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 (gₛ) and transpiration (E) did not vary significantly among treatments. Diurnal patterns for A were positively correlated with gₛ, 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 photosynthetic 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 Pearcy, 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 µmol·s⁻¹·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 µmol·s⁻¹·m⁻², 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 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.

Experiments 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, gₛ, 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 µmol CO₂/mol and dried to a constant 20% RH was pumped into the chamber at a rate of 0.375 liter·min⁻¹. Preliminary analysis of light response for A of mature leaves showed that the saturating PPF for maximum A of cocoyam was >750 µmol·s⁻¹·m⁻² (Schaffer and O’Hair, 1987). Therefore, all measurements were made at PPFs >800 µmol·s⁻¹·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, gₛ, and Ci, E, WUE, and lamina temperature were determined in the field 95 and 130 days after planting.
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 phonological 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 Marinini 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 K$_2$SO$_4$: 1 CuSO$_4$, and digestion was conducted for 4 hr at 400°C using 10 ml H$_2$SO$_4$ and 2 ml H$_2$O$_2$. 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 CO$_2$ assimilation rates were 8.4, 8.8, and 8.6 µmol CO$_2$/m per sec for the basal section, midsection, and tip, respectively, to the variation in E throughout the day [E = 1.6 + 9.8(rh) + 1.25; P < 0.05]. Specific leaf density was greater for 100% than for 30% sunlight-grown plants (Fig. 3).

**Discussion**

Although cocoyam has been reported to be shade-tolerant (Cesar, 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 photosynthetic production and likely more partitioning to underground storage organs.

Table 1. Effect of developmental light environment on A, g$_{st}$, Ci, and WUE of cocoyam determined under saturating PPF (800 µmol s$^{-1}$ m$^{-2}$).

| Sunlight (%) | A (µmol CO$_2$/m per sec) | g$_{st}$ (µmol CO$_2$/m per sec) | Ci (µmol CO$_2$/mol) | WUE (µmol 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 |

*Determinations for all experiments were pooled because slopes and intercepts were homogeneous.

NS • Nonsignificant and significant at P < 0.05, respectively.
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 gₕ (>200 mmol CO₂/m per sec) in the present study indicates that gₕ 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 µmol·s⁻¹·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 CO₂ 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 CO₂ 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 gₖ, E, WUE, and relative humidity and increased vapor pressure deficit. Stomatal conductance for CO₂ decreased throughout the day, possibly due to stomatal closure in response to increased vapor pressure deficit (Henson et al., 1989; Kuppers 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 ± se: 140 days after planting, and of six replications ± 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 ± se. In most cases se bars were smaller than the symbols.

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