

Biomass and Above-ground Productivity of Salt-marsh Plants in South-eastern Australia

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Abstract

The above-ground biomass of three dominant salt-marsh vascular plants (*Juncus kraussii*, *Sarcocornia quinqueflora* and *Sporobolus virginicus*) was measured to assess both spatial and temporal variation and to provide baseline data. Additionally, the culm dynamics of the rush *J. kraussii* were measured so that above-ground productivity could be estimated.

No distinct seasonal patterns were detected in above-ground biomass in *J. kraussii*. Averaged over all sites and times, the above-ground biomass of *J. kraussii* was 1116 g dry weight m⁻². Culms are replaced annually, hence standing crop approximated annual above-ground productivity. Much of the dead above-ground biomass appears to accumulate in the upper marsh, as evidenced by the elevated nutrient and organic carbon content of the soil there relative to the sediment in the mangrove zone. Above-ground biomass of the decumbent perennial grass *Sporobolus virginicus* and the procumbent perennial chenopod *Sarcocornia quinqueflora* showed no consistent spatial or temporal trends. The above-ground standing crops of these species were about one-third that of *J. kraussii*.

Introduction

Functional aspects of salt-marsh plant ecology have, for the most part, centred on either European or North American species, and there are few studies of salt-marsh plants in Australia (see Adam 1990). This inadequacy of salt-marsh research was emphasized in the review of research topics in Australian marine ecology by Fairweather (1990), in which the number of papers documenting salt-marsh research was the lowest for any marine habitat.

The production and ecological fate of organic matter produced by salt-marshes have been extensively studied in the Northern Hemisphere, particularly on the eastern seaboard of North America (Adam 1990). Biomass and productivity of salt-marsh plants in Australia have seldom been studied, although the values reported by Congdon and McComb (1980) for the rush *Juncus kraussii* in Western Australia are comparable with values reported for *J. roemerianus* in North America (Adam 1990).

Measurements of internode development, rate of culm extension and longevity of culms, together with measurements of standing crop, provide the basis for understanding the productivity of salt-marshes. Demographic methods have been widely used to analyse plant growth (McGraw and Garbutt 1990), to study leaf longevity of mangrove species (e.g. Gill and Tomlinson 1971; Saenger and Moverley 1985; Duke 1990; Clarke 1994), and to examine culm extension and longevity in salt-marsh plants (e.g. Congdon and McComb 1980; Eleuterius and Caldwell 1981). These methods were applied to salt-marsh plants as part of the present study.

Many studies of salt-marsh performance rely on extrapolation of measurements made in limited areas over a limited time to estimate productivity of whole marshes or regions (Adam 1990). In addition, few studies of salt-marsh performance have been designed to yield a quantitative baseline against which future changes in performance can reliably be detected.

Thus, estimates of spatial and temporal variation in performance, at a range of scales, are needed for a clearer understanding of salt-marsh performance, reliable detection of disturbance and cost-effective monitoring (Underwood 1993).

In south-eastern Australia, Jervis Bay and surrounding bays have been the focus of studies assessing the spatio-temporal variation in the distributions, abundances and performances of a wide range of biota (Ward and Jacoby 1992). During these studies, mangrove and salt-marsh distributions have been described in detail (Clarke 1993). Much of the upper salt-marsh at these localities is dominated by *Juncus kraussii*, whereas the lower salt-marsh, at the interface with the mangrove zone, is dominated by monospecific patches of *Sporobolus virginicus* or *Sarcocornia quinqueflora* (Clarke 1993).

This paper describes spatial and temporal variation in growth and above-ground biomass for *J. kraussii* and in above-ground biomass for *Sporobolus virginicus* and *Sarcocornia quinqueflora* in south-eastern Australia. In addition, it presents some preliminary information on the organic carbon and organic nitrogen content of the sediments.

