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Seedling growth and physiological responses of two sandplain *Banksia* species differing in flood tolerance

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Abstract

Banksia littoralis (Proteaceae) inhabits winter-wet locations and wetland fringes that are prone to seasonal flooding events on the Swan Coastal Plain. To survive in these locations, *B. littoralis* seedlings must be able to tolerate periods of flooding or complete submergence if establishment is to be successful. Flood tolerance was assessed in seedlings of *B. littoralis* subjected to 104 days of continual soil waterlogging by comparing changes in seedling growth and leaf ecophysiology with those of well-watered plants. Flood tolerance was also assessed in seedlings of *Banksia prionotes*, a species that grows in drier locations on the Swan Coastal Plain. As expected, *B. prionotes* was unable to survive long periods of soil waterlogging or submergence (97% mortality after 72 days of flooding). Both species responded to flooding by closing their stomates and reducing photosynthetic capacity, although *B. littoralis* was able to recover lost photosynthetic potential when flooded conditions subsided. After 72 days of flooding, there was a substantial decrease in relative growth rate in flooded *B. prionotes* seedlings, compared to that of well-watered plants, although this was not associated with significant differences in biomass allocation. Flood-affected *B. littoralis* seedlings were significantly smaller than well-watered seedlings after 72 days of flooding, but were the same size after 104 days. Flood tolerance enables *B. littoralis* seedlings to survive exceptionally wet winter-spring months when flooding events are more likely to occur, although surviving the annual summer drought may be more important to sustain seedling establishment.

Keywords: *Banksia littoralis*, *Banksia prionotes*, flooding, photosynthetic capacity, stomatal conductance, submergence

Introduction

Species confined to wetland fringes and winter-wet depressions are being lost from Perth's Swan Coastal Plain as a result of declining groundwater levels and poor groundwater recharge, due to local and regional abstraction, and successive years of below average rainfall (Aplin 1976; Groom *et al.* 2000, 2001). The loss of Swamp Banksia (*Banksia littoralis* R.Br.; Proteaceae) trees and its replacement by more xeric *Banksia* species has occurred over the past 40 years (Groom *et al.* 2001) as winter-wet swamps become filled with sand from the surrounding dunes (Heddle 1980; Muir 1983). This may have been because *B. littoralis* trees were unable to access sufficient moisture to meet their summer water-use requirements as soil moisture content and groundwater levels declined (Groom *et al.* 2001; Groom 2002; Zencich 2003).

Decreasing occurrence of flooding events may be an alternative explanation for the loss of tree species from wetland fringes, as it directly impacts seedling recruitment and establishment. Flooding is not necessarily required to sustain the recruitment and survival of wetland tree seedlings (Froend *et al.* 1993) but may provide sufficient soil moisture for seedlings to survive post-winter and subsequent dry summers. During flooding events, seedlings of wetland species must either be flood-tolerant or tolerate periods of submergence if seedling establishment is to be successful. The ability of seedlings to tolerate flooding or submergence may be an important contributor to a species' ecological distribution.

This paper compares the seedling flood response strategies of *Banksia littoralis*, a tree species known to tolerate flooding events, and a congener from the Swan Coastal Plain that typically grows in drier locations (*B. prionotes* Lindl.) (Groom 2004). Differences in flood responses and ability to tolerate complete submergence are measured in terms of changes in growth and leaf ecophysiology.

Methods

Setup and Design

Banksia seeds were obtained from Nindethana Seed Supply (Albany, WA). Seeds were imbibed in tap water for 30 min before being placed in plastic petri dishes lined with moist filter paper, and germinated at 15°C, the optimal germination temperature for other southwest

Australian *Banksia* species (Cowling & Lamont 1987). Once germinated, seeds were transferred to shallow seedling trays containing washed, coarse white sand in a temperature controlled glasshouse. In January 2001, 80 seedlings per species were transferred into square pots 18 cm tall by 8 cm wide, each containing coarse white sand with a top layer of small stones. Flooding trials began on 27 April 2001 and concluded 104 days later.

