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An ecophysiological study of cultivated *Nephrolepis exaltata* (L.) Schott cv. Bostoniensis (Boston Fern)

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The Boston Fern, a cultivar of *Nephrolepis exaltata* native to tropical and sub-tropical environments, is widely cultivated. There is substantial published horticultural research on its cultivation. However, there is less research published on its physiological ecology. This is a report of the physiological ecology of laboratory cultivated *N. exaltata* cv. Bostoniensis, particularly focusing on the following aspects: Net photosynthesis rate, dark respiration rate, leaf fluorescence (evidence of fundamental processes of light capture and electron transport during photosynthesis), as well as basic leaf physiological characteristics. The latter include chlorophyll content index (CCI), specific leaf area (SLA), percent water content, stomatal density, and transpiration rate expressed as stomatal water vapor conductance (g_w). These results provide evidence of *N. exaltata*'s capacity to adapt to environments of widely different light intensities that may partially explain its suitability for indoor cultivation as well as its ability to invade and naturalize in diverse habitats beyond its native range.

Key words: Environmental adaptation, leaf relative chlorophyll content, leaf chlorophyll fluorescence analysis, photosynthesis rate, specific leaf area, transpiration rate.

INTRODUCTION

Nephrolepis exaltata (L.) Schott cv. Bostoniensis, commonly known as the Boston Fern (Figure 1), is widely cultivated in gardens, conservatories and human habitations (Jones, 1987; Kumar et al., 2022); and it is of substantial economic value horticulturally and in some medicinal applications (Singh and Johari, 2018). It is a cultivated variant of the naturally occurring *N. exaltata* and was identified as a new variant approximately in 1896 among commercially available plants in Boston and Cambridge MA, USA (Morton, 1958). The crown of pale green leaves is sub-erect with slightly drooping leaves capable of growing up to 60 - 90 cm tall and 0.5 - 1 m wide. The sword-shaped leaves are entire to slightly toothed, measuring about 50 - 150 cm long and 5 - 10 cm wide. Lateral leaflets are alternately arranged and each measure about 3 - 8 cm in length.

The natural habitat of the species is tropical or sub-tropical environments including Florida, Mexico, Brazil, and West Indies (Jones, 1987). In some cases, it has escaped from cultivation and invaded geographic locations beyond its native habitats (de Almeida and Freitas, 2006; Henderson, 2007). It appears to be a relatively stable and successful plant in the natural environment and is currently listed as "Least Concern" (LC) by the IUCN Red List (Bárrios and Copeland, 2021).

A substantial amount of horticultural research has

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Figure 1. *Nephrolepis exaltata* (Boston Fern) in laboratory cultivation. Scale bar = 10 cm.
Source: Author.

been done reporting the effect of varying cultivation conditions on the growth, form, and survivability of *N. exaltata* (Dawson et al., 1991; Hvoslef-Eide, 1991; Mortensen, 1992; Parminder et al., 2014; Naveena et al., 2019; Beeson et al., 2020; Patil et al., 2020; Kumar et al., 2022; Vanlalhruaii et al., 2022; Sharanya et al., 2023). However, less research has been done on the physiological ecology of *N. exaltata* during its cultivation (Pass and Hartley, 1979; Gago et al., 2013; Seltsam and Owen, 2022). Although *N. exaltata* can be cultivated in moderately high light intensities (e.g., 300 µmol photons m^{-2} s^{-1}), its tolerance of lower light intensities is more typical of shade adapted plants. It grows effectively in light intensities as low as 15 to 20 µmol m^{-2} s^{-1} (Dawson et al., 1991), making it suitable for cultivation indoors and in outdoor locations where light intensities may be at the lower range of its tolerance.

