Terminal blades in *Macrocystis* and their unexplored links to functional biology

Understanding patterns of growth and primary productivity of the giant kelp, *Macrocystis pyrifera*, is of significant ecological and commercial value. Not only does the biogenic structure of this species provide food and shelter for a multitude of organisms (North 1971), but the floating canopies also allow harvest by boat of tissues for economic pursuits (Vásquez et al. 2014). Interest in predicting its productivity is, therefore, not surprising (Jackson 1987, Hadley et al. 2015). Success in doing so is challenged by the inherent difficulty in characterizing the biomass and rates of tissue turnover in a subtidal species as large and complex as *Macrocystis*. That whole fronds within a thallus are progressively senesced and replaced is widely recognized (North 1971, Arzee et al. 1985, North 1994), the phenomenon is identifiable via morphological characteristics (North 1971, Lobban 1978, van Tussenbroek 1989) and recent work suggests that frond age is an important predictor for rates of frond loss (Rodriguez et al. 2013). Monitoring age structure in *Macrocystis*, however, is an indirect metric for predicting fluxes in biomass because age is a construct of time without biological input: other factors that interact with time (e.g., abiotic conditions, growth rate) may modulate rates of senescence (Kirkwood and Melov 2011, Mencuccini and Munné-Bosch 2017). In terrestrial plants, determinate growth is frequently a biological precursor to senescence of the determinate organ and/or initiation of activity in adjacent organs (see Thomas 2013). Although determinate growth in *Macrocystis* is identifiable via morphological characteristics (North 1971, Arzee et al. 1985, North 1994), the phenomenon has been given minimal attention. In this note, I share observations of the prevalence of determinate growth in *Macrocystis* and comment on potential research directions that would advance our understanding of giant kelp development, ecophysiology, and predictions of biomass turnover.

In 2013 and 2014, I conducted a series of field-based studies, all of which monitored growth rates of *Macrocystis* fronds in southeast New Zealand (see Stephens 2015:95; Stephens and Hepburn 2014, 2016). While selecting appropriate fronds to tag and monitor, many of the existing mature fronds (defined as fronds reaching the surface of the water) displayed malformed pneumatocysts (air bladders) at the end of the stipe where the apical meristem is typically located. Instead of the stipe and new blade divisions reducing in thickness and size, asymptotically, towards a cluster of meristematic cells at the stipe apex (Fig. 1a), an elongated or bulbous pneumatocyst (with blade) formed (Fig. 1b–f). It was later determined that these “abnormalities” were likely terminal blades (see North 1971:27; Fig. 1g), which can sometimes lack terminal pneumatocysts (Fig. 1h,i; Arzee et al. 1985). In addition to the suspected terminal blades in my studies, tissues throughout these fronds were often darker (Fig. 1f). Although I did not measure the biomechanical properties of these tissues, they also appeared more brittle (personal observation) compared to tissues in adjacent fronds within the same thallus. Due to the distinct morphology, fronds with putative terminal blades were initially excluded from growth measurements.

Despite selecting only *Macrocystis* fronds with indeterminate apical meristems, numerous tagged kelp developed terminal blades after 30-d of growth. I assessed whether these stipe ends (Fig. 1b–f) reflect terminal blades, and thus determinate growth, by comparing the rates of adult blade elongation, stipe elongation, and new blade production in putative determinate fronds to those that were indeterminate (Fig. 1a). This was necessary because only once has growth in fronds with terminal blade morphology been empirically tested (Arzee et al. 1985), demonstrating a depression in growth in terminal frond tips. Unpublished data from Stephens and Hepburn (2014) show that blade and stipe elongation rates of indeterminate fronds were 1.5-fold and 1.3-fold higher in the summer, respectively, than those of determinate fronds (nested ANOVA, df = 5, \(P < 0.001\); \(df = 5, P < 0.001\)), and that the production of new blades was 3.5-fold higher in indeterminate fronds (\(t\) test, \(df = 5, P < 0.001\): Note: only indeterminate fronds were tagged for observation and the development of terminal blades occurred sometime during the 30-d period, thus allowing for the formation of new blades prior to determinate transformation). During the winter, blade and stipe elongation rates within indeterminate fronds were 2.1-fold and 0.32-fold higher, respectively (nested ANOVA, \(df = 5, P < 0.001\); \(df = 5, P = 0.041\)), and the production of new blades was also higher by 2.3-fold (nested ANOVA, \(df = 5, P = 0.013\)). These data support the notion that the terminal blades are, in fact, indicative of determinate growth in *Macrocystis*.

