaluate the contribution of diurnal PPF, relative humidity and lamina temperature to changes in net gas exchange.

Lamina N and chlorophyll concentrations were determined 140 DAP and again at harvest time in Expt. 3. Samples for N and chlorophyll determinations consisted of the oldest healthy fully expanded lamina of a plant, one sample per plant. Chlorophyll concentrations were determined as described by Marini and Marini (97) and Schaffer and Gaye (144). For N analysis, samples were digested using a modification of the aluminum block procedure of Gallaher et al. (62). The sample weight was 0.3 g, the catalyst used was 3.2 g of 9:1 $K_2SO_4$:$CuSO_4$, and digestion was conducted for 4 hr at 400C using 10 ml $H_2SO_4$ and 2 ml $H_2O_2$. Ammonia
concentration in the digestate was determined by semiautomated colorimetry (71) with a Technichron Autoanalyzer-II. Values for N concentration include organic and inorganic N.

Results

The effects of shading on net gas exchange of cocoyam was similar in each experiment (slopes of shade vs. gas exchange were homogeneous). Therefore, data from each experiment were pooled to determine effects of shade on net gas exchange. Net CO₂ assimilation rates were 8.4, 8.8, and 8.6 μmol CO₂ m⁻² s⁻¹ for the basal section, mid-section, and tip, respectively, of fully expanded laminas. Similarly, laminas of about the same age on the same plant had similar A rates (data not shown). In saturating light, A was greater for 100% sunlight than for shade-grown (30 or 50% sunlight) cocoyam (Table 4.1). Transpiration was similar among shade treatments, with mean E values of 8.1 mmol H₂O m⁻² s⁻¹. Water use efficiency increased with increased PPF during growth and Ci increased with increasing shade (Table 4.1).

Ninety five days after planting, A peaked at 1000 hr and then tended to decrease slightly until 1600 hr (Fig. 4.1A). Shade plants had lower A than 100% sunlight plants but the diurnal pattern was similar for plants grown in both PPF levels (Fig. 4.1A). Transpiration showed a similar diurnal pattern as A, with similar E values during the day for plants in both the 30% and
100% sunlight treatments (Fig. 4.1D). Although correlation coefficients were low, A was positively correlated with diurnal PPF \( (A = 2.83^{-3}(PPF) + 1.68; \ r = 0.36; \ P<0.01) \) and also with diurnal relative humidity \( (r = 0.17; \ P<0.01) \). Stomatal conductance decreased throughout the day in relation to decreased relative humidity \( (g_s = 6.32(RH) - 60.03; \ r = 0.97; \ P<0.05) \), and \( g_s \) decreased as vapor pressure deficit (VPD) increased \( (g_s = -71.61(VPD) + 456.20; \ r = 0.68) \). Relative humidity and PPF contributed 16% and 38%, respectively, to the variation in \( E \) throughout the day \( (E = 1.6^{-3}(PPF) + 9.8^{-2}(RH) + 1.25; \ P<0.05) \).

Nitrogen concentrations on a dry weight basis, increased with increased PPF 140 and 180 DAP (Fig. 4.2A). Nitrogen contents determined on lamina area (Fig. 4.2B) and chlorophyll bases increased with increased PPF, 140 DAP. Nitrogen : chlorophyll ratios were 3.7 for 30%, 4.2 for 50%, and 4.6 for 100% sunlight-grown plants. No significant differences were found in lamina chlorophyll contents between shade treatments 140 or 180 DAP; chlorophyll \((a + b)\) contents ranged from 0.39 to 0.42 mg cm\(^{-2}\). No differences in chla : chlb ratios were observed between treatments with ratios ranging from 1.4 to 1.8 when determined on both dry weight and lamina area bases. There was a positive relationship between N concentration (dry weight basis) and chlorophyll concentration (chlorophylls a and b, fresh weight basis) 180 DAP \( (N = 7.73(CHL) + 258.56; \ r = 0.49; \ P<0.05) \). Specific leaf density
was greater for 100% than for 30% sunlight-grown plants 140 and 180 DAP (Fig. 4.3).

Discussion

Although cocoyam has been reported to be shade-tolerant (22, 143, 168), it responded to increased PPF during plant development with increased A. Despite lower A, shade-grown plants had greater foliage and storage organ biomass (168) than full sun-grown plants. The increased leaf area in the shade resulted in increased photosynthate production and partitioning to underground storage organs.