This is a report of the photosynthesis, respiration, and physiological properties of Boston Fern leaves grown in controlled laboratory conditions. The aim was to more fully explore its physiological ecology and response to cultivation in artificial environments, including implications for its status in the natural environment. The leaf physiological variables examined include: 1) net photosynthesis rate (µmol CO_2 assimilated m^{-2} s^{-1}), 2) transpiration rate expressed as water vapor stomatal conductance (mmol m^{-2} s^{-1}), 3) leaf chlorophyll content index (CCI), a relative index measuring chlorophyll content per unit leaf area, 4) leaf chlorophyll fluorescence including: (i) evidence of quantum efficiency expressed as ratio of variable fluorescence to maximum fluorescence (Fv/Fm) and (ii) electron transfer per reaction center beyond the quinone intermediate (Q_A) in the electron-transport chain (ET_0/RC), and 5) dark respiration rate (µmol CO_2 released m^{-2} s^{-1}).

MATERIALS AND METHODS

Source of fern plants and experimental culture conditions

N. exaltata cv. Bostoniensis plants of varying maturity were obtained from a commercial supplier (Valli Florist, New York). Three plants were obtained (two with more mature leaves and one with younger leaves). Mature leaves at the base of the crown of leaves were several months old and younger leaves were several weeks old. The purpose was to obtain samples of leaves that were representative of plants in varying stages of maturity to more accurately obtain physiological evidence encompassing a breadth of maturational stages of *N. exaltata*. The containerized plants were grown in an environmentally controlled culture room at the Lamont-Doherty Earth Observatory of Columbia University. The growing conditions included a temperature of 25°C and a light cycle of 14 h of light followed by 10 h of darkness. The light was provided using

Table 1. Mean ± SEM net photosynthesis rate of *N. exaltata* leaves under controlled laboratory cultivation at 25°C at light intensities expressed as photosynthetic photon flux density (PPFD) of 10, 25, 50 and 100 µmol photons m^{-2} s^{-1}.

PPFD (µmol m^{-2} s^{-1})	Photosynthesis rate[a]		
	Per leaf area (nmol CO_2 g_{fw}^{-1} min^{-1})	Per leaf fresh weight (nmol CO_2 g_{dw}^{-1} min^{-1})	Per leaf dry weight (µmol CO_2 m^{-2} s^{-1})
10	0.45 ± 0.02	194.10 ± 12.81	1164.16 ± 93.40
25	0.99± 0.04	421.84 ± 22.94	2498.67 ± 159.96
50	1.48 ± 0.08	603.06 ± 44.24	3685.40 ± 213.76
100	2.21 ± 0.17	929.72 ± 72.00	5490.25 ± 450.05

[a]Mean data are based on 16 measurements (8 young leaves plus 8 mature leaves) for each parameter.

fluorescent illumination with an intensity of 100 µmol photons m^{-2} s^{-1}, and the relative humidity was maintained at 60% equivalent to a vapor pressure deficit (VPD) of 1.27 kPa.

Physiological analyses

The net photosynthesis rate of the leaves (expressed as µmol CO_2 assimilated m^{-2} s^{-1}) based on the leaf area in the chamber was assessed using an infra-red gas analyzer (IRGA) system (model BTA, Vernier, Beaverton Oregon), with an optically clear, 163 cm^3 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) at four different levels of light intensity typical of conditions likely encountered in shade environments and during cultivation; namely, photosynthesis photon flux density (PPFD) of 10, 25, 50 and 100 µmol m^{-2} s^{-1} (assessed by a LiCor solar monitor 1775, Biosciences, Lincoln, Nebraska, USA). Net photosynthesis rate was also calculated relative to leaf fresh weight (g_{fw}) and relative to leaf dry weight (g_{dw}). Relative humidity in the photosynthesis sample cuvette ranged from 85 to 90% equivalent to a VPD of 0.48 to 0.32 kPa that was a suitable level 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 leaf was *c*. 10 min. Mean respiration rate (expressed as µmol CO_2 released m^{-2} s^{-1}) was determined at 25°C using the same apparatus with a completely darkened assay chamber. The leaf 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. Leaf area, expressed as cm^2, was assessed using a Leaf Area Meter (Model AM-350, Opti-Sciences, Inc., Hudson, New Hampshire, USA).