Flooding was achieved using three 60 L clear plastic tubs each containing 10 pots per species. Tubs were filled with tap water until the pot, but not the seedling, was completely emersed. Another three tubs, set up exactly the same except with drainage holes, were watered twice a week for the duration of the flooding trial, and used as controls. Every two weeks seedlings were removed and all the tubs drained and scrubbed with tap water to remove the build up of algae on the tub walls. Seedlings were then put back into the tubs and refilled with fresh tap water. Four seedlings per species were removed from the tubs to assess the species' ability to recover after 36 days of flooding.

To examine the effects of submergence, 5–10 seedlings per species were placed in a 90 L clear plastic tub. This was filled with tap water until all plants were completely submerged. This tub was cleaned and refilled with fresh tap water every two weeks. Physiological data (stomatal conductance, chlorophyll fluorescence) were not collected from submerged plants because the leaves were constantly under water.

Stomatal conductance

Stomatal conductance and chlorophyll fluorescence data were measured approximately every 2 weeks from 4 plants per species and treatment. Midday stomatal conductance (g_s) was measured on recently formed, fully-expanded leaves using a portable infra-red gas analyser (LCi, ADC Bioscientific Ltd, Hoddesdon, England) attached to a leaf chamber. Measurements were taken on relatively cloud-free, sunny days, with data collected within 1 min of enclosing the leaf. Conductance data were collected at ambient humidity and CO_2 concentrations and when light intensity (PAR) was greater than 1000 µmol m^{-2} s^{-1}. Day time air temperature within the glasshouse varied from 23–25°C.

Chlorophyll fluorescence

Chlorophyll fluorescence was measured on attached leaves using a modulated chlorophyll fluorometer (OS1-FL, Opti-Sciences, Tyngsboro, Massachusetts, USA). Midday measurements of potential photochemical efficiency of Photosystem II (F_v/F_m) were recorded after a leaf dark adaptation time of 30 min using leaf clips provided by the fluorometer manufacturer. A reduction in the F_v/F_m ratio commonly indicates the occurrence of photoinhibition, particularly in plants exposed to periods of stress (Maxwell & Johnson 2000). Measurements were recorded from 4 plants per species and treatment.

Actual efficiency of Photosystem II photochemistry, or quantum yield (Φ_{PSII}), was measured under natural light conditions on light-exposed leaves, using an additional light pulse during the midday period. Φ_{PSII} was calculated by the instrument according to Genty *et al.* (1989). Φ_{PSII} was collected at PAR light intensity > 1000 µmol m^{-2} s^{-1} and is used as an indication of overall photosynthetic performance (Maxwell & Johnson 2000).

Seedling growth

Four seedlings per species and treatment were harvested at the beginning of the experiment (27 April 2001), towards the end (4 July) and at the end (7 August, *B. littoralis* only). Each seedling was separated into leaf, shoot (stem and side branches) and root components and

