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Productivity-decomposition dynamics of *Typha orientalis* at Kaitoke Swamp, Great Barrier Island, New Zealand

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Abstract The productivity and decomposition of *Typha orientalis* at Kaitoke Swamp on Great Barrier Island, New Zealand, were measured to determine the annual dynamics of its biomass. These interactions, including peat accumulation under nutrient-rich conditions, are often poorly understood. Annual productivity and maximum “standing” above-surface and below-surface biomass were measured using sequential harvest plots. Decomposition was determined using recently dead *T. orientalis* leaves in mesh litter bags placed on, above, and below the swamp surface.

The annual productivity of *T. orientalis* (c. 3 kg m⁻²) is within world-wide estimates for swamp wetland species. The order of decomposition of leaf litter at Kaitoke Swamp is: below surface > surface > above surface. Litter bag mesh size did not affect decomposition processes, indicating that larger decomposer animals probably do not have a significant influence on biomass loss in the site. Peat accumulation was estimated based on observations and measurements of the entrainment process. *T. orientalis* had low estimated peat accumulation, with 6.5% (0.19 kg m⁻² yr⁻¹) of the annual production remaining after all components had been underground for 5 years. Consequently a large amount of the annual production of biomass is lost from the site. The ratio of

maximum biomass to annual productivity was 2.2, also indicating low biomass accumulation.

Keywords annual production; biomass components; decomposition; entrainment process; growth cycle; peat accumulation; *Typha orientalis*; Great Barrier Island

INTRODUCTION

Minerotrophic wetlands are amongst the most productive ecosystems in the world due to a plentiful supply of nutrient-rich water and low water stress for much of the year (Teal & Teal 1969; Bradbury & Grace 1983; Wilen & Tiner 1993). However, wetlands are also notable for their slow decomposition processes (Whittaker 1975) and the accumulation of peat, or non-decomposed remains of dead plants. Peat colour, texture, water retention, or degree of decomposition vary according to the contributing plants (Johnson & Brooke 1998; Wheeler & Proctor 2000). For example, *Typha orientalis* commonly forms fen peats in New Zealand, with *Phormium tenax* and *Carex secta* contributing (Thompson 1987).

Multiple vegetation types with differing fertility, water quality, and peat production dynamics exist at Kaitoke Swamp, Great Barrier Island, New Zealand (Rutherford 1998). There are mesotrophic, or medium fertility, areas within the swamp, including large areas of almost monotypic *Baumea juncea* sedge vegetation, where nutrients are supplied by intermittent in-flowing water. Low fertility (oligotrophic) areas at Kaitoke, with water derived predominantly from rainfall, support stands of *Gleichenia dicarpa*. However, of primary interest in this study are the more eutrophic areas dominated by the native deciduous rhizomatous macrophyte, *Typha orientalis*. These areas are subject to abundant sediment and nutrient input from through-flowing water.

At Kaitoke Swamp, *T. orientalis* appears to make a significant contribution to annual swamp productivity because of its fast growth rate over summer, large size, and significant below-surface components.

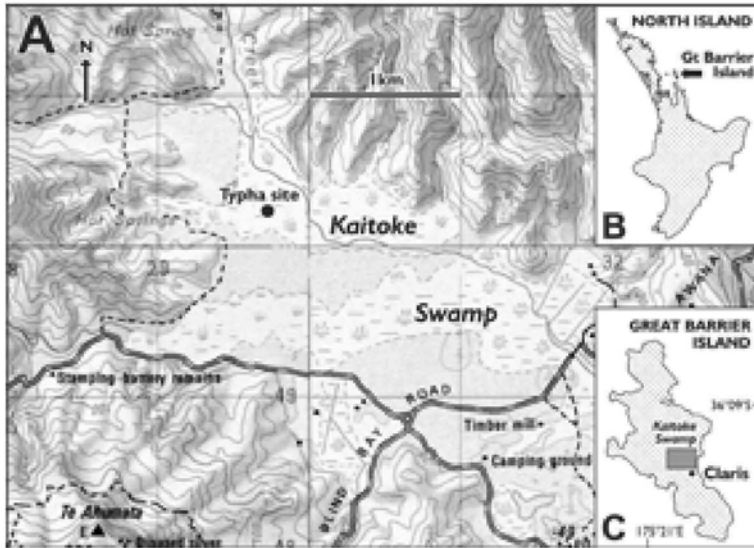


Fig. 1 Locations of A, *Typha* site; B, Great Barrier Island; C, Kaitoke Swamp.

