Developmental Light Environment and Net Gas Exchange of Cocoyam (*Xanthosoma sagittifolium*)

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Abstract. The effects of shade during leaf development on photosynthetic activity of cocoyam [*Xanthosoma sagittifolium* (L.) Schott] were investigated. Net gas exchange and N and chlorophyll concentrations were determined for cocoyam leaves growing in 30%, 50%, or 100% sunlight. Net CO₂ assimilation (A) and water use efficiency (WUE) were greater for plants grown in 100% sunlight than for plants grown in less sunlight. Substomatal CO₂ concentration increased with increased shading. Stomatal conductance (g_s) and transpiration (E) did not vary significantly among treatments. Diurnal patterns for A were positively correlated with g_s, lamina temperature, relative humidity, and photosynthetic photon flux (PPF). Lamina N concentrations, determined on lamina dry weight and lamina area bases, increased with increased PPF. Shade plants (30% and 50% sunlight) had greater chlorophyll : N ratios (dry-weight basis) and greater lamina area : lamina dry weight ratios than 100% sunlight-grown plants, which indicates increased photosynthate and N allocation to leaves of shade plants and maximization of light interception.

Cocoyam has been identified as shade tolerant (Caesar, 1980; Schaffer and O'Hair, 1987). Therefore, the potential exists for use 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 aroid species grown in moderate shade have equal (Miura and Osada, 1981), greater (Schaffer and O'Hair, 1987), or lower (Sims and Percy, 1989) A rates than sun-grown plants. Schaffer and O'Hair (1987) 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 ($>750 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$). Diurnal and seasonal gas exchange data are lacking for cocoyam growing at PPFs below the light saturation point.

Lamina N and chlorophyll concentrations can affect A (Field, 1983). Chlorophyll is important for light harvesting while N is an important component of several photosynthetic enzymes (Field, 1983; Evans, 1989). To our knowledge, no information exists that evaluates the role of lamina chlorophyll and N on shade acclimation of cocoyam.

Previous studies have shown that biomass accumulation and yield of cocoyam are greater for shade-grown than sun-grown plants (unpublished data). 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 (LI-COR, Lincoln, Neb.) was 2200, 1100, and 650 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$, respectively]. Mean integrated daily PPFs for the 100% sunlight treatments were 35.0 $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ for

Expts. 1 and 2, and 37.4 $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ for Expts. 3 and 4 as determined with pyranometer (Model PSP, Eppley Laboratory, Inc., Newport, R.I.). Shade treatments were provided by covering 3 × 3 × 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 peat : 1 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 and the last two began in late Dec. 1988.

A, E, G_s, and 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 analyzer (LCA-2, Analytical Development, Hoddesdon, Herts, U.K.), as described by Schaffer and O'Hair (1987). Outside air containing 340 ± 10 $\mu\text{mol CO}_2/\text{mol}$ and dried to a constant 20% RH was pumped into the chamber at a rate of 0.375 liter·min⁻¹. A preliminary analysis of light response for A of mature leaves showed that the saturating PPF for maximum A of cocoyam was $>750 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ (Schaffer and O'Hair, 1987). Therefore, all measurements were made at PPFs $>800 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ 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 analysis of variance and by orthogonal contrast analysis. Gas determinations within and between experiments were tested for homogeneity of slopes and intercepts. Gas exchange determinations from all experiments were pooled for statistical analysis when 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

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Abbreviations: A, net CO₂ assimilation; Ci, substomatal CO₂ concentration; E, transpiration; g_s, stomatal conductance; WUE, water use efficiency.