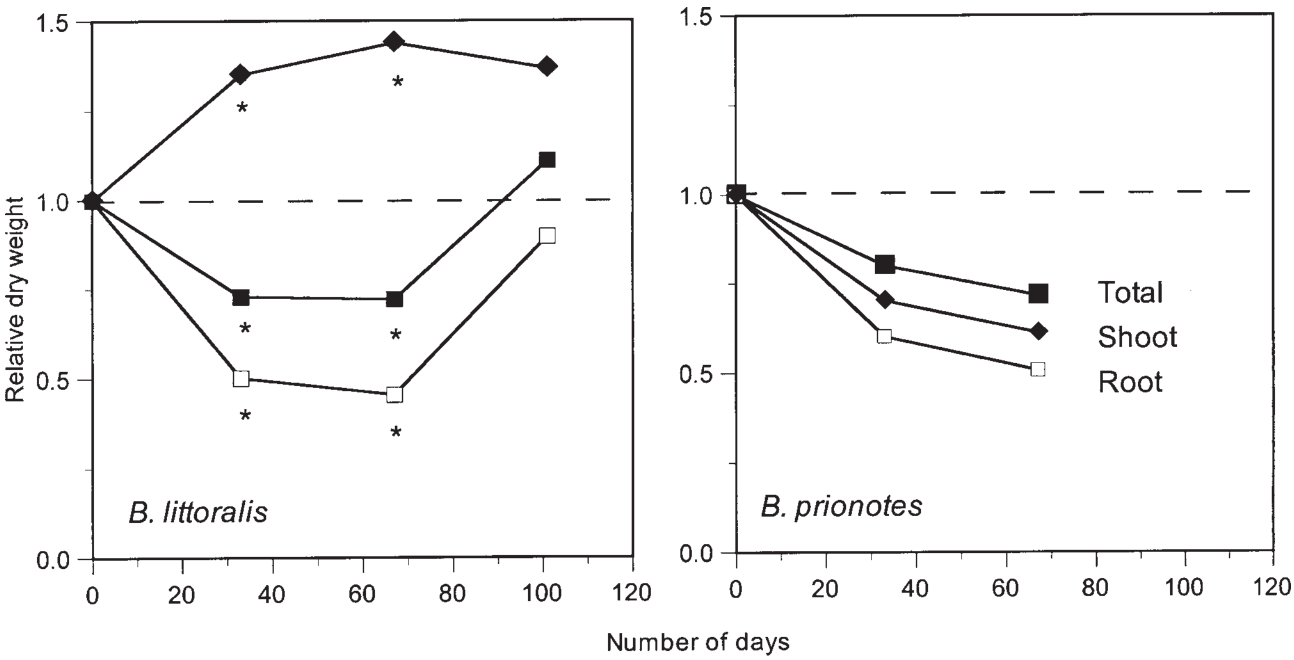

Figure 1. Relative total (closed square), shoot (diamond) and root (open square) dry weight of *Banksia* seedlings subjected to continuous flooding. Data are means of four replicates and relative to data obtained for well-watered (control) seedlings. Dashed line (at 1) indicates where flood and control data would be equal. Asterisk indicates significant differences ($P<0.05$) between flooded and well-watered seedlings. SE bars are not included because of their overlapping nature.

Table 1

Growth parameters of *Banksia littoralis* seedlings before and after an exposure to an extended flooding regime. Values are mean ± SD for 4 plants. % change indicates an increase (+) or decrease (-) in relation to the pre-flooding data. *P* values based on a *t*-test comparing well-watered and flooded data. RGR = relative growth rate; LAR = Leaf area ratio.

		72 days of flooding			% change	
	Before Flooding	Well-watered	Flooded	P	Well-watered	Flooded
Dry weight (g)						
Total	0.66 ± 0.06	1.80 ± 0.36	1.30 ± 0.19	0.0415	+173	+97
Shoot	0.24 ± 0.03	0.49 ± 0.11	0.70 ± 0.13	0.0465	+104	+192
Roots	0.42 ± 0.06	1.31 ± 0.28	0.60 ± 0.16	0.0042	+212	+43
Root:shoot ratio	1.80 ± 0.29	2.75 ± 0.52	0.88 ± 0.31	0.0009	+53	-51
RGR – total (mg g^{-1} day^{-1})		13.9	9.4			
RGR – shoot (mg g^{-1} day^{-1})		23.6	12.7			
LAR (mm^2/ mg shoot)	5.60 ± 0.42	4.46 ± 0.23	3.48 ± 0.52	0.0143	-20	+39
Seedling height (cm)	10.6 ± 2.1	14.6 ± 3.8	14.8 ± 3.2	0.7979	+38	+39
		104 days of flooding				
Dry weight (g)						
Total		1.70 ± 0.44	1.89 ± 0.80	0.8103	+158	+186
Leaves & shoots		0.77 ± 0.28	1.06 ± 0.40	0.2939	+221	+342
Roots		0.93 ± 0.27	0.84 ± 0.54	0.5373	+121	+100
Root:shoot ratio		1.30 ± 0.52	0.80 ± 0.40	0.1754	-28	-55
RGR – total (mg g^{-1} day^{-1})		9.1	10.1			
RGR – shoot (mg g^{-1} day^{-1})		11.2	14.3			
LAR (mm^2/ mg shoot)		3.79 ± 0.55	3.17 ± 0.28	0.0918	-32	-43
Seedling height (cm)		13.6 ± 3.6	13.9 ± 2.5	0.8253	+28	+31