This is not unexpected, since *Typha* species worldwide have high productivity (Claude & Hess 1969; Bradbury & Grace 1983; Odum et al. 1984; Wilen & Tiner 1993). However, this is offset against high decomposition processes in *Typha* stands, which can account for the loss of 90% or more of their primary productivity (Mason & Bryant 1975; Whittaker 1975; Davis & van der Valk 1977).

The aim of this study was to determine the fate of *T. orientalis* biomass by measuring net annual primary productivity and assessing decomposition rates of above-surface and below-surface components. Below-surface dynamics are not adequately investigated in many *Typha* studies, and consequently the overall biomass dynamics of swamps is often poorly understood (Claude & Hess 1969; Bradbury & Grace 1983; Odum et al. 1984; Wilen & Tiner 1993).

Study area

Great Barrier Island is situated in the Hauraki Gulf, 90 km north-east of Auckland, North Island, New Zealand, with Kaitoke Swamp located at 36°14'S, 175°26'E on the east coast of Great Barrier Island, north-west of Claris (Fig. 1). The study site was in the north-western part of the swamp (Fig. 1). The swamp is administered for the most part by the Department of Conservation.

Kaitoke Swamp comprises alluvial valley floors with slightly sloping surfaces (<4°), and maximum elevation of 20 m (Rutherford 1998). The average rainfall recorded at the nearest weather station (Port

Fitzroy on the west coast) between 1961 and 1997 was 1839 mm. The mean maximum temperature for February (the warmest month) is 23.8°C, the mean minimum temperature for July (the coldest month) is 15.3°C, and mean relative humidity is 82.2% (NIWA 1997).

At Kaitoke Swamp, *T. orientalis* occurs in association with abundant *Gleichenia dicarpa* and a small amount of *Baumea rubiginosa* (Fig. 2). Other species in the surrounding vegetation include *Baumea articulata*, *Leptospermum scoparium*, and *Coprosma robusta*. Within this vegetation, *T. orientalis* attains heights of up to 3.2 m at the site and *Gleichenia dicarpa* reaches 1.8 m. Recently dead *T. orientalis* stems and leaves are present alongside new live stems. This dead material (necromass) forms a significant proportion of the above-surface material.

Nomenclature

Native wetland angiosperm names follow Johnson & Brooke (1998). No exotic species were recorded at the site.

METHODS

Environmental measurements

The depth to water-table was measured using a "pismometer" that comprised a 5 cm diameter perforated plastic tube, closed at the bottom, inserted to 1.5 m below the swamp surface. Measurements of water

Fig. 2 **A**, *Typha* site at the start of the growth period showing recently dead *T. orientalis* shoots and inflorescence spikes; **B**, *Typha* site during the growth period showing live shoots amongst recently dead shoots. Note the *Gleichenia dicarpa* component.



levels within the tube relative to the swamp surface were obtained at different times over two years.

The depth to the base of the peat was measured with a 6.3 mm diameter stainless steel rod, extendible to 6 m in length. Sediment core samples were also taken with a D-section corer to gain a more accurate assessment of the substrate. Depth to the anaerobic peat layer was measured by inserting "Bright Grade" steel rods, 1.5 m long and 6.3 mm diameter, 1 m into the substrate. Preserving oil was removed from the rods just before placement in June 1999. After 3 months, the distance from the peat surface to the level on the rod where there was no rust was taken to be the depth to the fully anaerobic layer. The method follows that of Rutherford (1998).

Ten measurements of pH, conductivity, and salinity were taken in April 1999 in randomly selected decomposition plots (see below) where lower bags had been removed leaving small leachate pools derived from below-surface water. pH was measured in leachate using a Hanna pHep WP temperature-compensated hand-held pH electrode, Hanna Instruments, USA. Conductivity and salinity were measured with an Orion Thermo conductivity and salinity meter (model 115) and cell (011050) (Thermo Electron Corporation, USA).