Shaded cocoyam had greater yields than full sun-grown cocoyam (168). In the present experiment plants grown in full sun had both greater lamina N contents (on an area and chlorophyll bases) and A. Therefore, lamina N contents may play a role in the adaptation of cocoyam to varying developmental PPF as shown for several plant species (68, 100, 135, 147, 152, 162, 163, 165). Increased A with increasing developmental PPF has been reported for other plant species (54, 81, 82, 106, 161) including related aroids (152). Lower respiration rates for several shade-grown plants than for plants grown in direct sunlight (10, 65, 102, 152) may be a compensation for decreased A in the shade, resulting in an overall increased net biomass accumulation for shade-adapted plants grown in low PPFs (10). In the present
experiment the lower lamina dry weight on a lamina area basis for shade than for sun plants (Fig. 4.3) indicated that shade plants had lower respiration rates than 100% sunlight-grown plants (10, 65).

The PPF at which A reached its maximum value was similar to that reported for Colocasia (143, 152) but greater than that observed for Alocasia, another aroid (152). Alocasia is adapted to growing in deep-shaded forest understories (11), while both cocoyam and Colocasia, are often grown in monocultures which allow for greater light absorption by individual plants (143). The high gs (>200 mmol CO₂ m⁻² s⁻¹) in the present study indicate that gs was not limiting photosynthetic activity (86). The greater WUE obtained for 100% than for 30% sunlight-grown plants indicates that plants grown in full sun were better adapted to absorb and utilize the high PPFs (> 800 μmol m⁻² s⁻¹) under which the gas exchange measurements were taken.

The trend toward a diurnal decline in A observed at midday may be attributable to stomatal closure due to water and/or heat stress (140), or to inherent diurnal behavior (89). The diurnal decline in A coincided with a depletion of CO₂ in substomatal cavities. The depletion of CO₂ in substomatal cavities was greater for plants grown in full sun (Table 4.1, Fig. 4.1C) due to their greater photosynthetic activity compared to shade-grown plants. The declining trend in A from midday corresponded with
decreased $g_s$, E, WUE, and relative humidity, and increased vapor pressure deficit. Stomatal conductance for CO$_2$ decreased throughout the day in relation to increased vapor pressure deficit, possibly due to stomatal closure in response to increased vapor pressure deficit (73, 90, 109, 139).

The data obtained in this study indicate that gas exchange and N of cocoyam is affected by incident PPF during plant growth. The greater A (on a leaf area basis) for 100% sunlight-grown cocoyam may partially compensate for the lower leaf area for the 100% sunlight- compared to shade-grown plants (168). This may explain cocoyam's ability to grow and produce marketable yields in a wide range of light environments. Thus, cultural practices such as cropping system selection, planting patterns, and N fertilization can be devised for cocoyam to improve interception and marketable yields.
Table 4.1. Effect of developmental light environment on net CO₂ assimilation (A), stomatal conductance for CO₂ (gs), substomatal CO₂ concentration (Ci), and water use efficiency (WUE) of cocoyam determined under saturating PPF (800 μmol m⁻² s⁻¹).

<table>
<thead>
<tr>
<th>Sunlight (%)</th>
<th>A (μmol CO₂ m⁻² s⁻¹)</th>
<th>gs (mmol CO₂ m⁻² s⁻¹)</th>
<th>Ci (μmol CO₂ mol⁻¹)</th>
<th>WUE (mmol CO₂ mmol H₂O⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>8.82</td>
<td>237</td>
<td>263</td>
<td>1.2</td>
</tr>
<tr>
<td>50</td>
<td>8.1</td>
<td>231</td>
<td>269</td>
<td>1.1</td>
</tr>
<tr>
<td>30</td>
<td>6.7</td>
<td>210</td>
<td>273</td>
<td>0.9</td>
</tr>
</tbody>
</table>

Orthogonal contrasts

<table>
<thead>
<tr>
<th>Shade linear</th>
<th>*</th>
<th>NS</th>
<th>*</th>
<th>*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shade quadratic</td>
<td>NS</td>
<td>NS</td>
<td>*</td>
<td>NS</td>
</tr>
</tbody>
</table>

²Determinations for all experiments were pooled since slopes and intercepts were homogeneous.