their weight recorded after drying for 24 h at 60°C. Leaf area was measured on fresh samples using a digital image analyser (WinDIAS, Delta-T Devices, Cambridge, UK). Stem lengths were also recorded. Relative growth rates (RGR) were calculated on a shoot and total dry biomass basis as described by McGraw and Garbutt (1990).

Results

Banksia littoralis

After 72 days of flooding, flooded *B. littoralis* seedlings were significantly smaller (total dry weight) than the well-watered seedlings, with more dry mass allocated to their stem and leaves, but less leaf area per shoot weight (Table 1). The root:shoot ratios of well-watered seedlings were 53% greater than pre-flood seedlings, in contrast to flooded seedlings where root:shoot ratios were 51% lower. Overall shoot mass of flooded seedlings was significantly greater than that of the well-watered controls (Fig 1) whereas root mass was significantly lower. There was no significant difference between flooded and well-watered seedlings in any of the growth parameters measured after 104 days of flooding (Table 1). Well-watered seedlings had a greater relative growth rate than flooded seedlings after 72 days, in contrast to relative growth rate after 104 days. There was no seedling mortality during the 104 days of flooding.

There were significant declines in g_s, Φ_{PSII} and F_v/F_m

Table 2

Stomatal conductance (g_s), maximum (F_v/F_m) and actual quantum yield (Φ_{PSII}) of Photosystem II photochemistry of *Banksia littoralis* seedlings before and after exposure to an extended flooding regime. Values are mean ± SD for 4 plants. % change indicates an increase (+) or decrease (-) in relation to the well-watered data. *P* values based on a *t*-test comparing well-watered and flooded data.

		17 days of flooding			
	Before Flooding	Well-watered	Flooded	P	% change
g_s (mol m^{-2} s^{-1})	0.19 ± 0.07	0.25 ± 0.02	0.11 ± 0.04	0.0407	-56
Φ_{PSII}	0.43 ± 0.12	0.44 ± 0.03	0.19 ± 0.04	0.0008	-57
F_v/F_m	0.84 ± 0.02	0.82 ± 0.02	0.68 ± 0.09	0.0299	-17
		74 days after flooding			
g_s (mol m^{-2} s^{-1})		0.18 ± 0.06	0.07 ± 0.02	0.0164	-61
Φ_{PSII}		0.44 ± 0.06	0.32 ± 0.05	0.1230	-28
F_v/F_m		0.86 ± 0.02	0.76 ± 0.08	0.0454	-12