Productivity

Gross primary productivity is defined as the conversion of solar energy by green plants, through photo-

synthesis, into plant carbohydrate per unit area per unit time (Whittaker 1975; Brinson et al. 1981; Wilen & Tiner 1993). The amount available for harvest by consumers and decomposers (net primary productivity) excludes organic compounds used for respiration and internal repair (Newbould 1967; Jones 1979; Kvet & Westlake 1998). Annual net production is defined as the biomass produced in one growing season per unit area. Standing biomass is the total weight of organic matter present at one time (Whittaker 1975). A fraction of net primary production is consumed by bacteria, fungi, insects, mammals, birds, etc. Plant detritus may also be exported to adjacent habitats for secondary assimilation by bacteria, zooplankton, or fish (Crow & MacDonald 1979). The biomass accumulation ratio is the maximum biomass to annual productivity ratio and the inverse of this is net production per unit of biomass.

In *Typha*, photosynthetic biomass increases each year to a maximum in late summer, after which shoots die. Most of the dead leaf material produced is subsequently added to the substrate surface, so that the amount of standing dead biomass remains relatively constant from year to year. Rhizome death is associated with the movement of stored reserves from rhizomes to the developing shoots. Old rhizomes die after new ones have been initiated from the bases of the new shoots.

This study used the "harvest method" (Jones 1979; Bradbury & Grace 1983) to measure annual net primary production. This involved sequential harvesting from different plots of vegetation that undergoes an annual growth cycle, with annual net primary productivity estimated as the difference between the dry weights of live vegetation recorded at the beginning and the end of the growth cycle per unit area. Only one site was studied due to the very large volume and weight of biomass that had to be harvested and transported long distances on foot. Additionally, the site was the only example of a pure *T. orientalis* stand, determined after an extensive survey of Kaitoke Swamp (Rutherford 1998).

The study site was within an extensive *T. orientalis* stand, and divided into twenty-one 1 m × 1 m areas, arranged in three contiguous rows of seven. At each harvest, a 1 m × 1 m area was randomly selected from each row, and a 50 cm × 50 cm plot demarcated in the centre of each area. Already-sampled 1 m × 1 m areas were excluded from subsequent samples. This restricted stratified random sampling provided three replicate plots per harvest and minimised disturbance between the areas because a minimum distance of 1 m was left between

adjacent plots and most work was carried out from marginal tracks (Newbould 1967). Harvests were in November 1997, April 1998, September 1998, and April 1999, approximating the beginning and end (maximum biomass) of two growth periods. Live above-surface biomass was sampled at all four harvests. Dead above-surface biomass was harvested over the second annual cycle to estimate the dead matter present at the beginning and end of the growth period. Rhizomes and roots were collected in the second, third, and fourth harvests for an estimation of below-surface biomass (Table 1). Rhizomes were not harvested at the first harvest in order to observe the shoot regrowth from them. Consequently, total annual biomass production could be estimated only for the second year.

All above-surface standing biomass samples were obtained by inserting a 50 cm × 50 cm interlocking quadrat around the biomass in the centre of each 1 m × 1 m area, and trimming all plants at swamp-surface level (just above the decomposing litter) using hedge clippers. The harvested biomass was partitioned into live or dead components (including *Gleichenia dicarpa*) and dried at 80°C until constant in weight. Recently dead leaf sheaths of *T. orientalis* attached to current year live stems were considered part of the current year's live weight. The number and length of *T. orientalis* stems in each plot were recorded at each harvest. Weights are expressed as kg m⁻².

Typha orientalis rhizomes were harvested by digging out all dead and live rhizomes and roots from the entire 50 cm × 50 cm plots to approximately 80 cm depth or until no more solid below-surface biomass was encountered. All below-surface biomass was washed to remove sediment and was partitioned into live and dead rhizomes and roots, and dried as above.