NS, *, non-significant and significant (P<0.05), respectively.

Significance determined by orthogonal contrast analysis.
Figure 4.1. Diurnal net CO$_2$ assimilation (A), stomatal conductance for CO$_2$ (B), substomatal CO$_2$ concentration (C), transpiration (D), water use efficiency (E), and vapor pressure deficit (F) of cocoyam (*Xanthosoma sagittifolium*) grown in 100% and 30% sunlight. Each point represents the mean of 4 replications determined on 5 Apr. 1989 (95 days after planting). Vertical bars represent ± SE. In some cases SE bars were smaller than the symbols.
Figure 4.2. Effect of developmental light environment (% sunlight) on lamina nitrogen concentration on a lamina dry weight (A), and area basis (140 days after planting) (B) of cocoyam (*Xanthosoma sagittifolium*) in Expt. 3. Each point represents the mean of 10 replications 140 days after planting, and of 6 replications 210 days after planting. Vertical bars represent ± SE. In most cases SE bars were smaller than the symbols.
Figure 4.3. Effect of developmental light environment (% sunlight) on specific leaf density of cocoyam (*Xanthosoma sagittifolium*) in Expt. 3. Each point represents the mean of 10 replications 140 days after planting. Vertical bars represent ± SE. In most cases SE bars were smaller than the symbols.
CHAPTER 5
EFFECTS OF SHADE AND NITROGEN ON GAS EXCHANGE AND GROWTH OF COCOYAM

Introduction

Lamina nitrogen (N) concentration affects plant light utilization and absorption since N is a major constituent of assimilating tissues (91, 103, 147, 153), and is a component of ribulose bisphosphate carboxylase, an important regulator of photosynthetic activity (9, 56, 91, 160). Lamina N concentration has been positively correlated with net CO₂ assimilation (A) for several plant species (47, 60, 153, 163), including aroids such as Colocasia esculenta (152) and Alocasia macrorrhiza (147, 152). Nitrogen allocation appears to be involved in acclimation of plants to high photosynthetic photon fluxes (PPF) (57, 78, 114).

The mechanism by which N is allocated within a leaf varies among plant species (47) and is affected by environmental factors such as temperature, incident PPF, and soil fertility (60). Little is known about the interaction between N and PPF in the Araceae. Cocoyam, an important energy-rich food source in tropical areas, has been identified as shade tolerant with respect to growth (168) and photosynthetic activity (143). The perennial tropical herb, produces edible rhizome-like cormels which arise from the base of the corm below the soil surface. Sims and Pearcy (152) reported that N content on a lamina area basis increased
with increasing PPF for *Colocasia* and *Alocasia*, two close relatives of cocoyam. However, in their study, plants in the high PPF treatments were given almost twice as much N as plants in the shade treatments, introducing lamina N concentration as a possible confounding factor. Chow et al. (34) showed that *Alocasia*, which normally grows in deep-shade, can adapt to growth in a high light environment with respect to high A rates when given an 'adequate' N supply. However, that study also lacked N-free fertilizer controls. Since N deficits are common and N-fertilizer costs are often prohibitive in tropical agroecosystems, where cocoyam is often grown as an intercrop, information is needed to evaluate cocoyam N utilization under different environmental conditions. Such baseline information can help improve the efficiency of N utilization by cocoyam in agroecosystems where N is a limiting resource. The purpose of the present study was to determine the effects of PPF and N fertilization during plant development on net gas exchange and growth of cocoyam.

