
EXPLAINING RARITY OF THE NARROWLY ENDEMIC *DIPTEROCARPUS CF. CONDORENSIS* BY *IN SITU* PHYSIOLOGICAL MEASUREMENTS**Le Buu Thach⁽¹⁾, Christa Critchley⁽²⁾**

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ABSTRACT: Comparative physiological attributes, obtained by chlorophyll fluorescence and gas exchange techniques, of restricted *Dipterocarpus cf. condorensis* and widespread *Shorea roxburghii* species that are actually co-located in Ta Kou Nature Reserve - Binh Thuan Province, provided essential information for understanding rarity of *D. condorensis*. The narrowly endemic *D. condorensis* had similar photosynthetic performance to the locally abundant *S. roxburghii* in more common habitats in which ground water tables are deep (>20m), but had significantly higher photosynthetic activities in its specific habitat, where the ground water level is shallow (<10m). These differences are probably the consequence of evolutionary trade-offs, and represent specializations of the endemic *D. condorensis* which is only successful in habitat where the ground water is accessible. However, while adaptive in this habitat, these traits may reduce success in other more common habitats in this region.

Key words: Chlorophyll fluorescence; *Dipterocarpus cf. condorensis*; gas exchange; photosynthetic; rarity.

INTRODUCTION

Most of the dominant trees in forests of Southeast Asia belong to the *Dipterocarpaceae* family. Besides their role as ecological keystone species, they are major sources of wood and resin in the region. In Vietnam, dry open forests dominated by two dipterocarp species, *Dipterocarpus cf. condorensis* and *Shorea roxburghii* G. Don., play an important role in the balance of ecology and landscape along the southern coast. *Dipterocarpus cf. condorensis* is a newly recognised species, endemic to Vietnam and should be considered as critically endangered because of its limited

distribution in fragmented small populations, its sparse regeneration and severe human impacts [1]. By contrast, *Shorea roxburghii*, despite being assessed as endangered in the IUCN Red List, is a common dipterocarp in South-eastern Vietnam, unusual because it is adapted to withstand adverse climatic conditions and soil types [2]. *Shorea roxburghii* occurs in dry evergreen or deciduous forests and bamboo forests ranging from lowland to mid-elevation, often on sandy soils in several Asian countries including Cambodia, India, Lao People's Democratic Republic, Malaysia, Myanmar, Thailand and Vietnam.

A previous study suggested that the cause of rarity in *D. condorensis* may be restriction to a rare habitat [1]. It occurs as a dominant tree in forests that superficially resemble to those of the more common *S. roxburghii*, which dominates forests immediately adjacent to the *D. condorensis* populations.



Figure 1. Forests dominated by *D. condorensis* occur at low elevation (2-50 m), adjacent to wetland forest dominated by *Melaleuca cajuputi* (left), and are burnt frequently.

These two species grow in dry open forests with climatic conditions characteristic of tropical monsoonal climates: average annual temperatures of 26-27°C, annual rainfall of 1100 to 1500 mm, dry season lasting 5-6 months (i.e. from November to April) in which there are 3-4 months with no rain. For this reason, drought conditions are inherent in this type of forest, and combined with sandy soil, drought becomes very severe at the end of the dry season (February/March). In addition to a restriction in available water, soil drying induces a decrease in nutrient availability, in particular nitrogen with strong interactive effects on plant growth and function [3].

Comparisons of sites dominated by *D. condorensis* with climatically and edaphically

similar sites dominated by *S. roxburghii* and using co-occurring species composition as a relative measure of habitat specificity, found that sites dominated by *D. condorensis* were unique. Only two factors distinguished the two forests: ground water tables and forest fires. Forests dominated by *D. condorensis* are located in an area with a shallow ground water table (<10m) and are affected more frequently by forest fire than the forest dominated by *S. roxburghii*. In contrast, the forest dominated by *S. roxburghii* are characterized by a deep ground water table (>20m) and are not usually burnt.

It can be therefore assumed that the environmental conditions for the two species in their natural habitats are identical. The deeper ground water level in the forest dominated by *S. roxburghii* can be considered equivalent to the water stress treatment.