The maximum annual live *T. orientalis* above-surface production is estimated to be the live standing biomass of shoots at the end of the growth period, since *T. orientalis* is relatively ungrazed, fast-growing, and does not maintain significant live biomass for more than one growing period (Kvet & Westlake 1998). For *T. orientalis*, this is equivalent to the difference between the dry weights of live vegetation recorded at the beginning and the end of the growth cycle.

Below-surface annual productivity is estimated as the difference between live rhizome and root biomass at the end and beginning of the growth period, since live rhizomes present at the start of the growth period are derived from the previous season's productivity.

Decomposition

Decomposition was studied using the "litter bag" method (Suffling & Smith 1973; Mason 1977; Swift et al. 1979), where dried weighed plant material is enclosed in mesh bags which are placed in the environment and randomly harvested at time intervals to determine dry biomass losses. This was conducted in proximity to the productivity site to ensure the same macro-climatic conditions. Numbered small-mesh fibreglass litter bags (7.5 cm × 22.5 cm, with 2 mm² spaces) containing dried and weighed samples of recently dead *T. orientalis* leaves were attached to bamboo canes at three levels at the site. This simulated decay c. 50 cm above the swamp surface (still-attached material), litter layer or swamp-surface material, and material c. 20 cm below the swamp surface or in the peat layer (but above the water table at the time they were put in place). This reflects the fact that in swamps decomposition begins in aerial conditions and concludes in an aquatic environment (Davis & van der Valk 1977). The litter bags were secured on a total of 24 bamboo canes, placed 1 m apart, and six replicate canes were randomly collected at 127, 288, and 483 days after placement (Nov 1997) at the site, corresponding with the last three of the four productivity harvest dates (Table 1).

In addition, 12 bamboo canes each had one large-mesh (4 mm² space) litter bag at each level, to determine whether larger mesh sizes allowed larger invertebrates to enter the bags and affect decomposition rates. This allowed one harvest of 6 replicate large-mesh litter bags at 127 days and one at the end of the study (483 days).

Harvested litter bags were re-dried to constant weight at 80°C. Dead leaves (e.g., *Leptospermum*

scoparium) accidentally added to the bags in the field, or roots that had entered some of samples in the below-surface litter bags, were carefully removed before weighing.

A weight adjustment was made if there was sediment accumulation on the samples within the litter bags. Sediment contamination occurred especially in below-surface litter bags with increasing time. These contaminated samples were dried, weighed, and then heated at 550°C for one hour to remove organic material (Roxburgh et al. 1994). The percentage of ash remaining was compared with that in equivalent uncontaminated recently dead litter samples, and the decomposition rate adjusted for sediment accumulation.

Litter bag weight changes are expressed as percentage of initial dry weight remaining of components per square metre at each level.

Rates of decomposition of dead *T. orientalis* leaves at the three levels were determined. Decomposition occurs exponentially (Whittaker 1975; Swift et al. 1979), and the weight of a component of litter remaining after time t is:

$$M_t = M_o e^{-kt}$$

where M_o is the original weight of plant litter, and M_t is the weight of litter remaining after time t . The litter decay rate constants (k) were calculated as

$$k = -\ln(-RWL)$$

where $RWL = (M_o - M_t)/M_o$, the relative weight loss after time t .

The weight of litter remaining after t years (M_t) is the amount of that component added to the system as peat in the below-surface anaerobic layer. The half-life of decomposition is the time when $M_t = M_o/2$.

Table 1 Summary of harvesting schedule and replication for biomass dry weight components, and for leaf decomposition rates using small-mesh bags, for *Typha orientalis* (large-mesh bag decomposition harvests are shown in brackets). Leaves include the shoot, which is largely made up of leaf bases.

	Nov 1997 Spring 1	April 1998 Autumn 1	Sept 1998 Spring 2	April 1999 Autumn 2
Biomass harvests				
Leaves	3	3	3	3
Dead leaves	-	-	3	3
Rhizomes	-	3	3	3
Roots	-	3	3	3
Leaf decomposition rates				
Above swamp surface	Set up	6 (6)	6	6 (6)
Swamp surface	Set up	6 (6)	6	6 (6)
Below swamp surface	Set up	6 (6)	6	6 (6)

Peat accumulation

The amount of peat accumulated in a system is the difference between the annual income of plant litter and the weight lost through decomposition (Reader & Stewart 1972; cf. Clymo 1980). Income is annual, but loss of that income occurs over many years, so that account must be taken of the time that biomass components spend at each decomposition level in the ecosystem, and the proportion of each component that moves to different levels in any time interval. This is referred to as the "entrainment process".