**Materials and Methods**

Cocoyam cv. South Dade White was grown in 100%, 50%, or 30% sunlight (maximum PPF as determined on a cloudless day at 1300 hr with a LI-COR 190SA quantum sensor was 2200, 1100, and 650 μmol m⁻² s⁻¹, respectively) as described by Valenzuela, et al. (168). Mean integrated daily PPF for the 100% sunlight treatment was 37.4
mol m\(^{-2}\) day\(^{-1}\) as determined by a pyranometer (Model PSP, Eppley Laboratory, Inc., Newport, Rhode Island). Shade treatments were provided by 3 x 3 x 1.5 m cages covered with neutral woven polyethylene fabric of different mesh sizes. Propagules, approximately 300 g, consisting of the top portion of main corms were potted in 1:1 peat:sand (by volume) in 7.5-liter containers. The corms were potted 28 Dec. 1988 and the experiment was concluded on 4 July 1989. Plants were irrigated daily. The experimental design was a split-plot randomized block with four replications and four single-plant samples per replication. Shade treatments were the main plots and N treatments were the subplots. Each block consisted of a 'shade' cage (4 cages or replications per treatment) containing both N-fertilized plants (+N plants) and plants fertilized with a N-free nutrient solution (-N plants). Half of the plants were fertilized twice weekly with the N-free solution consisting of 178 mg MgCl\(_2\)-6H\(_2\)O, 265 mg MgSO\(_4\)-7H\(_2\)O, 165 mg K\(_2\)HPO\(_4\), 82 mg K\(_2\)HSO\(_4\), 20 mg sequestrene Fe, 7.2 mg MnCl\(_2\), 5.7 mg H\(_3\)BO\(_4\), 0.2 mg CuSO\(_4\)-5H\(_2\)O, 0.4 mg ZnSO\(_4\)-7H\(_2\)O, and 0.3 mg NaMoO\(_4\)-2H\(_2\)O per kg of nutrient solution. Nitrogen fertilized plants received 475 mg kg\(^{-1}\) N twice weekly from an ammonium nitrate solution plus the N-free solution. A chemical analysis of the growing media prior to the beginning of the experiment showed a pH of 7.5, an electrical conductivity of 50\(^{-4}\) dS m\(^{-1}\), 1 mg N, 2 mg P, 5 mg Ca, and 90 mg Cl per kg of growing medium.
Beginning 75 days after planting (DAP), four monthly determinations were made of lamina length along the mid-rib, maximum lamina width, petiole length and number, and stem diameter at the soil surface. Lamina area was determined at each sampling date from the lamina length and width, based on an equation developed previously by Valenzuela et al. (168). Plants were harvested 180 DAP and lamina, petiole, and corm fresh weights were determined. Tissue samples were then oven-dried at 80°C for 72 hours and tissue dry weights were determined.

Gas exchange determinations were determined as described previously by Schaffer and O’Hair (143) and Valenzuela et al. (169). Net CO₂ assimilation, stomatal conductance for CO₂ (gₛ), transpiration (E), and water use efficiency (WUE) were determined in the field by enclosing lamina sections in a Parkinson leaf chamber, connected to a portable CO₂ and water vapor exchange analyser (LCA-2, Analytical Development Co., Hoddesdon, Herts, U.K.). Outside air containing 340± 10 μmol CO₂ mol⁻¹ and dried to a constant 20% RH, was pumped into the chamber at a rate of 0.375 liters min⁻¹. A preliminary analysis of light response for A showed that the saturating PPF for maximum A of cocoyam was 750 μmol m⁻² s⁻¹ (data not shown). Therefore all determinations were made at PPF > 800 μmol m⁻² s⁻¹ using sunlight as the source. All determinations were made on cloudless days between 0930 hr and 1130 hr, to minimize diurnal effects on gas exchange activity.
Determinations were made on the youngest fully expanded leaves from six different plants, one leaf per plant. Lamina N and chlorophyll concentrations were determined 140 and 180 DAP. Chlorophyll concentrations were determined as described by Marini and Marini (97) and Schaffer and Gaye (144). Nitrogen, including organic and inorganic forms, was determined by a modified Kjeldahl procedure described by Valenzuela et al. (169). Data were analyzed by orthogonal contrast analysis. Slopes and intercepts of equations for N vs. growth and N vs. gas exchange were tested for homogeneity. If slopes and intercepts were homogeneous, N treatments were pooled to determine linear responses to shade.