Materials and Methods

Culm Dynamics of Juncus kraussii

Internode development, culm dynamics and culm growth of *J. kraussii* were measured in two inlets in Jervis Bay (Carama Inlet, 35°00'S, 150°47'E and Moona Moona Creek, 35°02'S, 149°40'E). Four plots (each about 400 m²) were selected in each inlet, and within each plot four randomly selected nodes were tagged during February 1989. The number of culms on each node was counted, and the initiation of new culms together with the death of older culms was recorded throughout the study. Each new culm was numbered, and the lengths of the living (green) and senescent (brown) components were measured separately at monthly intervals until December 1990. Growth and senescence of culms were assessed by means of the percentage of the total culm length represented by living material. Annual cumulative culm births and deaths and maximum green culm extension were compared among the four plots in a single-factor analysis of variance.

Above-ground Biomass

A pilot study was used to determine the size and number of quadrats required to achieve a 5% coefficient of variation for above-ground biomass of *J. kraussii*. As a result, all standing plant material was harvested from 0.5 x 0.5 m quadrats in three estuaries in south-eastern Australia (Port Hacking, Jervis Bay, and Batemans Bay). In Jervis Bay two inlets (Moona Moona Creek and Carama Inlet) were sampled, whereas one inlet was sampled in each of the other bays (Cabbage Tree Basin in Port Hacking, 34°08'S, 150°07'E, and Lattas Creek in Batemans Bay, 35°43'S, 150°11'E). In each inlet four plots were established, and within each of these plots four randomly selected replicate quadrats were harvested. Harvests were made at both inlets in Jervis Bay during 10 months: February 1989, 1990 and 1991; May 1989 and 1990, 1991; August 1989 and 1990; November 1989 and 1990. Harvests were made at the inlets in Port Hacking and Batemans Bay during six months: February 1990, May 1990, August 1989 and 1990, and November 1989 and 1990. Two harvests were partitioned into live culms, dead culms and reproductive components.

Analysis of variance (ANOVA) was used to assess variation in biomass among inlets, plots and times. Comparisons of biomass among the 10 harvests in the two inlets in Jervis Bay were made with a three-factor ANOVA. Harvests and inlets were fixed factors, and plots were nested as a random factor in inlets. Similarly, comparisons were made among the six harvests at Batemans Bay and at Port Hacking with a two-factor ANOVA. Harvests and plots were fixed factors. Comparisons were also made among the four inlets for harvests in November of 1989 and November 1990 with a one-way ANOVA.

Measures of above-ground biomass for *Sporobolus virginicus* and *Sarcocornia quinqueflora* were made in two inlets in Jervis Bay (Currabene Creek, 35°00'S, 150°39'E, and Carama Inlet). In each of the two inlets, two widely separated plots were established, and within each of these plots four randomly selected quadrats (0.5 x 0.5 m) were harvested. Harvests were made during eight months: February 1989 and 1990; May 1989 and 1990; August 1989 and 1990; and November 1989 and 1990. Comparisons of above-ground biomass were made among the eight harvests in the two inlets with a three-factor ANOVA. Harvests and inlets were fixed factors, and plots were nested as a random factor in inlets.

Soil Analysis

Sediment cores were collected from two inlets in Jervis Bay (Cararma Inlet and Moona Moona Creek), and in each inlet two plots within the salt-marsh were sampled: one in the *Juncus* zone and one at the interface between the salt-marsh and the mangrove zone, the *Juncus* plot being in the same location as the *J. kraussii* harvest. Three replicate samples of 500 mL volume were taken from two depths: 0–10 cm and 20–30 cm. Soil pH and redox potential were measured in the field at low tide during a period of neap tides. Samples were then returned to the laboratory, where they were oven-dried, sieved to remove root fragments, and analysed for particle size, total nitrogen and organic carbon.

Data Analysis and Archiving

All data were tested for homoscedasticity with Cochran's test, and where necessary they were log-transformed prior to ANOVA. Comparisons were made *post hoc* with Scheffe's test. Locations of plots and data on above-ground biomass and soils are archived in a database held by the Australian Department of Defence and the CSIRO Division of Fisheries.

