

Full Length Research Paper

An ecophysiological study of the lycophyte *Selaginella kraussiana*

O. Roger Anderson

Biology and Paleo Environment, Lamont-Doherty Earth Observatory, Columbia University, New York, USA.

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Selaginella kraussiana, native to Sub-Saharan Africa and Macaronesia, has become naturalized in many other regions worldwide, including parts of Europe, North America, South America, Australia, and New Zealand. As a widely studied lycophyte species in the family Selaginellaceae, it is representative of this class of spore-bearing, vascular plants that form a significant part of forest understory flora and other mesophytic environments. Consequently, additional research on its physiological ecology is warranted, particularly photosynthesis and dark respiration, which are important for documenting its role in ecosystem carbon balance. The objective of this study was to provide data on the photosynthesis rate, respiration rate, and leaf fluorescence properties for laboratory-cultivated *S. kraussiana* toward establishing a stronger base of evidence for its role in ecosystem dynamics. The mean maximum photosynthesis rate was measured as follows: $2.25 \pm 0.12 \mu\text{mol m}^{-2} \text{s}^{-1}$ per leaf area, $401.70 \pm 43.38 \text{ nmol g}^{-1} \text{min}^{-1}$ per leaf fresh weight, and $3,882.51 \pm 595.74 \text{ nmol g}^{-1} \text{min}^{-1}$ per leaf dry weight. In terms of mean dark respiration rates, the values were: $0.51 \pm 0.03 \mu\text{mol m}^{-2} \text{s}^{-1}$ per leaf area, $85.68 \pm 3.82 \text{ nmol g}^{-1} \text{min}^{-1}$ per leaf fresh weight, and $787.14 \pm 69.04 \text{ nmol g}^{-1} \text{min}^{-1}$ per leaf dry weight.

Key words: Chlorophyll concentration, dark respiration rate, leaf fluorescence data, leaf morphological data, maximum photosynthesis rate.

INTRODUCTION

Lycophytes, commonly known as club mosses, are distributed nearly worldwide (ranging from tundra to tropical forests) and encompass c. 0.4% of all extant vascular plant species on Earth (Mehltreter, 2022; Zier et al., 2015). They are living descendants of some of the earliest evolving vascular plants, arising in the Late Silurian and Devonian (Gensel and Berry, 2001). *Selaginella kraussiana* (Kunze) A. Braun, known

commonly as the African club moss, is a relatively widely studied species in the family Selaginellaceae, occurring naturally in parts of Sub-Saharan Africa and in Macaronesia. It is considered an invasive species in some geographical locations, especially New Zealand (Nessia et al., 2014) and Britain (Rumsey, 2021). Among the previously published studies of *S. kraussiana*, attention has been given to a variety of topics including: anatomy

E-mail: ora@ldeo.columbia.edu.

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Figure 1. *S. kraussiana*, surface view photographed from above the cultivated plant. Marker = 2.0 cm.
Source: The author.

and ontogenetic development (Burr and Evert, 1973; Harrison and Langdale, 2010; Jones and Drinnan, 2009; Sanders and Langdale, 2013; Slagg, 1932), genomics and cellular molecular mechanisms (Berrissou et al., 2024; Ge et al., 2016; Jernstedt and Mansfield, 1985; Van Sandt et al., 2007), biogeographic distribution and environmental adaptation (Bannister, 1984; Mingou et al., 2024; Sangry et al., 2024; Vernon and Ranker, 2013), and bioactive compounds (Santra and Banerjee, 2024).

Given that *S. kraussiana* is a broadly distributed representative of lycophytes that form a significant portion of forest understory flora, additional research is warranted on its physiological ecology, particularly photosynthesis and respiratory rate, which are potentially important aspects of its role in the environmental carbon cycle and energy flow of ecosystems where it is abundant. Relatively few published reports were found in a search of the literature on the physiology and photosynthesis of *S. kraussiana*. However, Jagels (1970) published a paper on the morphology and photosynthesis of *S. kraussiana* under varying light intensities. He measured light intensity in foot candles, which makes it difficult to compare his results to those from current research reports where light intensity is measured as photosynthesis photon flux density (PPFD) expressed as $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Also, the photosynthesis rate was expressed only in mg CO_2 assimilated per g dry weight per hour, and did not include the rate expressed per unit of leaf area as is typically reported in current research (that is, $\mu\text{mol CO}_2$ fixed $\text{m}^{-2} \text{ s}^{-1}$).