Results

Interactions between N and shade (P<0.05) were observed for lamina area per plant (Fig. 5.1C), and petiole length (data not shown), 165 DAP; stem number at all sampling dates (data not shown); top:corm ratio; and increased corm weight from planting to harvest (increased corm weight = corm fresh weight 180 DAP - corm fresh weight at planting) (Fig. 5.2B-C). There was no significant difference on lamina area per plant between N treatments for any shade treatment 75 DAP. However, by 75 DAP, there was a tendency for lamina area per plant to be greater for +N than for -N plants when shade treatments were pooled (Fig. 5.1A). Lamina area per plant was greater for +N than for -N plants from 105 DAP until the
last sampling date 165 DAP (Fig. 5.1B), when shade treatments were pooled. Pooled lamina area per plant 105 DAP was 1,408 and 1,296 cm² for +N and -N plants, respectively. Lamina area per plant increased with increased shade at both sampling dates for both N treatments (Fig. 5.1). Stem diameter and petiole weight, length and number increased with increased shade for plants in both N treatments, and also were greater for +N than for -N plants when shade treatments were pooled 165 DAP (data not shown). Petiole number for +N plants grown in 100% sunlight decreased from 2.3 to 1.8 between 75 and 165 DAP. Petiole number, however, increased from 2.7 to 3.3 between 75 and 165 DAP for +N plants grown in 30% sunlight. Weight of leaves, increase in corm fresh weights from planting to harvest, and top:corm ratios increased with increased shade (Fig. 5.2). In addition, these growth parameters were greater for +N than for -N plants, except for the 100% sunlight plants which showed similar corm weights and top:corm ratios between N treatments (Fig. 5.2). The +N plants showed a tendency toward greater corm dry weights than -N plants for all shade treatments. When shade treatments were pooled mean corm dry weight was 112 and 103 g for the +N and -N plants, respectively.

Interactions between applied N and shade (P<0.05) were observed for E and gs 90 DAP (Fig. 5.3). Transpiration and gs were higher for -N than for +N plants only for 100% sunlight plants 90 DAP (Fig. 5.3). For the -N plants, E increased with
increased PPF 90 DAP. The \(+N\) plants had greater \(E\) for 50% and 100% than for 30% sunlight plants 90 DAP. Transpiration and \(g_s\) were higher for \(+N\) than for \(-N\) plants when all shade treatments were pooled 120 DAP. The \(+N\) plants had a mean \(E\) rate of 7.1 compared to 6.5 mmol H\(_2\)O m\(^{-2}\) s\(^{-1}\) for \(-N\) plants when shade treatments were pooled 120 DAP. The \(+N\) plants had a mean \(g_s\) of 228 compared to 186 mmol CO\(_2\) m\(^{-2}\) s\(^{-1}\) for \(-N\) plants when shade treatments were pooled 120 DAP. Transpiration and \(g_s\) 120 DAP were similar among shade treatments for both \(N\) treatments. Transpiration among \(+N\) plants 120 DAP was 7.1 and 7.5 mmol H\(_2\)O m\(^{-2}\) s\(^{-1}\) for 30% and 100% sunlight plants, respectively. Stomatal conductance for \(+N\) plants 120 DAP was 279 and 214 mmol CO\(_2\) m\(^{-2}\) s\(^{-1}\) for 30% and 100% sunlight-grown plants, respectively. There was no difference in \(A\) between \(N\) treatments for plants in all shade levels, 90 DAP (Fig. 5.4A). However, a tendency was observed for higher \(A\) for \(-N\) than for \(+N\) plants 90 DAP, with mean \(A\) of 6.5 and 6.0 \(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\), respectively, when shade treatments were pooled. Net CO\(_2\) assimilation was greater for 100% sunlight than for 30% sunlight-grown plants for both \(N\) treatments 90 DAP (Fig. 5.4A). By 120 DAP, \(A\) was higher for \(+N\) than for \(-N\) plants, for 30% and 100% sunlight plants (Fig. 5.4B). Net CO\(_2\) assimilation increased with increased PPF for plants in both \(N\) treatments 120 DAP. When \(N\) treatments were pooled, no effect of shade was observed on WUE 90 DAP (data not shown), but WUE increased with.
increasing PPF 120 DAP. Mean WUE was 1.2, 1.4 and 1.7 mmol CO$_2$
mmol H$_2$O$^{-1}$ for 30%, 50% and 100% sunlight-grown plants,
respectively, when N treatments were pooled 120 DAP. Water use
efficiency was higher for +N than for -N plants when shade
treatments were pooled 120 DAP, with values of 1.5 and 1.3 mmol
CO$_2$ mmol H$_2$O$^{-1}$, respectively.