The leaf fresh weight and leaf dry weight after drying overnight at 60°C in a laboratory oven, were determined using a Sartorius digital balance (Göttingen, Germany). This data was also used to calculate the mean specific leaf area (leaf area in cm^2/dry weight in g) (Wolf et al., 1972). Stomatal water vapor conductance (g_w), an estimate of transpiration rate, was assessed using a SC-1 Porometer (Decagon Devices, Inc., Pullman, Washington, USA) in the laboratory with a relative humidity of 12% equivalent to a vapor pressure deficit (VPD) = 2.19 kPa and illumination with a light intensity of 100 µmol photons m^{-2} s^{-1} expressed as photosynthesis photon flux density (PPFD) from a LED light source. Thus, PPFD is the number of photons in the 400 to 700-nm wavelength band incident on the leaf surface per square meter per second.

The mean chlorophyll concentration index (CCI) for each leaf sample was obtained using a CCM-300 chlorophyll content meter (Opti-Sciences, Inc., Hudson, New Hampshire, USA). An OS-30p+ Chlorophyll Fluorometer (Opti-Sciences, Inc., Hudson, New Hampshire) was used to obtain leaf chlorophyll fluorescence data. This provides evidence of the energy level of the chlorophyll active site when illuminated, and to what extent the activated electrons are transferred from the chlorophyll active site to intermediate molecules in the chain of reactions leading to uptake of CO_2 and its chemical reduction resulting in an increase in the concentration of sugar compounds in the leaf. The leaf fluorescence data included leaf quantum yield efficiency expressed as variable fluorescence/maximum fluorescence (Fv/Fm), evidence of electron transport per reaction center (ET_0/RC) from photosystem II (PS II) to the quinone intermediate (Q_A) and beyond in the electron-transport chain, and ψo = probability that an electron, produced by photon excitation in PS II, will pass to the intermediate quinone and beyond in the electron-transport chain leading to reduction of CO_2. These were based on the JIP test application in the OS-30p+ instrument. Leaf samples were dark adapted for 20 to 30 min before the measurements were made to ensure that the reaction centers (RC) had come to equilibrium with the darkened state.

The estimate of mean stomatal density (number cm^{-2}), on the abaxial surface of the *N. exaltata* leaves, was made by using a leaf peel method (clear acetate varnish was applied to the abaxial surface, and after thoroughly drying, a replica of the leaf epidermis was obtained by gently peeling away the thin layer of hardened varnish). A wet mount slide preparation using deionized water was made, and 50 images of the stomata on the acetate peel were examined at a magnification of 400X using a Nikon phase contrast compound light microscope (Nikon Instruments, Melville, NY, USA) to obtain an estimate of the stomatal density. Concurrently, digital microscopic images were made of the stomata in the leaf peel and 50 stomata observed in three separate sections of the leaf peel were measured to obtain the estimated mean length and width of the stomata on the abaxial surface of the leaf.

All results of the assays are presented as the mean ± standard error of the mean (SEM) calculated using an Excel spreadsheet (Microsoft, Inc. Redmond, Washington, USA).

RESULTS

The results of the photosynthesis measurements within a PPFD range of 10 to 100 µmol m^{-2} s^{-1}, typical of the range of light intensities in shade or indoor cultivation, are presented in Table 1.

Mean dark respiration rates, measured per unit of leaf area, per gram fresh weight (g_{fw}) and per gram dry weight

Table 2. Mean ± SEM dark respiration rate for *N. exaltata* leaves under controlled laboratory cultivation at 25°C based on leaf area, leaf fresh weight and leaf dry weight.[a]

Per leaf area ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	Per leaf fresh weight ($nmol\ CO_2\ g_{fw}\ min^{-1}$)	Per leaf dry weight ($nmol\ CO_2\ g_{dw}\ min^{-1}$)
0.16 ± 0.03	63.25 ± 10.79	359.05 ± 59.10

[a]Mean data are based on 16 measurements for each column entry.