¹). Among other aspects, there was an examination of the photosynthesis rates for *S. kraussiana* plants replete with stored starch compared to those that were depleted in starch, and found that those with substantial starch reserves had a net photosynthesis rate that was c. 40% of the rate for plants with replete starch reserves. This research provides a context for studies of photosynthesis in *S. kraussiana* using modern research methods.

MATERIALS AND METHODS

Plants and growth conditions

Three healthy container-grown *S. kraussiana* plants (Figure 1) available from a commercial vendor (Valli Florist, New York, NY) were maintained in an environmentally controlled culture room at the Lamont-Doherty Earth Observatory of Columbia University. All experimental measurements were made using the three plants, including replicate measures of the assessed variables. Growing chambers were maintained at a temperature of 25°C and a light cycle of 14 h light and 10 h darkness. The light was provided using fluorescent illumination with an intensity of $60 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (simulating moderate light intensities in semi-shaded environments) with relative humidity of 60% equivalent to a vapor pressure deficit (VPD) of 1.27 kPa.

Photosynthesis measurements

Each photosynthesis measurement was made using a terminal segment of a fan-shaped branching stem of *S. kraussiana* containing

Table 1. Mean $\pm$ SEM morphological data for the terminal branching array of leaves of *S. kraussiana*.

Total leaf area (cm ²)	Leaf fresh weight (g)	Leaf dry weight (g)	Leaf percent water content (%)	Specific leaf area (cm ² /g)
16.4 $\pm$ 0.94	0.507 $\pm$ 0.051	0.062 $\pm$ 0.01	87.72 $\pm$ 0.32	284.36 $\pm$ 11.75

N = 20 branch leaf samples from three plants; SEM = standard error of mean.

closely spaced, alternately arranged microphyllous leaves (Figure 1). Only the apical, leafy, fan-shaped portion of the branch was enclosed in the assay chamber of an infra-red gas analyzer (IRGA) system (model BTA, Vernier, Beaverton Oregon), with an optically clear, 163 cm³ assay chamber (gas phase volume corrected for the volume of the leaf sample) at a temperature of 25°C, and illuminated with a Light Emitting Diode (LED). The light intensity was assessed by a LiCor solar monitor 1775, Biosciences, Lincoln, Nebraska, USA.

Maximum net photosynthesis rate $A_{\max}$ ($\mu\text{mol CO}_2$ assimilated $\text{m}^{-2} \text{s}^{-1}$), based on the leaf area enclosed in the assay chamber, was assessed for nine leaf-bearing branches from three plants. Maximum photosynthesis rate was achieved in a PPFD range of 400 to 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Relative humidity in the photosynthesis sample cuvette ranged from 85 to 90%, with a VPD of 0.48 to 0.32 kPa to reduce excessive transpiration loss. The CO_2 concentration in the assay cuvette was at ambient atmospheric concentration (417 ppm). The time for measurement of each assay was c. 10 min. The mean respiration rate of the apical fan-shaped leafy branch segment was determined at 25°C using the same CO_2 assay apparatus with a completely darkened assay chamber and based on three metrics for the released respiratory CO_2 ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$, $\text{nmol CO}_2 \text{ g}^{-1}$ fresh weight min^{-1} , and $\text{nmol CO}_2 \text{ g}^{-1}$ dry weight min^{-1}). The sample was maintained in the dark condition until the reaction centers of the photosystems of the leaves came to equilibrium with the darkened state (c. 2 min), and measurements were begun when there was a steady state respiration rate. Replicate samples of nine terminal leafy branches from three plants were used for the photosynthesis and dark respiration assays. Leaf area, expressed as cm^2 , was assessed using a leaf area meter (Model AM-350, Opti-Sciences, Inc., Hudson, New Hampshire, USA). The fresh weight and the dry weight of the leaf sample after drying overnight at 60°C in a laboratory oven were determined using a Sartorius digital balance (Göttingen, Germany).