Interactions between applied N and shade (P<0.05) were
observed for lamina N concentrations (dry weight and area bases)
(Fig. 5.5) and for chlorophyll content per plant (Fig. 5.6B).
Similar interactions were observed at both sampling dates (data
not shown). Nitrogen concentrations were higher for +N than for
-N plants only for the 100% sunlight plants and also increased
with increased PPF for both N treatments 140 DAP (Fig. 5.5) and
180 DAP (data not shown). Chlorophyll concentrations on a dry
weight basis ranged from 60 to 75 mg g$^{-1}$ and were similar between
N treatments when shade treatments were pooled 140 DAP.
Chlorophyll concentrations were greater for +N than for -N plants
only for the 30% and 50% sunlight plants, 180 DAP (Fig. 5.6A).
Chlorophyll concentrations were greater for 30% than for 100%
sunlight plants only for the +N plants, 180 DAP (Fig. 5.6A).
Chlorophyll contents on a lamina area basis were greater for +N
than for -N plants for all shade treatments. Mean chlorophyll (a
+ b) contents were 0.40 for +N plants compared to 0.33 mg cm$^{-2}$ for
the -N plants when shade treatments were pooled 180 DAP.
Chlorophyll contents on a lamina area basis were not affected by shade for both N treatments 140 or 180 DAP (data not shown). Lamina chlorophyll content per plant was greater for +N than for -N plants for all shade treatments, and increased with increased shade for both N treatments (Fig. 5.6B).

**Discussion**

Increased lamina area with increased N application rate has been documented for several plant species (18, 48, 60, 135, 147, 165). For cocoyam, the effect of N on lamina area per plant was greater for 30% sunlight plants than for 50% or 100% sunlight-grown plants, which indicates that 30% sunlight plants allocated more N toward lamina area production than the 50% and 100% sunlight plants. Similarly, shade plants (30% and 50% sunlight) exhibited greater foliage biomass and top:corm ratios at high N levels, than 100% sunlight plants. The greater lamina area for +N plants may result in greater yields since lamina expansion rates have been correlated with yields for several plant species (124), including cocoyam (168). Net gas exchange was similar for plants in both N treatments 90 DAP, which indicates that the growing media provided sufficient N for photosynthesis and growth. Since lamina area per plant for +N plants was 7.5% greater 75 DAP and 9% greater 105 DAP than that of the -N plants, when shade treatments were pooled, it would be expected that lamina area was also
greater for +N than for -N plants 90 DAP. Therefore, less lamina for the -N than for the +N plants 90 DAP indicates that the -N plants maintained increased A rates at the expense of reduced lamina area. Net CO₂ assimilation, gₛ, and WUE were higher for the +N than for the -N plants 120 DAP, especially for the 100% sunlight plants. Thus, by 120 DAP the limited N pool in the growing media had been depleted and -N plants lacked sufficient N for optimum gas exchange. The increase in lamina N concentration for +N than for -N plants observed in the present study also resulted in increased gₛ (43, 81, 94, 103), and increased WUE (16) for several other plant species. Among shade treatments, A of the 100% sunlight plants was higher for the +N than for the -N plants. This observation was also reported for Lepechinia calycina (59). Plants grown in full sunlight generally utilize more N than shade-grown plants (78) due to the increased demand for N necessary for the higher growth observed in direct sunlight (10, 50, 65). In addition, increased N increases a plant's ability to acclimatize to increased PPF (57, 78, 114, 147). Therefore N deficits may be more detrimental for 100% sunlight than for shade-grown plants, as reported for Flindersia brayleyana (165), Lepechinia (59) and as shown by data from the present study (Fig. 5.4B).

The effect of applied N on lamina chlorophyll concentration (dry weight basis) was greater for the shade plants (30% and 50% sunlight) than for those growing in direct sunlight indicating a
greater emphasis by the shade plants to allocate N toward light absorption. Seeman et al. (147) observed greater chlorophyll concentrations (dry weight basis) with increased shade for *Alocasia*. In the present study, chlorophyll contents on an area basis were greater for +N than for -N plants but were not affected by shade. Sims and Pearcy (152) also found similar chlorophyll contents on an area basis among shade treatments for *Alocasia* and *Colocasia*. However, in the present study, chlorophyll content determined on a whole plant basis was greater for shaded plants (30% and 50% sunlight) than plants grown in full sunlight.