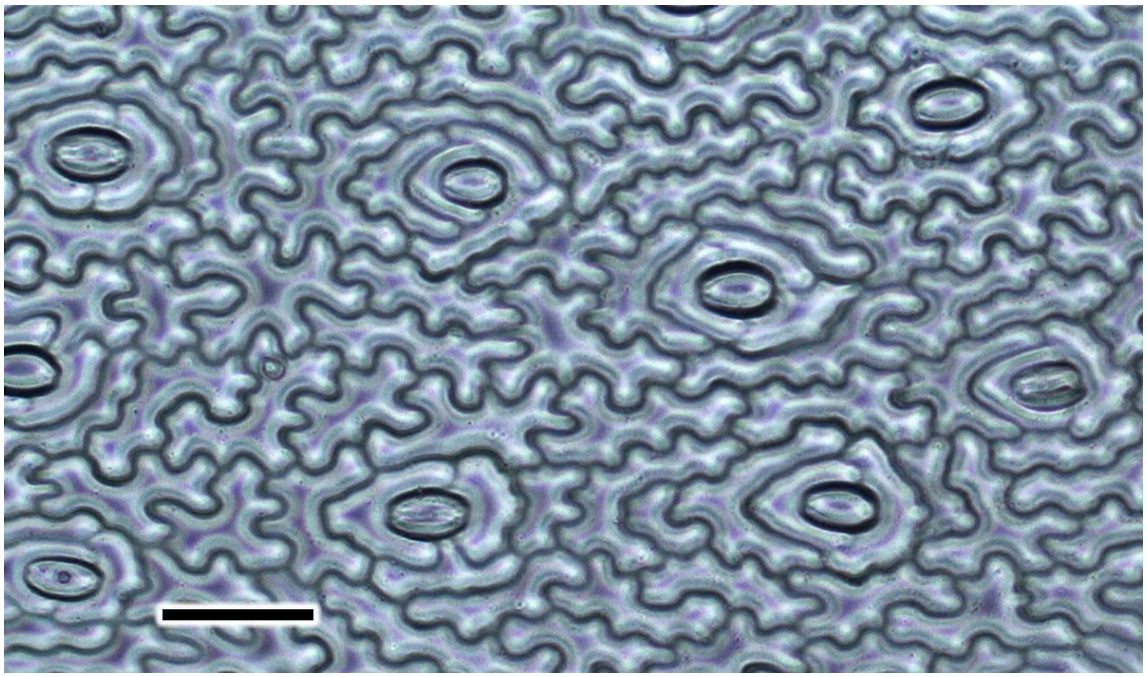

Figure 2. Abaxial leaf surface replica showing 8 oval-shaped stomata surrounded by closely interdigitated epithelial cells. Scale bar = 100 µm.
Source: Author.

(g_{dw}), are presented in Table 2.

The mean dark respiration rate of 0.16 ± 0.03 µmol CO_2 m^{-2} s^{-1} is clearly less than the lowest mean photosynthetic CO_2 gain (0.45 ± 0.02 µmol CO_2 m^{-2} s^{-1}) at PPFD of 10 µmol photons m^{-2} s^{-1}, indicating that this CO_2 fixation rate at the lowest PPFD is well above the loss due to respiration. Images of leaf stomata surrounded by epithelial cells on the abaxial leaf surface of *N. exaltata* are as shown in Figure 2.

The mean stomatal density per square cm of the abaxial leaf surface of *N. exaltata* based on 50 measurements was 3,738 ± 132 cm^{-2}. The stomatal mean length ± SEM = 40.2 ± 0.54 µm and mean width ± SEM = 22.9 ± 0.34 µm. Additional mean data for leaf physiological measurements are presented in Table 3.

DISCUSSION

A substantial amount of evidence has been gathered on the environmental conditions that support viability and growth of *N. exaltata* in cultivation, and some of these findings may provide evidence of why it has been capable of escaping from cultivation as an invasive species in widely different tropical and sub-tropical geographic locations, sometimes becoming part of the naturalized biota. Mortensen (1986) studied the effects of increasing relative humidity (RH) across a range of values from 55-60% to 90-95% on the growth of container-cultivated *N. exaltata* (PPFD = 80 µmol m^{-2} s^{-1}) and found that this increase in RH produced a 68% increase in dry weight, an amount substantially greater than gains in weight by other cultivated plants used for comparison. This can be further understood in the context of the daily evapotranspiration rate (ET_A) of container grown *N. exaltata* reported by Beeson et al. (2020) who found that depending on the growth conditions mean daily ET_A per plant varied from 69.5 to 74.0 ml. In this current study of laboratory cultivated *N. exaltata*, the mean stomatal water vapor conductance

Table 3. Mean ± SEM data for leaf physiological parameters for *N. exaltata*.