Results

Culm Dynamics of *Juncus kraussii*

Numbers of culms averaged about three per node and remained relatively constant throughout the year. Culm maximum length ranged from 320 to 1035 cm, with an average of 732 cm. No significant differences in maximum culm length were detected among plots ($F_{3,28} = 1.4, P > 0.2$).

Numbers of newly initiated culms averaged about one per node per year, and this rate of initiation was balanced by the rate of culm senescence (Fig. 1). Annual rates of initiation and senescence did not differ significantly among plots in Jervis Bay (initiation $F_{3,23} = 0.3, P > 0.5$; senescence $F_{3,24} = 0.2, P > 0.5$).

From the growth and senescence curves, culms were classified into three groups: those culms initiating at the beginning of the census (February), those assumed to have initiated in the previous spring, and those that had reached maximum length and begun senescing. Culms initiating early in the year grow rapidly during the summer months and more slowly during winter and had reached maximum length by October. Thereafter, culms rapidly senesced (Fig. 2). Culms assumed to have initiated in the previous spring appeared to have less rapid growth and senescence (Fig. 2).

Biomass

The above-ground biomass of *J. kraussii* in Jervis Bay ranged from 96 to 4400 g dry weight m^{-2} over the 10 harvests. No consistent patterns of change in biomass through time were

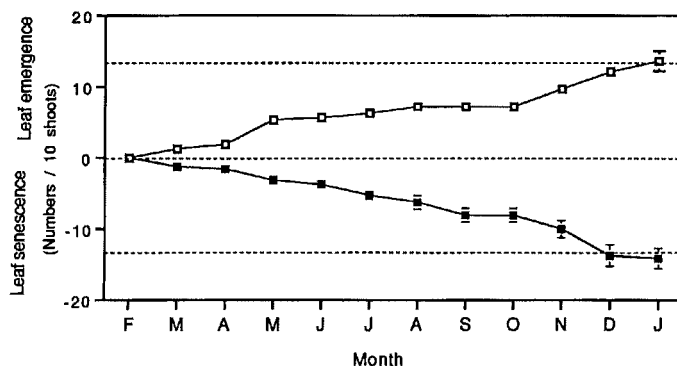


Fig 1. Mean (\pm s.e.) culm (\square) emergence and (\blacksquare) senescence for *Juncus kraussii* during 1989–90.

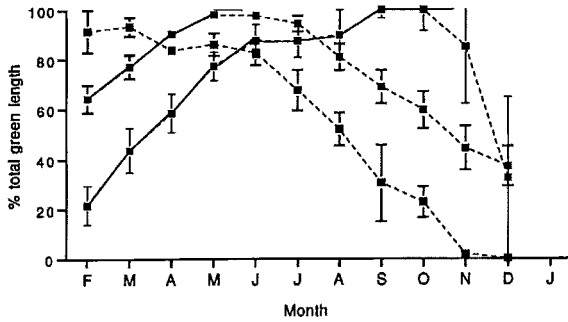


Fig. 2. Mean (\pm s.e.) culm (—) green extension and (---) death for three cohorts of *Juncus kraussii* leaves and culms.

detected, and no consistent differences were found between the two inlets in Jervis Bay (Figs 3a and 3b). Significant space and time interactions were detected in the ANOVA (harvest \times plots nested in inlets $F_{34,240} = 2.4, P < 0.01$), which is not surprising given the power of the analysis to detect small differences. Tests conducted *post hoc*, however, showed that most significant changes in biomass occurred between the first harvest and the rest (Figs 3a and 3b). Spatial variation was mostly due to differences between low-biomass plots in Moona Moona Creek and all other plots (Figs 3a and 3b).

The live (green) component of above-ground biomass accounted for 22% to 74% of the total biomass, and reproductive components (inflorescences) made up 0% to 22% of the total. The proportion of above-ground biomass devoted to live culms was significantly lower in February 1991 (35.4%) than it was in May 1991 (42.7%) ($F_{1,60} = 7.7, P < 0.01$).