Leaf measurements

Estimates of mean total leaf area (cm^2), mean leaf fresh weight, mean leaf dry weight, and mean percent water content were assessed using 20 branch leaf samples from three plants. Additionally, mean specific leaf area (SLA), using 20 branch leaf samples from three plants, was assessed as leaf area in $\text{cm}^2/\text{dry weight}$ in g (Wolf et al., 1972). The mean chlorophyll concentration index (CCI) for nine terminal branch leaf samples from three plants used in the photosynthesis assays was obtained using a CCM-300 chlorophyll content meter (Opti-Sciences, Inc., Hudson, New Hampshire, USA).

Leaf fluorescence measurements

The JIP test application within an OS-30p+ Chlorophyll Fluorometer (Opti-Sciences, Inc., Hudson, New Hampshire, USA) was used to obtain leaf fluorescence data for nine leaf-bearing branches from three plants used for the photosynthesis assays. The broad leafy terminal portion was enclosed in the fluorometer assay clamp. The fluorometer data included leaf quantum yield efficiency of

photosystem II (PSII), expressed as variable fluorescence/maximum fluorescence (F_v/F_m), evidence of electron transport per reaction center (ET_0/RC) from PS II to the quinone intermediate (Q_A) and beyond in the electron-transport chain, and y_0 representing the probability that an electron, produced by photon excitation in PS II, will pass to the intermediate quinone and beyond in the electron-transport chain. Leaf samples were dark-adapted for 15 min to ensure that the photosystem reaction centers (RC) were fully opened before the measurements were made.

RESULTS

The mean maximum photosynthesis rate ($A_{\max}$) expressed per leaf area was $2.25 \pm 0.12 \mu\text{mol m}^{-2} \text{s}^{-1}$. $A_{\max}$ per leaf fresh weight was $401.70 \pm 43.38 \text{ nmol g}^{-1} \text{min}^{-1}$, and per leaf dry weight $3,882.51 \pm 595.74 \text{ nmol g}^{-1} \text{min}^{-1}$. Mean dark respiration rate expressed per unit leaf area was $0.51 \pm 0.03 \mu\text{mol m}^{-2} \text{s}^{-1}$. The mean dark respiration per leaf fresh weight was $85.68 \pm 3.82 \text{ nmol g}^{-1} \text{min}^{-1}$, and per leaf dry weight, $787.14 \pm 69.04 \text{ nmol g}^{-1} \text{min}^{-1}$. Leaf morphological data are shown in Table 1, and leaf fluorescence data are shown in Table 2.

DISCUSSION

The maximum photosynthesis rates among various lycophyte species can differ significantly, as shown by published research. Zier et al. (2015) documented the maximum photosynthesis rates of four co-occurring temperate lycophyte species at Colgate University in Hamilton, NY: (*Lycopodium clavatum*, *Spinulum annotinum*, *Diphasiastrum digitatum*, and *Dendrolycopodium dendroideum*). They found that the maximum photosynthesis rate ($A_{\max}$) ranged from approximately $5.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *D. digitatum* to $6.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *S. annotinum*.

In another study, Pandey et al. (2010) investigated fully hydrated *Selaginella bryopteris*, a desiccation-tolerant species, and reported a net photosynthesis rate of $0.90 \mu\text{mol m}^{-2} \text{s}^{-1}$ at a moderately low PPFD of $300 \mu\text{mol m}^{-2} \text{s}^{-1}$. Soni et al. (2012) found that *S. bryopteris* achieved an $A_{\max}$ of $9.5 \pm 1.47 \mu\text{mol m}^{-2} \text{s}^{-1}$ at light-saturating intensities of $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$ in laboratory settings. Furthermore, in field studies, they recorded maximum photosynthesis rates of approximately $12 \mu\text{mol m}^{-2} \text{s}^{-1}$ during peak sunlight at noon, with a PPFD of $1,600 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Table 2. Mean $\pm$ SEM leaf fluorescence data obtained for *S. kraussiana*.