The present case study examined physiological differences between *D. condorensis* and *S. roxburghii* and any association with differences in their dominance. Le 2007 [4] suggested that physiological data, obtained by chlorophyll fluorescence and gas exchange techniques, may provide information for understanding rarity rare plant species.

MATERIAL AND METHODS

Study area

The study was carried out in the Ta Kou Nature Reserve, Binh Thuan province (Figure 2). This nature reserve extends from 10°

41°28'' to 10°53'01'' N latitude and from 107°52'14'' to 108°01'34'' E longitude. Two sites were chosen: a forest dominated by *D. condorensis* near the Headquarters of Ta Kou Nature Reserve management board premises and a forest dominated by *S. roxburghii* located in a central area of the Nature Reserve.



Figure 2. Location of Ta Kou Nature Reserve

Measurements and data analysis

Measurements were performed in February at the middle of the dry season when drought was becoming extreme.

Chlorophyll fluorescence measurement

Chlorophyll *a* fluorescence transients were measured with the Plant Efficiency Analyzer (Handy PEA; Hansatech Ltd., King's Lynn, Norfolk, UK). The fluorescence signal is digitised at different rates depending upon the different phases of the induction kinetic. For the first 300 μ s fluorescence is sampled at 10 μ s intervals. This provides excellent time resolution of minimal fluorescence intensity (F_0) and the initial rise kinetics. The time resolution of digitisation is then switched to slower acquisition rates as the kinetics of the fluorescence signal slow. A one second

measurement records 120 data points (Handy PEA Manual User's guide).

For chlorophyll fluorescence, 15 fast fluorescence transients were recorded on the upper surfaces of the youngest fully expanded leaves of 5 plants per species (three leaves per plant). During the measurement, the samples were shielded from ambient light by the clips to reach a dark adapted state (adaptation 30 min). Light intensity was 3000 μ mol photons $m^{-2}s^{-1}$ to generate maximal fluorescence intensity (F_m) for all species. Chlorophyll fluorescence data were analyzed according to the JIP test to calculate the performance index as described in Table 1.

Analysis of the chlorophyll fluorescence transient: the JIP test

The JIP-test [5] [6] [7] was used to analyse each chl *a* fluorescence transient. The shape of the OJIP transient has been found to be sensitive to stress such as excess light, temperature, drought, atmospheric CO_2 or ozone as well as chemical influences [8] [9] [10] [11] [12] [13].

The following data from the original measurements were used: maximal fluorescence intensity (F_m), minimal fluorescence intensity (F_0), fluorescence intensity at 300 μ s ($F_{300 \mu s}$) required for calculation of the initial slope (M_0) of the variable (*V*) component of the transient, and the fluorescence intensity at 2 ms (the J-step) denoted as F_j .

The JIP-test represents a translation of the original data to biophysical parameters that

quantify the energy flow through PSII. The initial stage of photosynthetic activity of a reaction center (RC) complex is regulated by three functional steps, namely absorption of light energy (ABS), trapping of excitation energy (TR) and conversion of excitation energy to electron transport (ET). The parameters which all refer to time zero (onset of fluorescence induction) of the flux ratios or yields are the maximum quantum yield of primary photochemistry ($\phi_{P_0} = TR_0/ABS = F_v/F_m$) and the efficiency ($\psi_0 = ET_0/TR_0$) with which a trapped exciton can move an electron into the electron transport chain beyond Q_A^- .

Recently, the performance index on an absorption basis, PI, was introduced as a multi-parametric expression of these three independent steps contributing to photosynthesis. The performance index was calculated as (for a review see Strasser *et al.* 2000, 2004)

$$PI = [\gamma_{RC}/(1 - \gamma_{RC})][(\phi_{P_0}/(1 - \phi_{P_0}))][(\psi_0/(1 - \psi_0))]$$

where γ is the fraction of reaction centre chlorophyll (Chl_{RC}) per total chlorophyll