Interactions between N and shade indicate that cocoyam response to N depends on incident PPF. A positive correlation may exist between A and lamina N concentration for cocoyam as was shown with many other plants (47, 60) and related aroids (147, 152). The interaction between A and lamina N concentration for cocoyam indicates a tendency toward maximizing A when grown in full sunlight. When grown in the shade, cocoyam allocated N toward light absorption in the form of greater foliage biomass. Cocoyam, thus exhibited a degree of adaptive plasticity with respect to N allocation within the lamina in response to light intensity and nutrition during plant development. Despite greater N allocation toward light absorption, shade-grown cocoyam had greater corm biomass than 100% sunlight plants for both N and N-free fertilized plants. The corm yield advantage for shade plants
is attributable to the greater crop growth rates observed for shade than for 100% sunlight-grown cocoyam (168). The greater foliage biomass for shaded cocoyam, resulted in increased light interception and translocation of photosynthates to the roots (168). The thinner leaves observed for shaded cocoyam also may result in decreased maintenance and respiratory costs than for 100% sunlight-grown plants (65, 165) as reported for Alocasia and Colocasia (152). The lower leaf temperatures commonly found in canopy understories also would contribute to decreased respiratory costs than for plants grown in direct sunlight. Thus, cocoyam has the potential to grow in moderate shade without sacrificing yields, especially in tropical agroecosystem polycultures where N deficits are common and where fertilizer costs are often prohibitive.
Figure 5.1. Effect of sunlight and nitrogen on lamina area per plant of cocoyam (Xanthosoma sagittifolium) 75 (A), and 165 (B) days after planting. Each point represents the mean of 16 values. Vertical bars represent ± SE. In most cases SE bars were smaller than the symbols.
Figure 5.2. Effect of sunlight and nitrogen on lamina dry weight (A), increase in corm fresh weight from planting to harvest (fresh weight of corm 180 DAP - fresh weight of corm at planting) (B), and tops:corm ratio (fresh weight) (C) of cocoyam (*Xanthosoma sagittifolium*). Each point represents the mean of 8 values 180 days after planting. Vertical bars represent ± SE. In some cases SE bars were smaller than the symbols.
Figure 5.3. Effect of sunlight and nitrogen on stomatal conductance for CO₂ (A), and transpiration (B) of cocoyam (*Xanthosoma sagittifolium*) 90 days after planting. Each point represents the mean of 6 determinations. Vertical bars represent ± SE.
\[
\text{SUNLIGHT} \quad \text{H}_2\text{O} \quad \text{m}^{-2} \text{s}^{-1} \quad \text{gs} \quad (\text{mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1})
\]

\[
\text{MO2} \quad \text{CO}_2 \quad 250
\]

\[
\begin{array}{c}
\text{A} \\
\text{B}
\end{array}
\]

\[
(\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1})
\]

\[
\text{E}
\]

\[
\text{% SUNLIGHT}
\]

\[
\begin{array}{c}
250 \\
200 \\
150 \\
100 \\
8 \\
6 \\
4 \\
20 \\
100
\end{array}
\]
Figure 5.4. Effect of sunlight and nitrogen on net CO$_2$ assimilation of cocoyam (Xanthosoma sagittifolium) 90 (A), and 120 (B) days after planting. Each point represents the mean of 6 determinations. Vertical bars represent $\pm$ SE. In some cases SE bars were smaller than the symbols.
Figure 5.5. Effect of sunlight and nitrogen on lamina nitrogen concentration of cocoyam (*Xanthosoma sagittifolium*) on a dry weight (A), and lamina area basis (B). Each point represents the mean of 10 values 140 days after planting. Vertical bars represent ± SE. In most cases SE bars were smaller than the symbols.
Figure 5.6. Effect of sunlight and nitrogen on chlorophyll concentration of cocoyam (Xanthosoma sagittifolium) on a dry weight (A), and on a per plant basis (B), 180 days after planting. Each point represents the mean of 5 or 6 values. Vertical bars represent ± SE.
Plant Growth