The entrainment process, from biomass production to its incorporation into peat, was not measured directly for each component. Rather, some rates were measured, and others were estimated by observing residence times.

Weight input rates of the different components were measured by sequential harvests. Losses by decomposition were measured (k values) for recently dead leaves at three levels. The residence time of visible components was estimated by observation over the 2 year period. Approximately one third of the live *T. orientalis* shoots produced in one year remained,

though now dead, above the swamp surface for one season after production, while the majority of the remaining two thirds reached the surface in the subsequent year. All remained at the surface for one year before entering the subsurface.

Time to incorporation below the surface was estimated by observing the speed with which surface litter bags became covered by dead plant material, and noting the shallow nature of the aerobic layer. The calculated maximum below-surface k value for leaves was applied to rhizome and adventitious root weights from their formation. Rhizomes are starch storing organs, but their contents are almost entirely used during the rapid spring growth phase. After this, new rhizomes are initiated and the old roots and rhizomes decompose rapidly due to their "spongy" nature.

Annual peat accumulation can be estimated by applying the k values obtained in the decomposition study to the weights of the annual dead biomass over a number of years. Five years was estimated to be the average time for all components, once below the surface, to reach the anaerobic layer and cease

Table 2 Mean (\pm SE) values of standing biomass (SB) and annual production of *Typha orientalis* based on three plots per harvest. Rhizomes and roots were not sampled in November 1997.

	Component	Start of season SB (kg m ⁻²)	End of season SB (kg m ⁻²)	Annual production (kg m ⁻² year ⁻¹)
Live components				
Nov 97–Apr 98	Shoots	0.32 \pm 0.19	1.75 \pm 0.71	1.75 \pm 0.71
Sep 98–Apr 99	Shoots	0.03 \pm 0.03	2.26 \pm 1.20	2.26 \pm 1.20
Sep 98–Apr 99	Rhizomes & roots	1.28 \pm 0.39	1.93 \pm 0.75	0.65 \pm 0.28
Sep 98–Apr 99	Total	1.31 \pm 0.30	4.19 \pm 0.64	2.91 \pm 0.67
Dead components				
Sep 98–Apr 99	Shoots	1.10 \pm 0.27	1.50 \pm 0.92	–
Sep 98–Apr 99	Rhizomes & roots	0.16 \pm 0.02	0.61 \pm 0.3	–

Table 3 Mean decomposition parameters (weight loss \pm SE, mean k values, and half life) for *Typha orientalis* leaf litter in small-mesh bags at different levels relative to the swamp surface over 483 days (k figure in brackets is maximum value). Values followed by different letters are significantly different from each other on using ANOVA at $P < 0.05$. Maximum subsurface k value is calculated, corresponding to minimum half life.

	% Weight loss \pm standard error	Mean k value (yr ⁻¹)	Half life (days)
Above swamp surface	20.9 \pm 1.5 b	0.178	1421
Swamp surface	40.5 \pm 2.9 a	0.345	733
Below swamp surface	42.6 \pm 3.3 a	0.387 (0.639)	653

decomposing. Calculations were also made for <5 and >5 years.

The “mass-balance” method we have used relies upon an assumption that, at some depth below the water or peat surface, anaerobic conditions reduce decomposition to zero. This assumption may not be strictly true, and the depth in question will vary and may be difficult to measure. Anaerobic decomposition is assumed to be negligible on the time scales considered here, and the weight remaining after the above times allows estimates of peat accumulation, assuming that further decomposition is negligible.

Statistics

Wilcoxon Signed Rank tests were used to compare the shoot productivity estimates between the same season in two different years. This test is analogous to the paired *t*-test, but examines data that do not fulfil assumptions of normality (Zar 1984).

ANOVA was applied to decomposition results, with Bonferroni comparisons (modified *t*-tests on small numbers of pairs of means; Zar 1984) adjusting the observed significance level for the fact that multiple comparisons were made.