Fv/Fm	ET ₀ /RC	ψ_o	CCI
0.72 $\pm$ 0.01	1.06 $\pm$ 0.03	0.68 $\pm$ 0.01	6.35 $\pm$ 0.48

N = Nine leaf samples from three plants. Fv/Fm = variable fluorescence/maximum fluorescence (maximum quantum yield of Photosystem II), ET₀/RC = evidence of electron transport per reaction center from PS II to the quinone intermediate (QA) and beyond in the electron-transport chain, ψ_o = the probability that an electron, produced in PS II, will pass to the intermediate quinone and beyond in the electron-transport chain, and CCI = chlorophyll concentration index.

Notably, Soni et al. (2012) also provided graph data indicating a net photosynthesis rate of 0.90 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *S. bryopteris* in the early morning when the PPFD was 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$. This finding aligns with the results from Pandey et al. (2010), who reported similar net photosynthesis under the same PPFD in their laboratory study.

Wang et al. (2010) studied the effects of dehydration and rehydration on the desiccation tolerant lycophyte *Selaginella tamariscina* that grows naturally on exposed rocks of hills in the region of Jingpo Lake, Heilongjiang Province, China. In addition to extensive physiologic and proteomic analyses of this lycophyte during desiccation and rehydration, they reported that the A_{max} of fully hydrated *S. tamariscina* was 6.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Similarly, the photosynthesis A_{max} for *Selaginella pallescens*, growing in a tropical deciduous forest, was estimated to be 5.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Brodribb et al., 2009).

In a study of *Selaginella martensii*, Ferroni et al. (2021) reported maximum photosynthesis rates expressed per leaf area ($\mu\text{mol m}^{-2} \text{s}^{-1}$) under varying light intensities as follows: extreme shade (1.54 $\pm$ 0.26), intermediate shade (2.68 $\pm$ 0.24), and full sunlight (3.43 $\pm$ 0.55). This is within the range found here for *S. kraussiana* (2.25 $\pm$ 0.12 $\mu\text{mol m}^{-2} \text{s}^{-1}$) grown under moderate fluorescent light intensity at a PPFD of 60 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Based on a search of the literature, it appears that among the few reported photosynthesis studies of lycophytes, *Selaginella* is presently the most studied genus.

Based on the mean data shown in Table 1, for total leaf area (cm^2), leaf fresh weight (g), and leaf dry weight (g), and using the mean A_{max} reported for each of these parameters, it is possible to compute the mean total CO₂ assimilated per fan-shaped leafy branch segment for each of these leaf parameters as follows: 16.4 cm^2 (A_{max} = 221.40 nmol min^{-1}) for total leaf area, 0.507 g (A_{max} = 203.66 nmol min^{-1}) for leaf fresh weight, and 0.062 g (A_{max} = 240.72 nmol min^{-1}) for leaf dry weight.

The mean dark respiration rate of *S. kraussiana* expressed per unit leaf area was 0.51 $\pm$ 0.03 $\mu\text{mol m}^{-2} \text{s}^{-1}$. This is comparable to a respiration rate (R_d) of 0.41 to 0.51 $\mu\text{mol m}^{-2} \text{s}^{-1}$ reported by Ferroni et al. (2021) for *S. martensii* at varying locations from low to high light intensity. The carbon balance (percent of C respired to C assimilated by photosynthesis) was obtained for *S.*

kraussiana in this study was c. 20% when measured at a temperature of 25°C.

Based on the fluorescence analyses reported here, the mean Fv/Fm value for *S. kraussiana* was 0.72 $\pm$ 0.01. This is similar to the mean Fv/Fm value of 0.69 reported by Li et al. (2019) for hydrated *S. tamariscina*. Ferroni et al. (2016) reported a mean value of Fv/Fm = 0.80 for *S. martensii*, and Pandey et al. (2010) reported a Fv/Fm = c. 0.78 for fully hydrated *S. bryopteris*. Yu et al. (2021) reported a Fv/Fm ratio of 0.80 for hydrated *Selaginella pulvinata* in laboratory culture.