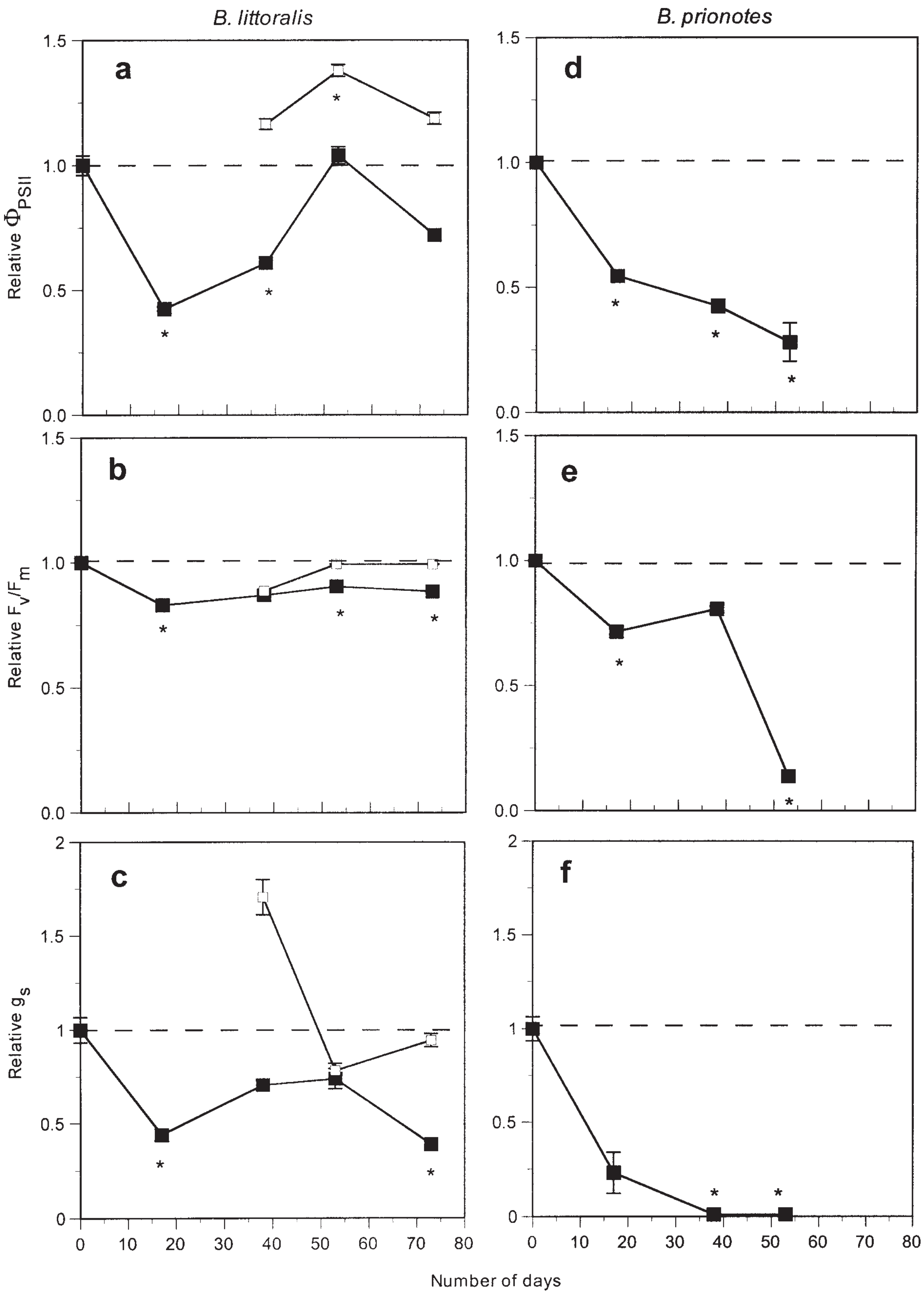

Figure 2. Relative fluorescence (Φ_{PSII}, F_v/F_m) and stomatal conductance (g_s) of *Banksia littoralis* (a–c) and *B. prionotes* (d–f) seedlings subjected to continuous flooding. Closed squares represent flooded seedlings, open squares (*B. littoralis* only) represents seedlings removed from the flooding process and allowed to recover. Data are mean ± SE for four replicates and are relative to data obtained for well-watered (control) seedlings. Dashed line (at 1) indicates where flood and control data would be equal. Asterisk indicates significant differences (P<0.05) between flooded affected and well-watered seedlings.

Table 3

Growth parameters of *Banksia prionotes* seedlings before and after an exposure to an extended flooding regime. Values are mean ± SD for 4 plants, including some recently dead plants. See Table 1 for details on statistics and abbreviations.