RESULTS

Environmental measurements

Sediment cores showed 3.4 m depth of organic material. There was 38–40 cm of semi-decomposed (mainly *Typha*) plant material at the swamp surface. The pisometer water table level was 0.2–21 cm below the swamp surface for all measurement periods. The mean depth from swamp surface to the fully anaerobic peat layer was 1.33 cm during winter.

The mean pH of leachate (soil water containing dissolved minerals and ions) in the site was 5.28, conductivity was 0.62 mS, and salinity was 300 parts per million.

Productivity

Typha orientalis shoot productivity was ≥ 1.75 kg m⁻² in both years, with no significant difference between years at $P < 0.05$, while total productivity (shoots + rhizomes + roots) was 2.94 kg m⁻² in the second season (Table 2). The harvested plots also contained smaller amounts of *Gleichenia dicarpa*, with estimated shoot production of 0.42 kg m⁻² yr⁻¹ and total productivity of c. 0.52 kg m⁻² yr⁻¹. Thus, site productivity in the 1998–1999 season was c. 3.5 kg m⁻² yr⁻¹.

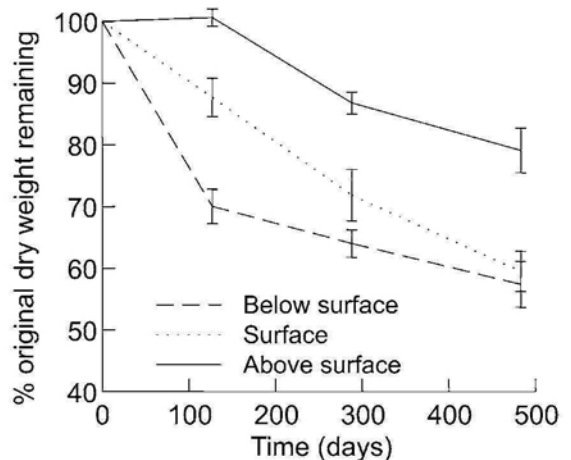


Fig. 3 Decomposition of recently dead *Typha orientalis* leaf litter at three levels (with standard error bars).

Biomass dynamics and allocation

The relative proportions of the different components changed from early spring (before significant shoot growth) to late summer when there was maximum shoot growth (Table 2). The live biomass in September was predominantly below-surface (rhizomes), while in April shoots predominated. However, dead material comprised at least one third of the total biomass, even in summer. The biomass accumulation ratio (maximum biomass to annual productivity) was 2.2 and the net production per unit of biomass was 0.46.

Decomposition

Weight changes in small-mesh litter bags at different levels in the system showed that surface and below-surface decomposition rates converged as the surface material was buried (Table 3; Fig. 3). Decomposition increased significantly once the material reached the swamp surface, and remained high even at c. 20 cm depth. No significant differences in decomposition rates were found between different mesh sizes, indicating that decomposition is mainly due to fungi and bacteria or small invertebrates (such as amphipods and millipedes which were found in small-mesh bags) rather than larger invertebrates.

Projected peat production

Assuming that all above-surface biomass reaches the swamp surface by 3 years after its initial production, then after 8 years all components would have been below the surface for at least 5 years (Fig. 4). If these

