



# *Nerium oleander* indirect leaf photosynthesis and light harvesting reductions after clipping injury or *Spodoptera eridania* herbivory: High sensitivity to injury

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## ABSTRACT

Variable indirect photosynthetic rate ( $P_n$ ) responses occur on injured leaves after insect herbivory. It is important to understand factors that influence indirect  $P_n$  reductions after injury. The current study examines the relationship between gas exchange and chlorophyll a fluorescence parameters with injury intensity (% single leaf tissue removal) from clipping or *Spodoptera eridania* Stoll (Noctuidae) herbivory on *Nerium oleander* L. (Apocynaceae). Two experiments showed intercellular  $[CO_2]$  increases but  $P_n$  and stomatal conductance reductions with increasing injury intensity, suggesting non-stomatal  $P_n$  limitation. Also,  $P_n$  recovery was incomplete at 3 d post-injury. This is the first report of a negative exponential  $P_n$  impairment function with leaf injury intensity to suggest high *N. oleander* leaf sensitivity to indirect  $P_n$  impairment. Negative linear functions occurred between most other gas exchange and chlorophyll a fluorescence parameters with injury intensity. The degree of light harvesting impairment increased with injury intensity via lower (1) photochemical efficiency indicated lower energy transfer efficiency from reaction centers to PSII, (2) photochemical quenching indicated reaction center closure, and (3) electron transport rates indicated less energy traveling through PSII. Future studies can examine additional mechanisms (mesophyll conductance, carbon fixation, and cardenolide induction) to cause *N. oleander* indirect leaf  $P_n$  reductions after injury.

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## 1. Introduction

Plants allocate resources to growth, maintenance, and reproduction, while also using resources to resist or tolerate abiotic and biotic stresses. When a constitutive plant defense (e.g., secondary metabolites) is breached, resources have already been allocated to the failed constitutive defense and additional resources may be allocated to induced defense responses. In cases where resource allocation to chemical defenses limits resource allocation to compensatory responses to injury, this may help explain a trade-off between plant chemical defense and growth [1] or tolerance [2] that can have fitness consequences [3,4]. Indirect  $P_n$  reduction (reduced activity on remaining tissue near sites of herbivory injury)

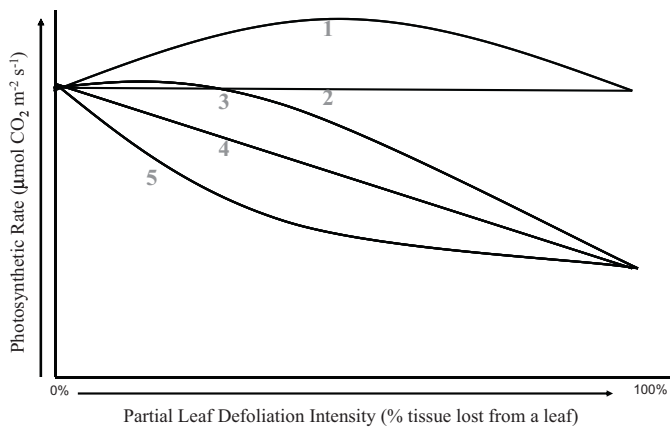
has been suggested to result from a secondary metabolism trade-off with primary physiology, since resources allocated to chemical defense are unavailable for, or cause downregulation of, photosynthesis [5–7; but see 8]. Yet, only a subset of plant species tested have indirect  $P_n$  reductions from defoliation herbivory [9–12], and variable responses can occur within a single species [8]. The degree of chemical defense investment by a plant can correlate with degree of indirect  $P_n$  reductions after herbivory [6; but see 8], so chemically well defended plants may be more prone to experience indirect  $P_n$  reductions after herbivory. Studying individual leaf  $P_n$  responses to injury are relevant because leaves are important for mediating whole plant responses to herbivory [13] and  $P_n$  is a highly sensitive leaf response assay to herbivory [10,14]. At the scale of a leaf one can study mechanisms by which injury affects photosynthesis on the leaf and neighboring uninjured (or regrowth) leaf  $P_n$  responses [9].

Plant responses to herbivory can be studied by comparing injured leaf responses across an injury intensity continuum relative to responses of uninjured leaves (zero injury intensity). Plant damage response curves indicate whether a plant performance parameter changes after injury and the relevant range(s) of injury intensity if the parameter changes. Several theoretical damage response functions (Fig. 1) are possible [derived from 15]: overcompensation ('1'), tolerance ('2'), tolerance at low injury intensities that transitions to negative linear reductions at higher injury levels

**Abbreviations:** ETR, electron transport rate;  $C_i$ , intercellular  $[CO_2]$ ; JA, jasmonic acid;  $F_v/F_m$ , light-adapted leaf maximal photochemical efficiency;  $F_m$ , maximal light-adapted leaf fluorescence;  $F_o$ , minimal light-adapted leaf fluorescence;  $q_p$ , photochemical quenching;  $P_n$ , net photosynthetic rate; PSI, photosystem I; PSII, photosystem II; PI, post-injury; SAW, *Spodoptera eridania*-southern armyworm;  $F'_v$ , steady state light-adapted leaf fluorescence;  $g_s$ , stomatal conductance;  $F'_v$ , variable light-adapted leaf fluorescence.

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**Fig. 1.** Some basic theoretical leaf photosynthetic response curves to single leaf injury intensity are shown to represent different major leaf responses to injury. These functions include: (1) overcompensatory function (positive slope over part of the injury range), (2) photosynthetic tolerance function (slope of zero), (3) compensatory function (initial slope of zero transitioning to a negative slope), (4) negative linear function (consistent negative slope), and (5) high injury sensitivity function (initial highly negative slope transitioning to a slope near zero).