		72 days of flooding			% change	
	Before Flooding	**Well-watered**	**Flooded**	***P***	**Well-watered**	**Flooded**
Dry weight (g)						
Total	0.53 ± 0.14	1.14 ± 0.51	0.70 ± 0.17	0.1604	+115	+32
Shoot	0.34 ± 0.10	0.57 ± 0.26	0.41 ± 0.12	0.3735	+68	+21
Roots	0.22 ± 0.064	0.57 ± 0.25	0.30 ± 0.08	0.6370	+159	+36
Root:shoot ratio	0.57 ± 0.14	1.01 ± 0.12	0.72 ± 0.22	0.0791	+77	+22
RGR – total (mg g^{-1} day^{-1})		10.6	3.9			
RGR – Shoot (mg g^{-1} day^{-1})		7.2	2.6			
LAR (mm^2/ mg shoot)	5.37 ± 0.89	6.22 ± 1.37	3.61 ± 0.51	0.0205	+16	-33
Seedling height (cm)	0.9 ± 0.4	1.6 ± 0.8	0.8 ± 0.3	0.0323	+78	-11

resulting from flooding on the 17th day (Table 2), resulting in 17% to 56% decreases in relation to pre-flood values. After 74 days of flooding, all three variables were less than those of well-watered seedlings (Fig. 2), although there was no significant different in Φ_{PSII} between well-watered and flooded seedlings (Table 2). Stomatal responses were overall linearly positively correlated with Φ_{PSII} (r = 0.65, P < 0.05), with *B. littoralis* possessing a higher g_s at a given Φ_{PSII} than *B. prionotes.*

There was no significant difference in the physiology of seedlings after 8 days recovery from flooding compared with well-watered seedlings (Fig 2 a–c). This was despite Φ_{PSII} and g_s displaying greater values than the well-watered controls. Φ_{PSII} was the only parameter to show significant differences after 18 days of recovery (P = 0.0454). There was no significant physiological difference between recovered and control plants after 38 days of recovery (Fig 2 a–c).

Banksia prionotes

After 28 days of flooding 22% of *B. prionotes* seedlings had died. An additional 14 seedlings died 4 days later taking the cumulative mortality to 45%. After 53 days of flooding seedling mortality was 83%. The experiment was concluded after 72 days, with only two of the original 60 seedlings still alive. All seedlings used to monitor post-flooding recovery died after 8 days.

After 72 days of flooding the percentage difference in dry weight increased by 21 to 36% (Table 3) compared to pre-flood values, and was less than that for control plants (68 to 159%). This difference between flooded and well-watered plants is reflected by the relative growth rate values over the same time period. There was no significant difference in total dry weights, the weights of the stem and roots, or root:shoot ratios (Table 3) between well-watered and flooded after 72 days of flooding. Despite this, well-watered seedlings were significantly taller (P = 0.0323), and produced more leaf area per shoot dry weight. Throughout the period of flooding, total, shoot and root dry weights of flooded seedlings were consistently less than that of the well-watered seedlings (Fig 1), but there was no significant difference between the two treatments.

After 17 days of flooding there was a significant decline in stomatal conductance (g_s), compared with that of pre-flooded seedlings (P = 0.0097). This was despite no significant difference in g_s between well-watered and flooded treatments measured on the 17th day, attributed to the larger standard deviation of well-watered seedlings. After 38 days of flooding g_s was <0.01 mol m^{-2} s^{-1} and remained so when remeasured after 54 days (Fig 2).

There was a significant decline in actual (Φ_{PSII}) and maximum (F_v/F_m) efficiency of photosystem II

Table 4

Stomatal conductance (g_s), maximum (F_v/F_m) and actual quantum yield (Φ_{PSII}) of Photosystem II photochemistry of *Banksia prionotes* seedlings before and after exposure to an extended flooding regime. See Table 2 for details.