Below-ground biomass of *J. kraussii* was measured once, when soils were sampled, and it ranged from 150 to 1640 g m⁻² for surface samples (mean 535 g m⁻²), whereas samples taken from a depth of 10–20 cm ranged from 46 to 480 g m⁻² (mean 187 g m⁻²).

Standing crops of *J. kraussii* at Port Hacking and at Batemans Bay ranged from 196 to 2276 g dry weight m⁻² over the six harvests. No consistent patterns in space or time were

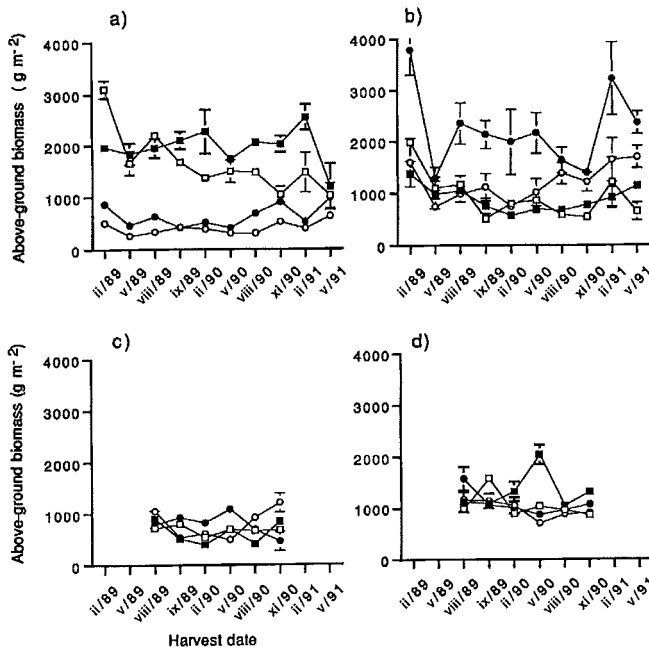


Fig. 3. Mean (\pm s.e.) above-ground biomass of *Juncus kraussii* at (a) Moona Moona Creek, Jervis Bay; (b) Cararra Inlet, Jervis Bay; (c) Cabbage Tree Basin, Port Hacking; and (d) Lattas Creek, Batemans Bay. Nested plots within each inlet are denoted by different symbols.

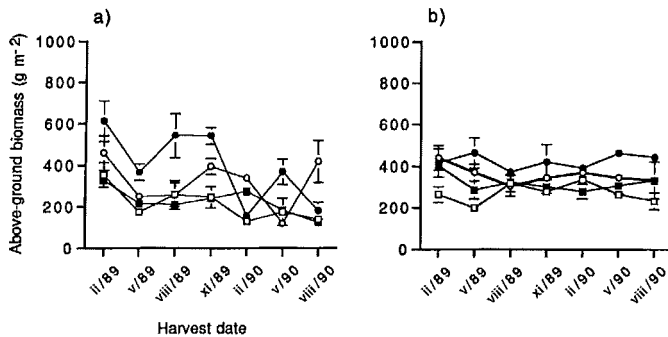


Fig. 4. Mean (\pm s.e.) above-ground biomass of (a) *Sarcocornia quinqueflora* and (b) *Sporobolus virginicus* in Jervis Bay. Plots are denoted by different symbols.

detected (Figs 3c and 3d), and space and time interactions were significant (Port Hacking, harvest \times plots $F_{15,72} = 5.3$, $P < 0.01$; Batemans Bay, harvest \times plots $F_{15,72} = 3.7$, $P < 0.01$).

Comparisons of *J. kraussii* biomass among the four inlets (Cabbage Tree Basin, Moona Moona Creek, Cararma Inlet and Lattas Creek) showed no consistent year-to-year differences (ANOVA $F_{1,96} = 2.2$, $P > 0.1$). There were, however, differences between inlets, with Cabbage Tree Basin averaging about 350 to 440 g m^{-2} lower in biomass than the other inlets (Fig. 3c).