($Chl_{RC+Antenna}$). Therefore, $\gamma/(1-\gamma) = Chl_{RC}/Chl_{Antenna} = RC/ABS$. This expression can be de-convoluted into two JIP-test parameters and estimated from the original fluorescence measurements as $RC/ABS = [(F_{2ms}-F_0)/4(F_{300\mu s} - F_0)] \cdot (F_v/F_m)$. The factor 4 is used to express the initial fluorescence rise per 1 ms. The expression RC/ABS represents the active RC density on a chlorophyll basis. The decrease of RC/ABS means an increase in the size of the chlorophyll antenna serving each reaction center. The contribution of the light reactions to primary photochemistry is estimated according to the JIP-test as $[\phi_{P_0}/(1 - \phi_{P_0})] = F_v/F_0$. This component of the PI represents the performance due to the trapping probability (P_{TR}). The contribution of the dark reactions is derived as $[\psi_0/(1-\psi_0)] = (F_m - F_{2ms})/(F_{2ms} - F_0)$. It is the performance due to the conversion of excitation energy to electron transport (P_{ET}). The formulae in Table 1 illustrate how each of the above-mentioned biophysical parameters is calculated from the original fluorescence measurements [5] [12].

Table 1. Summary of formulae and definitions of some JIP test parameters

Parameter	Calculation	Description
Extracted and technical fluorescence parameters		
Relative variable fluorescence at 2 ms: V_J	$= (F_{2ms} - F_0)/(F_m - F_0)$	For unconnected PSII units, equals the fraction of closed RCs at 2ms expressed as a proportion of the total number of RCs that can be closed.
Net rate of PSII closure: $(dV/dt)_0$	$= 4 (F_{300\mu s} - F_0)/(F_m - F_0)$	An approximation of the slope at the origin of the fluorescence rise $(dF/dt)_0$ which is a measure of the rate of the primary

or Mo		photochemistry. It is a net rate because the reduced Q_A can be reoxidised via electron transport beyond Q_A .
The flux ratios or yields		
Trapping probability: TRo/ABS or ϕ_{P_0}	$= (1 - F_0)/F_m$ $= F_v/F_m$	The probability that an absorbed photon will be trapped by the PSII RC with the resultant reduction of Q_A .
Electron transport probability: ψ_0 or ET _o /TR _o	$= 1 - V_j$	The probability that an electron residing on Q_A will enter the electron transport chain.
Performance index PI	$= [\gamma_{RC}/(1 - \gamma_{RC})][(\phi_{P_0}/(1 - \phi_{P_0}))][(\psi_0/(1 - \psi_0))]$ $= (RC/ABS)(P_{TR})(P_{ET})$	Multi-parametric expression of these three independent steps contributing to photosynthesis.
RC/ABS $= \gamma_{RC}/(1 - \gamma_{RC})$	$= (V_j \cdot \phi_{P_0})/M_0$ $= [(F_{2ms} - F_0)/4(F_{300\mu s} - F_0)] \cdot (F_v/F_m)$	The contribution to the PI of the active RC density on a chlorophyll basis.
Performance due to ϕ_{P_0} (P_{TR})	$= [\phi_{P_0}/(1 - \phi_{P_0})]$ $= F_v/F_0$	The contribution to the PI of the light reactions for primary photochemistry
Performance due to ψ_0 (P_{ET})	$= [\psi_0/(1 - \psi_0)]$ $= (F_m - F_{2ms})/(F_{2ms} - F_0)$	The contribution to the PI of the dark reactions

Among several parameters obtained from the chlorophyll fluorescence measurements, the F_v/F_m ratio (= TR_o/ABS) and the performance index PI were selected for comparison of statistically significant differences. The reason for this choice was that the F_v/F_m ratio is the most widely used photosystem II efficiency indicator. This parameter has been shown to correlate with the number of functional PSII complexes. Many studies have used this ratio as an indicator for stress tolerance or sensitivity [14] [15] [16]. However, some studies have shown this parameter to be quite insensitive to change [17] [18] [10] [5] [13]. Force *et al.* (2003) [19]

demonstrated the advantage of using a number of JIP test derived fluorescence parameters to evaluate PSII function, rather than using only the F_v/F_m ratio. Recently, (for a review see [5] [12]), the PI was introduced and has been used as to quantify the effects of environmental factors such as chilling, heat, drought, chromate, ozone or urban injuries on photosynthesis in several studies [20] [9] [21] [22] [13]. According to the definitions of Strasser *et al.* (2000, 2004) [5] [12], the PI combines 3 values quantifying the three functional steps of photosynthetic activity by a PSII reaction center complex, from light energy absorption, trapping of excitation energy and

conversion of this energy to electron transport occurring in PSII. Research by Hermans *et al.* (2003) [22] showed that PI is more sensitive to environmental change and correlates well with plant vigour and performance. In order to understand in more detail the response in structure and behavior of PSII to the environment, the three components of the PI were compared.