In addition to growth metrics, the expression of terminal blades may not be randomly distributed across time. In one study (Hepburn and Stephens 2014; unpublished data), frond growth was measured across a water motion gradient in two geographically distinct regions (three sites each, \(n = 90\) per site) and across two seasons. Terminal...
blades formed in 36.1% ± 2.5% (mean ± SE) and 17.2% ± 4.0% of tagged fronds in the summer and winter, respectively, and the development of terminal blades did not significantly vary across regions (t test, df = 5, P = 0.861), sites (nested ANOVA, df = 5, P = 0.749), or the flow gradient within sites (nested ANOVA, df = 2, P = 0.890). In an independent year-long study, data (Stephens 2015) show that the fraction of terminal blades vacillates between 8.3% and 69.2% of total apical blade number (Appendix S2). Prevalence of terminal blades is highest during the spring/autumn and lowest during the summer/winter. It is important to note that spring and autumn are periods of transition between light limitation (winter) and nitrogen limitation (summer) in southeast New Zealand and that growth rates are typically highest in these seasons (Stephens 2015, Desmond et al. 2015). The fraction of terminal blades does not correlate with either blade or stipe elongation rates (blade growth, P = 0.14; stipe growth: P = 0.44) but it is difficult to ignore similarities in their seasonal patterns (Appendix S2).

Considering that ~70% of functional apical meristems can develop terminal blades after only 30 d, it is surprising that terminal blades have received so little attention. What factors contribute to determinate growth and eventual senescence, and why? As mentioned above, terminal blades were found only in mature fronds, after which, the biomechanical properties of tissues within those fronds appear more brittle and it is possible that rates of senescence in aged fronds (Rodriquez et al. 2013) are enhanced by drag forces inflicted upon these older, more brittle tissues (see Krumhansl and Scheibling 2012). In fact, tissue loss was 4.4-fold higher for canopy...
blades on terminal fronds compared to those growing on indeterminate fronds (Stephens and Hepburn 2014; unpublished data). Both the experimental removal (Geange 2014, Fox 2016) and natural senescence of canopy tissues (Rodriquez et al. 2013) resulted in increased initiation and growth rates of juvenile fronds in Macrocystis, implying that Macrocystis “perceives” losses in canopy biomass and responds by replacing it with new biomass, the tissues of which are likely more productive (see Jurik 1980, Rodriguez et al. 2016). A chicken-and-egg scenario then forms: is frond senescence a byproduct of factors associated with time-dependent age and associated reductions in physiological fitness (non-programmed), or does determinate growth trigger frond senescence to facilitate ecophysiological adaptation via new fronds (programmed; see Kirkwood and Melov 2011, Thomas 2013)? Within macroalgal research, the former is generally assumed while the latter is largely colloquial, and although the two are quite different and often opposing, they are sometimes confused as one in the same.

Whether ageing and senescence are programmed is an interesting and ongoing discussion in the literature (Kirkwood and Melov 2011, Skulachev 2011). Regardless, biological programming must first be rejected before accepting non-programmed senescence. When addressing the validity of programmed senescence in Macrocystis, the biological function of two tissue-turnover hypotheses described in terrestrial botany must be considered (see Chabot and Hicks 1982): (1) age-related physiological cost–benefit balancing with regard to productivity and (2) adaptive, physiological plasticity in response to a temporally heterogeneous environment. For the first, consider a kelp frond as an organ that accumulates carbon. Older leaf tissues have reduced photosynthetic efficiency and nutrient uptake, and therefore reduced carbon fixation and productivity (see Chabot and Hicks 1982). It is possible that older tissues within Macrocystis are voluntarily senesced to prioritize productivity in younger tissues, which is partially supported by Rodriguez et al. (2013), who found that frond age explained 28% of frond loss rates. My studies do not track frond age, but terminal blades were observed in only mature fronds, which were also the oldest. Alternatively, it is also possible that Macrocystis senescences fronds to adapt to a changing environment. Some terrestrial plants, for example, replace springtime leaves that are adapted to high light with shade-adapted leaves after the canopy thickens and reduces light penetration (Jurik 1980). That the fraction of terminal blades is highest during the periods of environmental transition (i.e., spring and fall, Fig. 1e) and that this fraction increases when elongation rates are declining rapidly during periods of environmental stress (i.e., low nutrients and low light; see Stephens 2015), could suggest that fronds ill-adapted to existing environmental conditions are voluntarily shed to prioritize the growth of new fronds that are physiologically adapted to these environmental conditions. In fact, North (1994) noted that during stressful conditions, fronds that do not reach the water’s surface (non-mature) may develop terminal blades, supporting the second tissue-turnover hypothesis.

The work discussed here suggests that the presence and dynamics of terminal blades are a non-random attribute of Macrocystis biology, the formation of which is associated with determinate growth. Further corroboration of this, alone, is enough to advance our knowledge about the functional and evolutionary biology of kelps because determinate growth is typically not referred to as a developmental trait in seaweeds. If determinate growth is, in fact, linked to rates of progressive senescence and frond initiation, terminal blade morphology could prove to be a useful tool in assessing and predicting standing crop biomass and biomass flux. Lastly, the potential connections to adaptive physiological plasticity as a modular species need to be investigated and may help explain Macrocystis’ success as a large, cosmopolitan species that thrives in habitats frequently characterized by seasonal stressors.

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Appendix S1

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Fig. S1. Temporal variation in the prevalence of terminal blades (gray shading, %) plotted against rates of blade elongation (solid line, RGR d$^{-1}$) and stipe elongation (dashed line, RGR; d$^{-1}$). Error bars represent ±SE (n < 11). Note: the terminal blade data are derived from initially indeterminate fronds that were tagged for growth studies, these indeterminate fronds developed into determinate fronds (as indicated by the presence of a terminal blade) within a 30-d period.