Standing crops of *Sarcocornia* ranged from 52 to 1184 g m^{-2} , with an average of 317 g m^{-2} . No consistent temporal trends or spatial trends were detected, ($F_{21,96} = 4.9$, $P < 0.01$) (Fig. 4a).

Standing crops of *Sporobolus* ranged from 148 to 852 g m^{-2} , with an average of 349 g m^{-2} . No consistent temporal were detected, although significant differences were apparent among harvests and plots ($F_{7,96} = 6.3$, $P < 0.01$) (Fig. 4b).

Soil Analysis

Soil pH in the *Juncus* zone ranged from 5.4 to 6.6, with an average of 6.3. Redox potentials ranged from -115 to $+200$ mV. No significant differences in pH or redox potentials were detected with depth of samples. Concentrations of total nitrogen (TN) and organic carbon (OC) were both higher in the surface samples than in the deeper samples (0.31% versus 0.15% for TN and 5.9% versus 3.7% for OC). The ratio of clay:silt: fine sand: coarse sand was, on average, 5:2:18:75.

Soil pH in the interface between the lower salt-marsh and the mangrove zone ranged from 6.0 to 6.8, and redox potentials ranged from -306 to $+150$ mV. No significant differences in pH were detected with depth of samples, although the average redox potential decreased from a mean of -52 mV (0–10 cm) to -108 mV (10–20 cm). Concentrations of total nitrogen and organic carbon were higher in the surface samples than in the deeper samples (0.25% versus 0.11% for TN and 4.8% versus 2.1% for OC). The ratio of clay:silt: fine-sand: coarse sand was similar to that in the upper salt-marsh.

Discussion

Spatial Variation

Spatial variation in standing crop was relatively consistent through time at high- and low-biomass sites in Jervis Bay. Plots with low above-ground biomass ($<1 \text{ kg m}^{-2}$) were usually at the interface between the *Juncus* zone and the *Sarcocornia-Sporobolus* complex (Clarke 1993), whereas biomass was highest ($>2 \text{ kg m}^{-2}$) in plots adjacent to *Casuarina glauca* forest. Single samples of above-ground biomass from Botany Bay (1.9 kg m^{-2}) (Clarke 1986) and from Myall Lakes (Clarke, unpublished) were also high adjacent to *C. glauca* forest. This pattern may relate to the seepage of groundwater into the upper marsh because *J. kraussii* attains

maximal growth when salinity is low in cultivation (Heinsohn and Cunningham 1991); alternatively, nitrogen fixation by *C. glauca* may enhance the concentration of nutrients in this zone and promote growth.

Above-ground biomass of *J. kraussii* was consistently lower in Cabbage Tree Basin than in the other three inlets. The reasons for this are not clear, but they may relate to soil salinity and nutrient concentrations or to disturbance by feral deer. Over all sites and times, above-ground standing stocks (mean 1116 g m⁻², s.e. 31.7 g m⁻², range 51–4832 g m⁻², coefficient of variation 0.64, $n = 512$) were similar to those reported for a range of locations within an estuary in Western Australia (mean 1424 g m⁻², $n = 103$, Congdon and McComb 1980). In contrast, the standing crops for *Sarcocornia* (317 g m⁻²) and *Sporobolus* (349 g m⁻²) were about half those previously reported for a single site in Botany Bay (Clarke 1986). This difference demonstrates the need for future attempts at spatial comparisons to take into account variability within and among estuaries.

Temporal Variation

Culms of *J. kraussii* are initiated throughout the year, and these 'births' are balanced by an equivalent annual mortality. Culm initiation appears to be high before, and after, a summer period of flowering and fruiting. For the single cohort that could be followed from birth to death, the average time to reach maximum length was about 10 months. Culms rapidly elongate during their first few months of growth, and they reach a maximum height of about 73 cm. Culm longevity of 12 months was similar to that found for this species in Western Australia (Congdon and McComb 1980) but less than that typically found in *J. roemerianus* from marshes of the Gulf and South Atlantic coasts of the United States (Eleuterius and Caldwell 1981; Christian *et al.* 1990).