A search of the literature produced little published data on leaf percent water content or leaf specific area (SLA) of lycophytes. The mean SLA of *S. kraussiana* shown in Table 2 is 284.36 $\pm$ 11.75. Each microphyllous leaf of *S. kraussiana* is thin (c. 30 μm thick), with a mesophyll largely one to two cells thick, extending from the midvein almost to the leaf margins (Jagels, 1970). The alternately arranged micro leaves along the branching, fan-shaped stem are relatively slender, and the mean total area of the *S. kraussiana* terminal fan-shaped array of microphyllous leaves (Table 1) is 16 cm^2 . For comparison, the SLAs of some shade-dwelling ferns published by Bannister and Windish (1982) are as follows: *Asplenium bulbifera* (336 cm^2/g), *Dryopteris filix-mas* (345 cm^2/g), and *Polystichum vestitum* (255 cm^2/g). However, for ferns with relatively thin leaves, such as *Adiantum capillus-veneris*, the SLA can be relatively large (615 cm^2/g) (Anderson, 2023). Wylie (1948) measured leaf thickness in *A. capillus-veneris* and reported a mean blade thickness for portions of the leaf varying in mesophyll thickness as follows: two mesophyll layers (120 μm), one layer (98 μm), and for portions without mesophyll (51 μm).

Given their global distribution and potential for significant contributions to local biogeochemical cycles (Halder et al., 2021), it is important to expand the range of ecophysiological studies of lycophytes in varying biogeographical settings, including broad-scale biogeographic studies of lycophyte communities as well as autecological and ecophysiological studies of representative individual lycophyte species. For example, Tosens et al. (2016) examined the photosynthetic capacity in 35 ferns and fern allies, focusing on mesophyll CO₂ diffusion as a key trait. They studied two lycophyte species (*Lycopodium annotinum* and *L. clavatum*) growing in

shrublands and conifer forests. They concluded that low mesophyll conductance to CO₂ was the main cause for low photosynthesis in ferns and fern allies, which, in turn, was associated with thick cell walls and reduced chloroplast distribution towards intercellular mesophyll air spaces.

Campany et al. (2019) measured a suite of functional traits from seven species of *Selaginella* and six fern species in a lowland rain forest in Costa Rica. Using the convergence of trait function, they categorized *Selaginella* species into different habitats. *Selaginella* spp. in heavily shaded environments had higher chlorophyll concentrations and lower light compensation points compared with open habitats. However, species occupying open habitats had lower foliar nitrogen and higher stomatal densities. *Selaginella* spp. had denser and smaller stomata, lower leaf mass per area, and lower foliar nutrient content than ferns, revealing how these plant groups optimize ecophysiological function differently in tropical forest floors.

Among the seven species of *Selaginella* sampled in a lowland forest by Campany et al. (2019), the net photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) varied from 1.8 ± 0.25 (*Selaginella atirrensensis*) to 5.8 ± 0.49 (*Selaginella eurynota*), with the majority of results in a range of 2.1 to $3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$. The photosynthesis data were collected at a standard PPFD of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, which previously was shown to produce maximum photosynthetic rates for shade-adapted understory terrestrial plants (Watkins et al., 2010). Their PPFD is within the range used in this study (400 to $600 \mu\text{mol m}^{-2} \text{s}^{-1}$), where the A_{max} for *S. kraussiana* was $2.25 \pm 0.12 \mu\text{mol m}^{-2} \text{s}^{-1}$, a value comparable to the findings of Campany et al. (2019) for the seven understory lycopphyte species in their study.

Conclusions

This study, and prior ones reviewed earlier, indicate increasing evidence of the role of lycopphytes in ecosystem dynamics. However, additional research is warranted, including greater clarity regarding the range and diversity of the rate of carbon fixation by photosynthesis and loss by respiration among communities of lycopphytes. Moreover, further studies are needed focusing more on the community level of lycopphytes to better document their contribution to productivity compared to other members of the co-occurring plant community; and to examine the ecophysiology of lycopphytes in varying environmental settings, and their response to changing climatic conditions.

CONFLICT OF INTERESTS

The author has not declared any conflict of interests.

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