(DAP) for plants grown in 100% or 30% sunlight in Expt. 4. Diurnal gas exchange determination dates were separated by ≈ 1 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 5 min before 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 (1983) and Schaffer and Gaye (1989). For N analysis, samples were digested using a modification of the aluminum block procedure of Gallaher et al. (1975). The sample weight was 0.3 g, the catalyst used was 3.2 g of 9 K₂SO₄ : 1 CuSO₄, and digestion was conducted for 4 hr at 400C using 10 ml H₂SO₄ and 2 ml H₂O₂. Ammonia concentration in the digestate was determined by semiautomated calorimetry (Hambleton, 1977) with a Technicon Autoanalyzer-II (Technicon, Tarrytown, N.Y.). Values for N concentration include organic and inorganic N.

Results

The effects of shading on net gas exchange of cocoyam were similar in each experiment (slopes of shade vs. gas exchange were homogeneous). Therefore, data from all experiments were pooled to determine effects of shade on net gas exchange. Net CO₂ assimilation rates were 8.4, 8.8, and 8.6 $\mu\text{mol CO}_2/\text{m per sec}$ for the basal section, midsection, 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 1). Transpiration was similar among shade treatments, with mean E values of 8.1 mmol H₂O/m per sec. Net CO₂ assimilation increased with increased shade and WUE increased with increased PPF during growth (Table 1).

Ninety-five days after planting, A peaked at 1000 HR and then tended to decrease slightly until 1600 HR (Fig. 1A). Shade plants had lower A than 100% sunlight-grown plants, but the diurnal pattern was similar for plants grown in both PPF levels (Fig. 1A). Transpiration and WUE showed a similar diurnal pattern as A (Fig. 1D and E). Transpiration was similar during

the day for plants exposed to 30% or 100% sunlight, while the 100% sunlight-grown plants had greater WUE values during the early morning hours. Although correlation coefficients were low, A was positively correlated with diurnal PPF [$A = 2.83^{-3}(\text{PPF}) + 1.68$; $r = 0.36$; $P < 0.01$] and also with diurnal relative humidity ($r = 0.17$; $P < 0.01$). Stomatal conductance decreased throughout the day (Fig. 1C) in relation to decreased relative humidity [$g_s = 6.32(\text{RH}) - 60.03$; $r = 0.97$; $P < 0.05$], and decreased as vapor pressure deficit (VPD) increased [$g_s = -71.61(\text{VPD}) + 456.20$; $r = 0.68$] (Fig. 1 B and F). Relative humidity and PPF contributed 16% and 38%, respectively, to the variation in E throughout the day [$E = 1.6^{-3}(\text{PPF}) + 9.8^{-2}(\text{RH}) + 1.25$; $P < 0.05$].

Nitrogen concentrations on a dry-weight basis increased with increased PPF 140 and 180 DAP (Fig. 2A). Nitrogen contents determined on lamina area (Fig. 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 chl a : chl b 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 [$N = 7.73(\text{CHL}) + 258.56$; $r = 0.49$; $P < 0.05$]. Specific leaf density was greater for 100% than for 30% sunlight-grown plants 140 and 180 DAP (Fig. 3).

Discussion

Although cocoyam has been reported to be shade-tolerant (Ceasar, 1980; Schaffer and O'Hair, 1987), it responded to increased PPF during plant development with increased A. Despite lower A, shade-grown plants had greater foliage and storage organ biomass (unpublished data) than full sun-grown plants. The increased leaf area in the shade resulted in increased photosynthate production and likely more partitioning to underground storage organs.

Shaded cocoyam yielded more than cocoyam grown in full sun (unpublished data). In the present experiment, plants grown in full sun had both greater lamina N contents (on an area and a chlorophyll basis) and A. Therefore, lamina N content may play a role in the adaptation of cocoyam to varying developmental PPF as shown for several plant species (Sims and Percy, 1989; Syvertsen and Smith, 1984; Thompson et al., 1988).