No distinct seasonal pattern in the standing crop of *J. kraussii*, *S. virginicus* or *S. quinqueflora* was detected, although significant differences in the standing crop of *J. kraussii* were detected in Jervis Bay between the first harvests in early 1989 and subsequent ones. Higher efficiency of sampling at the initial harvest is one possible explanation, although care was taken to ensure similar sampling effort and random placement of quadrats in all sampling periods. Another possible explanation is that growth was enhanced by high rainfall at the beginning of 1989 that ameliorated the dry conditions of the years prior to harvesting.

Seasonal patterns in live standing crop were detected in Western Australia, but they were not consistent among sites (Congdon and McComb 1980). It is possible that similar patterns occur in Jervis Bay, because comparison of harvests in February and May of 1991 revealed significant differences in live biomass, although the total above-ground biomass was similar.

Productivity

In macrophytes that produce leaves or culms sequentially, above-ground net primary productivity cannot be easily estimated by direct harvesting or by the clip method. Instead, information about rate of culm growth, longevity and the relative proportions of live and dead biomass is required to estimate productivity. Some of the information collected for *J. kraussii* in Jervis Bay allows productivity to be estimated. The key measurements were taken during 1989, when culms were tagged. The product of (1) the proportion of the year that culms take to reach maximal height, (2) the ratio of maximum height to average total height during the period of growth, and (3) the average biomass of growing culms provides an estimate of above-ground net primary productivity (Christian *et al.* 1990). On this basis, it was calculated that an average of 0.81 kg m⁻² year⁻¹ of *J. kraussii* was produced in Jervis Bay during 1989. This is within the range estimated for south-western Australia (0.3 to 1.3 kg m⁻² year⁻¹, Congdon and McComb 1980) and within the range recorded for *J. roemerianus* marshes in North Carolina (0.79 kg m⁻² year⁻¹ Williams and Murdoch 1972, and 0.81 kg m⁻² year⁻¹, Christian *et al.* 1990). Productivity of *J. kraussii* is higher than the above-ground productivity estimates for *Avicennia marina* (0.31 kg m⁻² year⁻¹) and *Aegiceras corniculatum* (0.21 kg m⁻² year⁻¹) (Clarke 1994) in

the adjacent mangrove community. However, on a total area basis the mangroves would be more productive than the salt-marsh in Jervis Bay.

One contrast between *Juncus* salt-marshes in North America and those of eastern Australia is that, in North America, higher biomass and productivity are usually associated with the lower marsh. In New South Wales, however, mangroves occupy the lower intertidal zone and dense stands of *J. kraussii* occur mainly in the upper salt-marsh. In these salt-marshes, much of the *J. kraussii* productivity appears to accumulate in the salt-marsh soils, as reflected by higher concentrations of organic matter and nutrients compared with those in the lower salt-marsh and the mangrove zone (Clarke 1986). Concentrations of soil organic matter, organic nitrogen, and inorganic nitrogen have also been reported as being higher in a Victorian salt-marsh compared with the adjacent mangrove zone (Boon and Cain 1988).

Metabolic rates of organic nitrogen compounds in sediments from mangrove and salt-marsh areas in Victoria were similar (Boon and Cain 1988). However, studies of above-ground decomposition of senescent salt-marsh plants and mangrove leaves in a nearby estuary showed that *Sarcocornia quinqueflora* stems decompose less rapidly than do *Avicennia marina* leaves within their respective habitats (van der Valk and Attiwill 1993, 1984). Thus, low shore detritus may be more readily decomposed by invertebrates and marine fungi, whereas frequent tidal flushing could deplete the nutrient and organic content of the lower salt-marsh and mangrove zone. It has been suggested that the upper salt-marsh, where organic matter and nutrients appear to accumulate, may provide a source of nutrients for mangroves (Clarke 1983). However, the processes of decomposition and nutrient cycling of salt-marsh and mangrove detritus remain to be fully elucidated, as do the mechanisms for importing or exporting nutrients and organic matter in temperate Australian estuaries.

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