SLA[a]	% H_2O[a]	CCI[a]	g_w[b]	F_v/F_m[a]	ET_0/RC[a]	ψo[a]
429.29±1.80	82.52±0.53	12.00±0.48	102.38±2.85	0.80±0.004	1.15±0.02	0.74±0.01

SLA = Specific Leaf Area, % H_2O = leaf percent water content, CCI = Chlorophyll Content Index (mg chlorophyll m^{-2}), g_w = stomatal water vapor conductance (mmol m^{-2} s^{-1}), F_v/F_m = variable fluorescence/maximum fluorescence, ET_0/RC = electron transport in PS II per reaction center; and ψo = probability that an electron, produced by photon excitation in PS II, will pass to the intermediate quinone and beyond in the electron-transport chain. [a]Means based on 16 measurements, [b]Mean based on 30 measurements.

(g_w) is 102.38 ± 2.85 mmol m^{-2} s^{-1}, and presently may be the only published value for this fern species based on a search of the literature. Additional detailed studies of the rate of g_w for *N. exaltata* when grown at different temperatures within its tolerance range and variations in vapor pressure deficit (VPD) are needed to better describe its habitat requirements. Moreover, a more systematic study of its resilience to desiccation is needed, although there is evidence that it may be more resistant than some other commonly cultivated mesophytic ferns (Anderson, 2023), and more research is needed to compare the desiccation tolerance of *N. exaltata* relative to other ferns and major groups of plants (Perera-Castro et al., 2020).

The intensity of light during growth, expressed as the daily light integral (DLI), influences growth of *N. exaltata* cultivars (Seltsam and Owen, 2022). For most cultivars of *N. exaltata*, the growth index, which is an integrated measurement of height and diameter, decreased linearly as the DLI increased from 3.2 to 17.2 mol m^{-2} d^{-1}, resulting in smaller compact plants. However, dry mass generally increased as the DLI increased incrementally from 3.2 to 10.7 and ultimately to 12.4 mol m^{-2} d^{-1} for most cultivars.

An optimum growth temperature for cultivated *N. exaltata* is in the range of 25°C, and lower temperatures are increasingly deleterious; particularly at the lowest studied temperature of 15°C (Hvoslef-Eide, 1991) where growth stagnates and eventually results in death. This temperature range may partially account for its restricted habitats largely within tropical and sub-tropical locations that seldom are cooler than c. 20°C. Based partially on the aforementioned evidence, a temperature of 25°C was selected for growth and physiological measurements in the study of *N. exaltata*.

In the present study (Table 1), the mean net photosynthesis rate was reported per leaf area (cm^2) as typically is used in ecological studies. In addition, the mean net photosynthesis rate was tabulated in relation to leaf fresh weight and dry weight expressed in grams. Net photosynthesis expressed per unit of leaf weight, especially dry weight, has the added advantage in ecological studies of indicating how much photosynthetically fixed carbon is added relative to existing leaf biomass, and can serve as an indicator of efficiency in plant primary production. At the highest light intensity used in this study (100 µmol m^{-2} s^{-1}), the net photosynthesis gain per unit dry weight was c. 5,490 nmol CO_2 g_{dw}^{-1} min^{-1}, equivalent to 1,497 nmol carbon g_{dw}^{-1} min^{-1}.

To provide a broader context for the results of this study, Table 4 provides data on the mean net photosynthesis rate of *N. exaltata* in this study compared to prior results with other fern species either obtained by the author, or published by other researchers who obtained estimates of photosynthesis under sufficiently similar environmental conditions and measurement metrics to those used in this study. Most of the estimates summarized in Table 4 are for typically mesophytic species that may be reasonably compared to the data for *N. exaltata* obtained in this research study. However, some were cultivated ferns while others were studied in the natural environment.