Table 1. Effect of developmental light environment on A, g_s, Ci, and WUE of cocoyam determined under saturating PPF (800 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$).^z

Sunlight (%)	A ($\mu\text{mol CO}_2/\text{m per sec}$)	g _s (mmol CO ₂ /m per sec)	Ci ($\mu\text{mol CO}_2/\text{mol}$)	WUE (mmol CO ₂ /mol H ₂ O)
100	8.8	237	263	1.2
50	8.1	231	269	1.1
30	6.7	210	273	0.9
Orthogonal contrasts				
Shade linear	*	NS	*	*
Shade quadratic	NS	NS	*	NS

^zDeterminations for all experiments were pooled because slopes and intercepts were homogeneous.

NS,*Nonsignificant and significant at $P < 0.05$, respectively.

Fig. 1. Diurnal patterns of 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 grown in 100% or 30% sunlight. Each point represents the mean of four replications $\pm$ SE determined on 5 Apr. 1989 (95 days after planting). In some cases SE bars were smaller than the symbols.

Increased A with increasing developmental PPF has been reported for other plant species (Evans, 1989), including related aroids (Sims and Pearcy, 1989). Lower respiration rates for several shade-grown plants than for plants grown in direct sunlight (Bjorkman, 1981; Givnish, 1988; Miura and Osada, 1981; Sims and Pearcy, 1989) 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 (Bjorkman, 1981). In the present experiment, the lower tissue biomass on a lamina area basis for plants in 30% sunlight than for plants in 100% sunlight (Fig. 3) indicated that shade plants had lower maintenance costs than plants grown in 100% sunlight (Bjorkman, 1981; Givnish, 1988).

The PPF at which A reached its maximum value was similar to that reported for *Colocasia* (Schaffer and O'Hair, 1987; Sims and Pearcy, 1989) but greater than that observed for *Alocasia*, another aroid (Sims and Pearcy, 1989). *Alocasia* is adapted to growing in deep-shaded forest understories, while both cocoyam and *Colocasia*, are often grown in monoculture that allow for greater light absorption by individual plants (Schaffer and O'Hair, 1987). The high g_s ($>200 \text{ mmol CO}_2/\text{m}^2 \text{ per sec}$) in the present study indicates that g_s was not limiting photosynthetic activity (Kirschbaum and Pearcy, 1988). The greater WUE obtained for 100% than for 30% sunlight-grown plants indicates that the former were better adapted to absorb and use the high PPFs ($>800 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$) at 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, or to inherent diurnal behavior (Kirschbaum et al., 1988). However, the diurnal decline in A coincided with an increase of CO_2 in the substomatal cavity. Although recent studies indicated that Ci may be overestimated from gas exchange calculations (Downton et al., 1988), increased Ci with decreasing A generally indicates a nonstomatal limitation to gas exchange (Farquhar and Sharkey, 1982). Therefore, during prolonged periods of high PPF, sun- and shade-grown cocoyam leaves may be photoinhibited. Photoinhibition due to prolonged exposure to high PPF has also been observed for *Vitis vinifera* L. leaves (Correia et al., 1990). The depletion of CO_2 in substomatal cavities was greater for plants grown in full sun (Table 1, Fig. 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, possibly due to stomatal closure in response to increased vapor pressure deficit (Henson et al., 1989; Kupperts and Schulze, 1985; Nowak et al., 1988; San Jose, 1983).

The data obtained in this study indicate that gas exchange and N content of cocoyam are 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-grown plants compared to shade-grown plants (unpublished data). This compensation may explain cocoyam's ability to grow and produce marketable yields in a wide range of light environments.

Fig. 2. Effect of sunlight on lamina N concentration on a lamina dry weight (A), and area basis (140 days after planting) (B) of cocoyam in Expt. 3. Each point represents the mean of 10 replications $\pm$ SE 140 days after planting, and of six replications $\pm$ SE 210 days after planting. In most cases SE bars were smaller than the symbols.

Fig. 3. Effect of sunlight on specific leaf density (SLD) of cocoyam in Expt. 3. Each point represents the mean of 10 replications $\pm$ SE. In most cases SE bars were smaller than the symbols.

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