Gas exchange measurements

Leaf gas exchange was measured, between 08:00 am and 12:30 pm, using a portable photosynthesis system LI-6400 (Li-Cor, Inc., Lincoln, NE, USA) equipped with an artificial light source 6400-02B Red-Blue. Light intensity used is $1500 \mu\text{mol m}^{-2}\text{s}^{-1}$ which was equal to ambient light intensity in both species. The air CO_2 concentration entering the leaf chamber was $400 \mu\text{l l}^{-1}$ and airflow rate was $500 \mu\text{mol s}^{-1}$. All gas exchange measurements were performed over 6 cm^2 of leaf on attached, intact, youngest fully expanded leaves with 15 replicates (5 plants, 3 leaves per plant) for each species. Five readings were recorded for each leaf after net CO_2 assimilation rate had reached steady state and were.

Intercellular CO_2 concentration (C_i , $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$), transpiration rate ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and stomatal conductance for water vapour (g_s in $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) were simultaneously determined. The equations used to calculate all gas exchange parameters in this study were essentially derived by von Caemmerer and Farquhar (1981). Instantaneous water use efficiency (WUE) was

calculated as described by Leffler *et al.* (2004) [23]: $\text{WUE} (\text{mmol mol}^{-1} \text{ s}^{-1}) = \text{CO}_2 \text{ assimilation rate} (\mu\text{mol m}^{-2}\text{s}^{-1}) / \text{transpiration rate} (\text{mmol m}^{-2} \text{ s}^{-1})$.

Statistical analyses were performed using SPSS 10.0 software (SPSS Inc.: Chicago, USA). One-way ANOVA (Bonferoni post-hoc test) at $P < 0.05$ was used to test whether there were significant differences between mean values.

RESULTS AND DISCUSSION

The performance index (PI) of the two dipterocarp species were similar in the forest dominated by *S. roxburghii*, while significant differences in PI ($P < 0.05$) between *D. condorensis* and *S. roxburghii* were found in the forest dominated by *D. condorensis* (Figure 3). These results indicate that the two species exhibited similar photosynthetic performance in sites where the ground water level is deep. In contrast, the higher PI of *D. condorensis* in the forest dominated by *D. condorensis*, was consistent with its dominance in this forest, where the ground water level is shallower.

Two previous studies [1] [24] reported that *D. condorensis* may be better able to reach the ground water because it has a deep root system to 10m depth [1] and maintains higher leaf water potentials than other canopy species in the dry open forest dominated by dipterocarp species [24]. By maintaining higher water uptake in the dry season, *D. condorensis* can maintain a higher number of active reaction centers, indicated by higher RC/ABS (Table 2,

$P < 0.05$), and thus maintain higher photosynthetic rates than *S. roxburghii*.

Table 2. Chlorophyll fluorescence and gas exchange parameters of *D. condorensis* and *S. roxburghii* in the forest dominated by *S. roxburghii* and forest dominated by *D. condorensis*. Values are averages of 15 replicates (\pm SEM). Different superscript letters indicate significant differences between the two species in each type of forest (ANOVA, Bonferoni post-hoc test, $P < 0.05$).