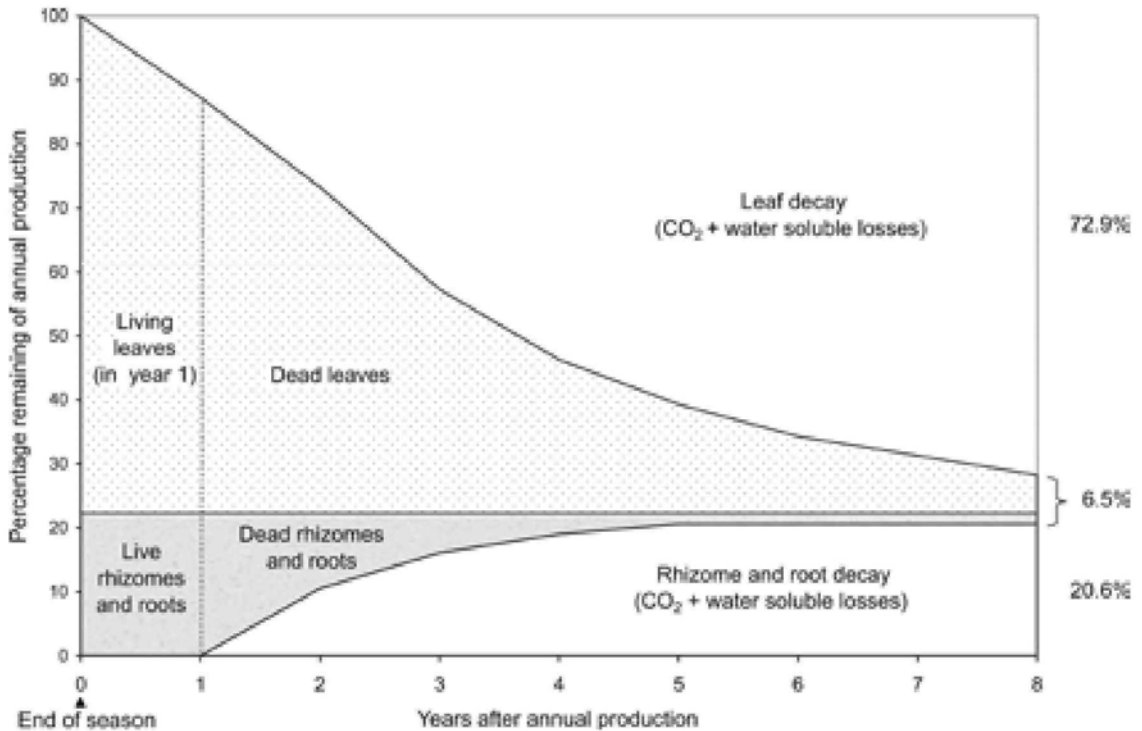


Fig. 4 Decay of the annual production, and peat production derived from *Typha orientalis*. All components assume below-surface decomposition rates after 3 years and cease decomposing at Year 8.

components reached the anaerobic layer and ceased decomposing 5 years after entering the subsurface, the estimated amount added to the system as peat would be $0.19 \text{ kg m}^{-2} \text{ yr}^{-1}$ (6.50%; Fig. 4).

DISCUSSION

The total annual productivity (shoot + root + rhizome) of *Typha orientalis* at Kaitoke Swamp ($c. 3 \text{ kg m}^{-2} \text{ yr}^{-1}$) is high, even equal to that of some tropical forests and cultivated areas (Whittaker 1975; Wilen & Tiner 1993). Annual shoot productivity ($2.26 \text{ kg m}^{-2} \text{ yr}^{-1}$) is near the top of the range of various shoot values reported for swamps and marshes by other authors (e.g.; $0.8\text{--}3.5 \text{ kg m}^{-2} \text{ yr}^{-1}$, Whittaker 1975; $0.4\text{--}3 \text{ kg m}^{-2} \text{ yr}^{-1}$, Wilen & Tiner 1993). Similar studies to that reported here were carried out at Pukepuke Lagoon in the Manawatu district of New Zealand in the 1970s (Ogden 1981). Annual total production there was $3.1 \text{ kg m}^{-2} \text{ yr}^{-1}$ for pioneer *T. orientalis* stands (<5 years old) and $2.34 \text{ kg m}^{-2} \text{ yr}^{-1}$ for mature (>30 year old) stands, which agrees closely with

the results for Kaitoke Swamp. Shoot productivity at Kaitoke Swamp ($2.26 \text{ kg m}^{-2} \text{ yr}^{-1}$) is higher than that for the same species in the USA ($1.49 \text{ kg m}^{-2} \text{ yr}^{-1}$, Bradbury & Grace 1983). Comparisons with other species of *Typha* indicate that total *T. orientalis* productivity at Kaitoke Swamp is similar to that for *T. angustifolia* ($2.61 \text{ kg m}^{-2} \text{ yr}^{-1}$) and *T. latifolia* ($3.19 \text{ kg m}^{-2} \text{ yr}^{-1}$) studied mainly in the USA (Claude & Hess 1969; Bradbury & Grace 1983; Odum et al. 1984; Wilen & Tiner 1993).