The mean net photosynthesis rate of *N. exaltata* reported in this research is moderately high compared to available data for some other representative fern species (Table 4), particularly for results at a light intensity of 100 µmol m^{-2} s^{-1}. In previous research, Gago et al. (2013) reported photosynthesis rates for young fully developed leaves of cultivated *N. exaltata*. Based on their published graphical data of mean net photosynthesis rates, the results they obtained for young leaves for varying light intensities (PPFD) of 10, 25, 50 and 100 µmol m^{-2} s^{-1} were as follows: 0.34, 1.04, 2.00, 2.90 (expressed as µmol CO_2 m^{-2} s^{-1}). For comparison, data are presented for eight young leaves analyzed in this study. The respective mean net photosynthesis rates for the same range of PPFD values were 0.49, 1.02, 1.59, and 2.72. Based on this evidence, the photosynthesis results obtained here are fairly comparable to estimates based on data published by Gago et al. (2013), particularly considering possible differences in conditions of cultivation, origin of the *N. exaltata* plants and the analytical equipment used to obtain the photosynthesis data. Furthermore, Gago et al. (2013) reported a mean dark respiration rate of 0.15 µmol CO_2 m^{-2} s^{-1} for *N. exaltata* compared to 0.16 µmol CO_2 m^{-2} s^{-1} obtained in this study (Table 2). The fluorescence mean leaf F_v/F_m value of 0. 80 (ET_0/RC = 1.15 and ψo = 0.74), shown in Table 3, is comparable to other data for fern species in favorable growth environments, but it can be much lower when the ferns are under stress (Sivanesan et al., 2014;

Table 4. Comparative data for mean photosynthesis rates among some examples of fern species.

Species	Photosynthesis photon flux density (PPFD) (µmol m^{-2} s^{-1})			
	10	25	50	100
	Mean photosynthesis rate (µmol CO_2 m^{-2} s^{-1})			
Adiantum capillus-veneris[a]	0.31	0.67	1.07	1.38
Adiatnum tibeticum[a]	0.36	0.64	0.91	1.08
Asplenium finlaysonianum[b]	0.60	1.20	2.00	2.60
Asplenium platyneuron[a]	0.25	0.40	0.63	1.63
Blechnum discolor[c]	0.50	1.00	2.30	3.10
Blechnum gibbum[d]	0.30	0.80	1.70	2.90
Dryopteris lepidopoda[a]	0.34	0.82	1.26	1.57
Dryopteris marginalis[e]	0.92	1.95	2.90	3.64
Nephrolepis exaltata[a]	0.45	0.99	1.48	2.21
Polystichum acrostichoides[f]	0.20	0.90	1.20	2.50
Pteridium aquilinum[c]	0.52	1.00	2.00	3.60
Rumohra adiantiformis[g]	0.20	0.28	1.20	1.84

Source: [a]Author's data, [b]Zhang et al. (2009), [c]Hollinger (1987), [d]Gago et al. (2013), [e]Sessa and Givinish (2014), [f]Prats and Brodersen (2020), and [g]Stamps et al. (1994).

Winkel and Wood, 2022).

Additional systematic research on the desiccation tolerance of *N. exaltata* cv. Bostoniensis with comparison to naturally occurring *Nephrolepis* species is needed to more clearly delineate the properties of the cultivar that make it amenable to indoor and garden cultivation. This may elucidate more clearly why the Bostoniensis cultivar is so readily adapted to cultivation, and also to delineate its survival strategies compared to those of naturally occurring species.

Moreover, from an evolutionary and ecological perspective, it would be advantageous to have additional physiological ecology studies comparing *N. exaltata* to other terrestrial species (e.g., *Nephrolepis cordifolia* (L.) Presl. and *Nephrolepis pectinata* (Willdenow) Schott.) and those that are also found as epiphytes such as *Nephrolepis biserrata* (Sw.) Schott. and *Nephrolepis undulata* J. Sm. This may provide additional evidence to complement current studies on the molecular genetic, phylogenomic, and biogeographic relationships among *Nephrolepis* spp. *(*Hennequin et al., 2010; Yahaya et al., 2016).

CONFLICT OF INTERESTS

The author has not declared any conflict of interests.

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