Cocoyam growth in the shade was found to be similar to that of other shade-tolerant crops (10, 13, 65). In response to shading, cocoyam exhibited increased foliage biomass and top:corm ratio, which resulted in greater assimilating area. When light was the limiting growth factor, cocoyam allocated photosynthates toward maximization of light interception and absorption by increasing lamina size and area per plant, stem diameter, petiole length and number, and chlorophyll content on a leaf area basis. A similar response was documented for several other plant species which allocated greater amounts of photosynthates to compensate for the deficiencies created by limiting nutrient, water or light levels (26). Even though foliage biomass was increased in the shade, underground storage organ yields were similar or greater for shade- than for full sunlight-grown cocoyam. Thus, the potential exists for improving the productivity of agroecosystems by growing cocoyam as an understory crop. Several studies have shown that efficiency of resource utilization (space, nutrients, water or light) is often improved in polyculture systems (2). Species exploit available resources at different efficiency levels, with some plants having a competitive advantage over others with respect to resource utilization. A well-designed polyculture system should minimize competition for resources.
among plant species and total productivity should be improved through an efficient use of the available resources (2). The efficient use of available resources is an important decision-factor in farm enterprises where resources (such as land, fertilizers or water) are in limited supply and/or prohibitively expensive. Since this is the case in most of the tropics, the efficient light-harvesting characteristics of cocoyam, make of it an ideal understory-component in polyculture systems.

Nitrogen Utilization

An interaction between shading and N utilization in relation to cocoyam growth was observed in the present studies. A similar growth response was also reported for several other plant species (see: Chapter 5). When grown in the shade, N was utilized by cocoyam to increase foliage biomass through increased assimilating areas. In the shade, however, A rates were similar between +N and -N treatments, indicating that N applied to shade plants was utilized to maximize lamina area rather than to maximize photosynthetic efficiency. A smaller photosynthetic apparatus is sufficient for shade-grown cocoyam to utilize the lower PPFs found in the shade (10). Although not evaluated in this study, the smaller photosynthetic apparatus for cocoyam grown in the shade (indicated by lower A, specific leaf densities, and net assimilation rates) also may result in lower costs of structural support, maintenance and
respiration as has been shown for several other plants (10), and aroids (152). The small reduction in A for the -N plants grown in the shade indicate that cocoyam may be able to maintain adequate productivity when grown in N-deficient soils as an understory crop.

The addition of N to cocoyam grown in a low N growth media helped to compensate for the poor growth observed in full sunlight, by increasing A on a lamina area basis. Therefore, in full sunlight the productivity of cocoyam was increased on a lamina area basis (as shown by higher A, specific leaf densities, and net assimilation rates) when the plants were given N in a N-free growth media. This helps to explain the high productivity of cocoyam grown in monoculture commercial fields. When grown in monoculture, planting distances are reduced to increase canopy shading within plants, and N is applied to increase lamina productivity on an area basis. Thus, high density plantings and high N application rates in full sun increase productivity for cocoyam on a leaf area basis resulting in greater harvestable yields.

Future Research Prospects.

Cocoyam is outstanding, among terrestrial crops, in its ability to accumulate photosynthates under shaded conditions. The unique potential exists to increase the productivity of tropical agroecosystems by introducing cocoyam as an understory component of polyculture systems. In areas where cocoyam is already utilized as
an intercrop, the introduction of alternative cultural practices such as planting distances, planting patterns, and time of plantings may improve light interception patterns and efficiency of nutrient utilization. Since very little is understood about patterns of light interception in polyculture systems, a great deal of information is needed to understand which planting designs can best exploit the light harvesting characteristics of cocoyam. Some relevant aspects of light interception that are in need of research include planting patterns (63), planting distances (116, 130), timing of operations (63), choice of cultivars, and other management practices such as N fertilization, leaf harvesting for human consumption and disease and pest control (2). Crop improvement of cocoyam offers bright opportunities for research, since the genetic diversity in the Araceae has yet to be exploited (127, 128, 159), through traditional techniques including breeding and tissue-culture (110) or through novel biotechnology techniques.
LITERATURE CITED


BIOGRAPHICAL SKETCH

Hector R. Valenzuela was born in Mexico City on February 11, 1961, as a twin brother of Lourdes Valenzuela. Since then he has lived for several years each in Guatemala, Paraguay, El Salvador, Nicaragua, Washington State and Florida, U.S.A. Hector also lived for several months in Brazil. In 6th grade, as an elementary student, Hector earned a meritory award for hard work. In high school Hector was one of two, out of eighteen students, to complete an 'Advanced' program from the American School of Guatemala in 1979. Hector earned B.S. and M.S degrees in agronomy and horticulture (vegetable crops), respectively, both from Washington State University. Hector's research interests focus on a systems research approach toward applied crop ecology to improve resource utilization, pest management and productivity in vegetable crops.
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Stephen K. O'Hair, Chairman
Associate Professor of Horticultural Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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