(‘3’), consistent parameter decreases with each unit of injury (‘4’), and high injury sensitivity at low injury levels (‘5’) transitioning to little additional reduction at higher injury levels. The meaning of a damage response curve depends on the scale of the parameters. Damage response curves were initially studied to examine yield relationships with defoliation intensity at a field scale [16], which indicated the range of injury at which a particular crop was sensitive to yield loss and helped to develop economic injury levels [15,17]. Damage response curves applied to the scale of individual plants [17] are used to study plant tolerance and fitness consequences of injury [18]. Here the functions are considered for a single leaf (Fig. 1), where  $P_n$  is the dependent variable examined in response to % single leaf tissue loss as the independent variable to indicate the degree of  $P_n$  change that occurs on remaining tissue of an injured leaf [12,14,19–21]. This informs us about leaf  $P_n$  sensitivity to change after injury and at which range(s) of tissue loss  $P_n$  has large (or small) changes per unit of injury. Several leaf gas exchange and chlorophyll a fluorescence parameters can also be measured to provide insights about why  $P_n$  changes [22], and which parameters are most closely associated with  $P_n$  changes after injury [6,23].

### 1.1. Study species

*Nerium oleander* L. (Apocynaceae) is an evergreen perennial dicot shrub/bush native to Mediterranean regions, but has been planted in most tropical and subtropical regions globally. It is grown as a yard and street median ornamental plant in southern USA states [24]. Common oleander shrubs vary from 1 to 6 m in height and have variable numbers (~5–100) of branches. Many complete, narrow lanceolate leaves occur along a branch. A single leaf (see Fig. 2A) can be 5–21 cm long, 1–4 cm at the widest part of the leaf, and cover 10–40 cm<sup>2</sup> (personal observation). Leaf drop is rare, so a leaf can remain on a plant >1 year. Only a few specialist insect and no vertebrate herbivores feed on *N. oleander*. This is because *N. oleander* is a chemically well defended plant that contains high total cardenolide levels and specific compounds like oleandrin and nerine [25]. Oligophagous specialist defoliators of *N. oleander* inside the USA include larvae of the oleander polka dot moth (*Syntomeida epilais* Walker) [24] and the spotted oleander moth (*Empyreuma affinis* Rothschild) [26], while outside the USA there are the oleander hawkmoth (*Daphnis nerii* L.) and common crow butterfly (*Euploea core* Cramer). These four herbivore species were not observed at the study site. However, the generalist southern armyworm moth

(SAW; *Spodoptera eridania* Stoll) has been observed to feed on *N. oleander* (personal observation) and was able to be used in one experiment.

### 1.2. Research and hypothesis

I chose to study *N. oleander* leaf physiological responses to herbivory because it is a chemically well-defended species. Delaney [21] showed that mechanical clipping injury to single *N. oleander* leaves resulted in indirect  $P_n$  reductions on single injured leaves that had 50% tissue removal. Yet, what are the mechanisms that contribute to injured leaf indirect  $P_n$  reduction? The reported experiments extend Delaney [21] by examining *N. oleander* gas exchange and chlorophyll a fluorescence parameter response curves across a single leaf injury intensity continuum (% tissue loss from a single leaf), using clipping injury in two experiments and SAW larval herbivory in a third. Since  $P_n$  reductions had already been documented on injured *N. oleander* leaves [21], neither  $P_n$  overcompensatory (‘1’ from Fig. 1) nor tolerance (‘2’ from Fig. 1) response curves were expected. The specific objectives addressed with the reported experiments were: (1) to determine which leaf  $P_n$  theoretical responses (‘3’, ‘4’, or ‘5’ from Fig. 1) apply to *N. oleander* after clipping injury or SAW herbivory and (2) to compare the  $P_n$  relationship to leaf injury intensity with other gas exchange and light-adapted leaf chlorophyll fluorescence parameters. Mechanical injury is useful to examine leaf time course response to injury because the injury is imposed immediately, so post-injury (PI) gas exchange measurements in the first 120 min are relative to a specific injury time. Insect herbivory is spread out over temporal scales of minutes or hours, so it is extremely difficult in the first 120 min post-injury to be compared with a specific injury reference time. Gas exchange parameters were measured to indicate whether injury leads to stomatal or non-stomatal limitations to photosynthesis, and chlorophyll a fluorescence parameters provided insights about how injury affected light harvesting reactions. Non-stomatal limitations to photosynthesis after herbivory can include mesophyll limitations due to light harvesting impairment [6,8,12,23,27–30], and impairment of photosynthetic carboxylation reactions [20,30,31].

## 2. Materials and methods

Experimental *N. oleander* plants were located ~500 m north of the Xavier University of Louisiana (XULA) campus in New Orleans, LA. Plants received ambient precipitation, which is 150 cm annually for New Orleans. I was able to limit photosynthetic measurements to one leaf from a given branch on an oleander plant, and each plant was used in only one experiment.

### 2.1. Clipping injury

Baseline and post-injury photosynthesis measurements were collected with an infra-red gas analyzer. The measurement location (1.6 cm diameter circle) was located halfway along the length of each *N. oleander* leaf whether it remained uninjured (Fig. 2A) or subsequently had tissue removal (Fig. 2B–D). Baseline measurements were collected and immediately followed by clipping injury on the measured leaf in each of two experiments. A ruler was used to measure leaf length and width; leaves included in the experiment were 12–15 cm long and 3–4 cm wide. Leaf clipping with scissors removed ~10% of the length on one side of a leaf without any midrib injury to result in a ~5% photosynthetic tissue removal section (Fig. 2B). When there was >1 tissue removal section, a ~2 mm wide strip of tissue separated each tissue removal section (Fig. 2C and D). Leaves with ≤45% tissue removal had all removal sections located along the same side of the leaf relative

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