		17 days of flooding			
	Before Flooding	**Well-watered**	**Flooded**	***P***	**% change**
g_s (mol m^{-2} s^{-1})	0.14 ± 0.05	0.13 ± 0.11	0.04 ± 0.01	0.2765	-69
Φ_{PSII}	0.41 ± 0.05	0.43 ± 0.02	0.24 ± 0.09	0.0312	-44
F_v/F_m	0.80 ± 0.04	0.84 ± 0.02	0.60 ± 0.15	0.0222	-29
		54 days after flooding		***P***	
g_s (mol m^{-2} s^{-1})		0.12 ± 0.06	<0.01	-	-
Φ_{PSII}		0.54 ± 0.06	0.15 ± 0.11	0.0044	-72
F_v/F_m		0.84 ± 0.01	0.11 ± 0.08	0.0001	-87

Table 5

Shoot and root dry weights of *Banksia prionotes* and *B. littoralis* seedlings after 54 days of total submergence in comparison to well-watered seedlings. Values are mean ± SD for 4 plants. % change indicates an increase (+) or decrease (-) in relation to pre-flood data. *P* values based on a *t*-test comparing well-watered and submerged data.

	54 days of submergence			% change
	Well-watered	**Submerged**	***P***	**Submerged**
B. prionotes				
Dry weight (g)				
Total	1.14 ± 0.51	0.33 ± 0.08	0.0070	-38
Shoot	0.57 ± 0.26	0.18 ± 0.08	0.0166	-47
Root	0.57 ± 0.25	0.16 ± 0.02	0.0038	-27
Root:shoot ratio	1.01 ± 0.12	1.1 ± 0.63	0.7774	+93
RGR - total (mg g^{-1} day^{-1})	14.5	-8.7		
RGR - shoot (mg g^{-1} day^{-1})	9.7	-12.5		
B. littoralis				
Dry weight (g)				
Total	1.80 ± 0.36	1.02 ± 0.23	0.0236	+54
Shoot	0.49 ± 0.11	0.37 ± 0.07	0.1801	+35
Root	1.31 ± 0.28	0.65 ± 0.25	0.0227	+55
Root:shoot ratio	2.75 ± 0.55	1.83 ± 0.90	0.1483	+2
RGR – total (mg g^{-1} day^{-1})	18.9	8.2		
RGR – shoot (mg g^{-1} day^{-1})	13.5	8.4		

photochemistry after 17 days of flooding compared with that of pre-flooded seedlings (Fig 2), and a significant difference when compared with well-watered seedlings (Table 4). As flooding continued, there was a significant decrease in both fluorescence parameters, resulting in a -72 to -87% change after 54 days. A decrease in Φ_{PSII} was associated with decreased stomatal conductance, as the two variables were positively linearly correlated (r = 0.88, P < 0.01).

Submergence

All submerged *B. littoralis* seedlings survived after 54 days, although many of the existing leaves were a lighter green compared to controls. Φ_{PSII} measurements taken on the 17th day were not significantly different (P = 0.3500) between well-watered (0.44 ± 0.03) and submerged seedlings (0.32 ± 0.20). Submerged plants had significantly lower total and root dry weight than well-watered plants, but not shoot dry weight (Table 5), with a 54% increase in total dry weight in relation to pre-flood seedlings. There was no significant difference in root:shoot ratios between the control and submerged plants.

All *B. prionotes* seedlings died after 54 days of submergence. Φ_{PSII} measurements taken on the 17th day showed a significant difference (P = 0.0050) between well-watered (0.41 ± 0.03) and submerged seedlings (0.21 ± 0.05). Submerged plants had significantly lower dry weight than well-watered plants (Table 5), with a 38% reduction in total dry weight in relation to pre-flood seedlings, represented by negative RGR values. There was no significant difference in root:shoot ratios between controls and submerged plants.