Species Parameters	Forest dominated by <i>S. roxburghii</i>		Forest dominated by <i>D. condorensis</i>	
	<i>D. condorensis</i>	<i>S. roxburghii</i>	<i>D. condorensis</i>	<i>S. roxburghii</i>
Chlorophyll fluorescence parameters				
Fv/Fm	0.80 (0.005)	0.79 (0.01)	0.81 (0.003)	0.80 (0.005)
RC/ABS	0.56 (0.01)	0.58 (0.01)	0.66 (0.01) ^a	0.59 (0.01) ^b
P _{TR}	4.05 (0.12)	3.81 (0.12)	4.37 (0.10)	3.94 (0.11)
P _{ET}	0.91 (0.07)	1.09 (0.07)	1.19 (0.05)	1.10 (0.05)
PI	2.20 (0.16)	2.50 (0.13)	3.46 (0.14) ^a	2.70 (0.13) ^b
Gas exchange parameters				
A _{max}	1.10 (0.23)	0.69 (0.21)	4.70 (0.42) ^a	1.52 (0.06) ^b
g _s	0.14 (0.01)	0.016 (0.001)	0.08 (0.01) ^a	0.037(0.004) ^b
C _i	357 (2.27)	309 (14.56)	263 (1.43)	261(11.72)
WUE	0.11 (1.42) ^b	2.92 (0.99) ^a	0.60 (0.01) ^b	1.04 (0.11) ^a

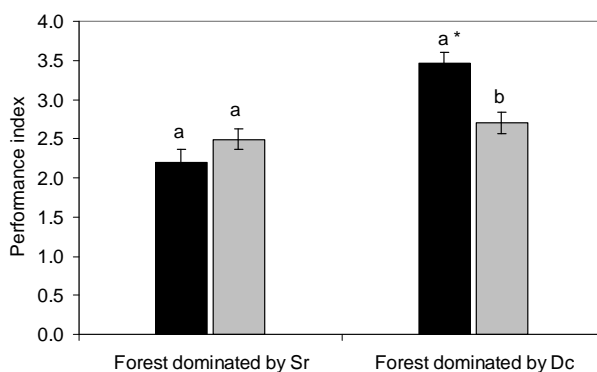


Figure 3. The performance index PI of *D. condorensis* (Dc, black bars) and *S. roxburghii* (Sr, grey bars) in the forest dominated by *S. roxburghii* (left) and forest dominated by *D. condorensis* (right). Values are averages of 15 replicates (\pm SEM). Different letters indicate significant differences between the two species in each type of forest. The asterisk indicates significant difference between the two forest types (ANOVA, Bonferoni post-hoc test, $P < 0.05$).

Gas exchange data measured in *D. condorensis* and *S. roxburghii* in the two forest types were consistent with chlorophyll fluorescence data, showing similar values between the two species in the forest dominated by *S. roxburghii*, but not in *D. condorensis* dominated forest (Figure 4 and Table 2). The lower PI (as well as their three components), coupled with lower A_{max} of the two dipterocarp species in forest dominated by *S. roxburghii*, compared to values in *D. condorensis* dominated forest indicated that

plants were suffering more severe drought in the site with deeper ground water level. Under extreme drought conditions, the plants' fitness in the field depends on its ability to efficiently use and take up water. Water use efficiency of *S. roxburghii*, measured in *S. roxburghii* dominated forest, was 26-fold higher than that of *D. condorensis* ($P < 0.001$, Table 2). This difference was much less in the forest dominated by *D. condorensis*, i.e. only 1.7-fold ($P < 0.05$).

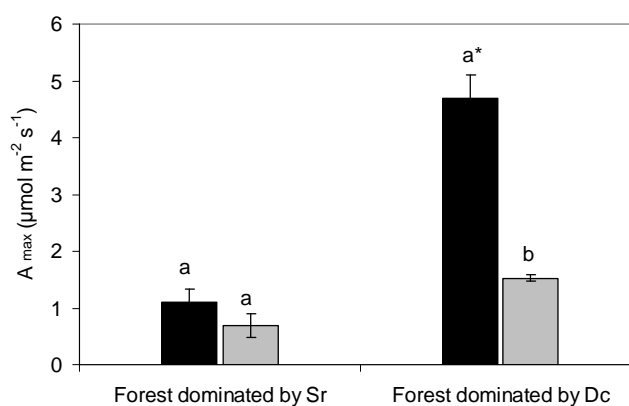


Figure 4. Maximum CO₂ assimilation rates of *D. condorensis* (Dc, black bars) and *S. roxburghii* (Sr, grey bars) in the forest dominated by *S. roxburghii* (left) and forest dominated by *D. condorensis* (right). Values are averages of 15 replicates (\pm SEM). Different letters indicate significant differences between the two species in each type of forest. The asterisk symbol indicates significant differences for each species between the two forest types (ANOVA, Bonferoni post-hoc test, $P < 0.05$).

S. roxburghii exhibited adaptive capacity to low water availability by using less water, increasing water use efficiency and thus being more tolerant and resistant to water deficits. It, therefore, dominates the forest where the ground water level is deep, partly because of high elevation, or inaccessible with only a thin layer of rocky soil.

The narrowly endemic *D. condorensis* appeared to be adapted to habitat with a shallower ground water table, by increasing root length to take up water better than *S. roxburghii*. Thus, *D. condorensis* can maintain considerable carbon fixation during the dry season which leads to higher growth rates and dominance in the forest where the ground water table is shallow (<10m). However, investing

heavily into root growth most likely contributes to this species' success in this habitat but may make it less competitive in habitats where ground water becomes inaccessible. This explanation is consistent with the hypothesis that edaphic endemics are genetically fixed specialists, with physiological and morphological adaptations necessary for survival in their specific environments. In other habitats these relatively fixed traits may be maladaptive and incur a fitness cost [25] [26].

CONCLUSION

The narrowly endemic *D. condorensis* had similar photosynthetic performance to the locally abundant *S. roxburghii* in more common habitats of coastal sandy soil region in which ground water tables are deep (>20m), but had significantly higher photosynthetic activities in its specific habitat, where the ground water level is shallow (<10m). These differences between the endemic *D. condorensis* and locally abundant *S. roxburghii* are probably the consequence of evolutionary trade-offs, and represent specializations of the endemic *D. condorensis* which is only successful in habitat where the ground water is accessible. However, while adaptive in this

habitat, these traits may reduce success in other more common habitats in this region. *S. roxburghii* probably have higher photosynthetic performance in wet season when water availability is high. Thus, physiological attributes and water potential should be tested in wet season to find out this possibility. With regard to conservation, because the endemic *D. condorensis* is restricted by its water demand, the sites for reforestation programs of this species should be considered where these meet its water requirements.

Findings in this field study confirmed the usefulness of the comparative approach based on physiological profiles to explain plant rarity. The Performance Index (PI), obtained from Chlorophyll fluorescence measurement, emerged as a more sensitive indicator for environmental stress than F_v/F_m . The Performance Index and its three components are useful quantitative and non-destructive indicators of plant stress which can be used in situ to assess plant populations. In addition, using gas exchange technique will provide the photosynthetic carbon gain at the leaf level and confirm the results of Chlorophyll fluorescence technique.

GIẢI THÍCH TÍNH PHÂN BỐ HỢP QUA KHẢO SÁT ĐẶC ĐIỂM SINH LÝ CỦA
DẦU CÁT -*DIPTEROCARPUS CF. CONDORENSIS*

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TÓM TẮT: Các kỹ thuật huỳnh quang diệp lục và trao đổi khí đã được sử dụng để so sánh các đặc điểm quang hợp của loài Dầu Cát -*Dipterocarpus cf. condorensis* (đặc hữu hẹp) và loài Sến-*Shorea roxburghii* (thông thường) tại Khu BTTN Tà Kóu - Tỉnh Bình Thuận. Kết quả khảo sát đã góp phần giải thích nguyên nhân phân bố hẹp của Dầu Cát. Dầu Cát có hiệu suất quang hợp tương tự như Sến ở các khu vực cả hai loài cùng mọc nơi có mực nước ngầm sâu (> 20m), nhưng có hoạt động quang hợp cao hơn ở nơi mực nước ngầm cạn (<10m). Quá trình tiến hóa đã hình thành các đặc tính chuyên biệt của Dầu Cát, giúp cho loài này phát triển mạnh ở những nơi có mực nước ngầm cạn. Tuy nhiên, những thuộc tính này có thể là nguyên nhân làm giảm sức cạnh tranh của Dầu Cát ở các môi trường sống khác phổ biến hơn trong khu vực.

Từ khóa: Huỳnh quang diệp lục, *Dipterocarpus cf. condorensis*, trao đổi khí, quang hợp.

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