Discussion

Mortality, physiology and growth data support the hypothesis that *B. littoralis* seedlings are more flood tolerant than *B. prionotes* seedlings. *Banksia prionotes* was unable to survive long periods (> 70 days) of flooding, and displayed many of the physiological and morphological responses typical of flood-intolerant species. These include stomatal closure, which has been associated with a decrease in root hydraulic conductivity (Davies & Flore 1986; Else *et al.* 2001), a decline in photosynthetic capacity, reduced growth and increased mortality. *Banksia littoralis* also displayed a reduction in stomatal conductance and photosynthetic performance (Φ_{PSII}) in response to flooding, but not to the same extent as *B. prionotes* and, like most flood tolerant species, was able to resume photosynthesis after the flooding treatment ceased.

There is evidence to suggest that a decrease in stomatal opening and its limitation on CO_2 intake, followed by a decrease in total leaf area, are the main factors contributing to reduced carbon uptake and reduced whole plant biomass in flooded seedlings (Smith & Moss 1998; Mielke *et al.* 2003). This is partially supported by this study, except that photosynthetic processes were directly affected by damage sustained to photochemical reaction centres (as indicated by a reduction in F_v/F_m and Φ_{PSII} ratios). Despite this reduction in photosynthetic performance, *B. littoralis* was able to maintain levels of Φ_{PSII} that were > 50% of that in well-watered plants, resulting in an increase in biomass that was 97% greater than pre-flood plants after 72 days of flooding. For flooded *B. prionotes* seedlings a reduction in relative growth rate can be directly linked to a reduction in photosynthetic activity, despite the lack of significant differences in biomass allocation.

The higher rate of *B. prionotes* mortality may be closely linked to the roots inability to survive and function under oxygen-deficient conditions. This caused severe physiological dysfunction, resulting in a progressive decline in photosynthetic performance. For *B. littoralis* seedlings to survive more than 100 days of flooding implies adaptations that promote oxygen and nutrient uptake. This may include the formation of aerenchyma tissues or presence of hypertrophied lenticels (Kozlowski 1997), although these were not examined.

Although flood survival is important for *B. littoralis* seedlings, flooding events are episodic in nature and restricted to winter and spring months. Surviving the annual summer drought may be more important for seedling recruitment. Physiological data suggests that *B. littoralis* is inherently less water-use efficient (assuming $\Phi_{PSII}/g_s \approx$ photosynthesis/water transpired) than xeric congeners, and is similar to results obtained for *B. littoralis* under drought conditions (Groom 2002). Seedlings of *Banksia littoralis* can be classified as 'water spenders' in response to flooding (this paper) and gradual summer drought (Groom 2002). By maintaining a relatively high rate of stomatal conductance (0.1–0.2 mol m^{-2} s^{-1}; 50–75% of well-watered plants) during flooding, *B. littoralis* was able to support sufficient photosynthetic activity to allow shoot growth to occur at a rate similar to, or greater than, well-watered plants. *Banksia littoralis* seedlings are able to maintain stomatal conductance between 0.2–0.3 mol m^{-2} s^{-1} until volumetric soil moisture contents drop below 2% (Groom 2002). For *B. littoralis* seedlings, an overall higher g_s, as compared to more xeric congeners, may be viewed as a flood survival technique and/or a response to year-round access to reliable water sources.

The lack of post-flooding physiological recovery and the greater sensitivity of *B. prionotes* to waterlogging is not surprising considering this species characteristically occurs on well-drained, sandy soils (Taylor & Hopper 1988). *Banksia littoralis* inhabits winter-wet locations and wetland fringes, tolerating up to 104 days of water inundation (this study), without detrimental impacts on leaf ecophysiology once waterlogging ceased. This enables *B. littoralis* seedlings to survive exceptionally wet winter-spring months when flooding events are more likely to occur. *Banksia littoralis* seedlings also survived and sustained growth after being fully submerged for 54 days, although in this experiment the leaves tended to discolour and were prone to epiphytic algae growth. Although the impact of submergence on seedling recruitment in *B. littoralis* has yet to be quantified, species that grow well when waterlogged or grown in flood conditions are unlikely to do as well when subjected to extensive periods of submergence (Parolin 2001; Mauchamp & Méthy 2004).

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