Decomposition rates were greatest below the surface of the swamp. This implies that aerobic conditions prevailed at least some of the time even though the depth of the aerobic layer we measured was only 1.33 cm. However, this was measured mainly over the winter period, when water levels were high and oxygen levels probably minimal. Elsewhere in *Typha* stands at Kaitoke Swamp, Rutherford (1998) measured aerated layers as deep as 29 cm in summer. The maximum below-surface decomposition rate ($k = 0.639 \text{ yr}^{-1}$) is similar to surface decomposition rates ($k = 0.64\text{--}0.69 \text{ yr}^{-1}$) for *T. angustifolia* in Norfolk, England (Mason & Bryant 1975).

However, the decomposition rates at Kaitoke Swamp are low overall compared with other studies which have used recently dead *Typha* leaf litter. For example, the surface k value for *T. glauca* in Iowa, USA, was 1.05 yr^{-1} (Davis & van der Valk 1977) compared with 0.345 yr^{-1} at Kaitoke Swamp. The apparently minor role played by larger invertebrates at Kaitoke Swamp, or seasonal and climatic conditions, may be factors.

Standing dead biomass ranged from 49% of the total biomass (including necromass) at the start of the growing season to 33% when the living green shoots were dominant during summer (Table 2). Due to the dynamic nature of gains and losses, the actual amount of standing dead matter remained remarkably constant over most of the year (Table 2). However, a tendency for standing dead material to accumulate through time has been observed in other studies. For example, Ogden (1981) found values of 55% for dead biomass in summer in the oldest stands at Pukepuke Lagoon but only 6% in the pioneer stands bordering on the lagoon. The *T. orientalis* stand at Kaitoke Swamp was also similar to the Pukepuke *T. orientalis* stand in values of biomass accumulation ratio (2.2 cf. 2.5) and net production per unit of biomass (0.46 cf. 0.40).

The rate of peat accumulation depends on the time taken for the dead material of any one year to cease decomposing. Although we have no reliable measures of this time, we can make approximations based on our observations. Fig. 4 presents a speculative model using the estimated productivity (Table 2) and decay rates (Table 3), assuming that all decomposition is exponential and has ceased after all components have been below the swamp surface for 5 years (i.e., in Year 8 for all components, having taken 3 years for all components to reach the surface). We also assume that decay rates for roots and rhizomes can be approximated by using the maximum k value obtained for leaves below the swamp surface. With these assumptions, after 8 years only 6.5% of the original productivity will remain in the system, the other 93.5% having been lost as carbon dioxide during the respiration of the decomposers or as water soluble components. If decomposition stops sooner, more material will accumulate. For example, if decomposition stops after only 2 years of burial (Year 5 in Fig. 4) then 25.14% would remain. This figure is very close to the value of 26.1%, estimated over the same time period in *T. orientalis* stands in the Manawatu district, New Zealand (J. Ogden unpubl. data). On the other hand, if decomposition continues for more than 5 years subsurface, then

<6% will accumulate. These figures cannot yet be adequately tested or assessed in an absolute way, although they will allow comparisons to be made between ecosystems or plant species using the same methods. For example, the small percentage of annual productivity apparently being incorporated into the system beneath the *T. orientalis* stand at Kaitoke Swamp contrasts strongly with the situation under stands of *Baumea juncea* and *Gleichenia dicarpa* at the same swamp. Although these stands are much less productive than *T. orientalis*, their aerial components decompose very slowly once buried, so that these species are more effective peat accumulators (Pegman 1999).

Observations made while digging out the *Typha* rhizomes demonstrated interesting stratigraphy in the top 80 cm. A layer of *Baumea* rhizomes was overlain by *Gleichenia* rhizomes and roots, which in turn was overlain by living *Typha* rhizomes. This suggests a temporal invasion sequence so that the underlying peat has not all been derived from vegetation similar to that now occupying the site. This is supported by observations on an adjacent area, where an initially pure stand of *Gleichenia* was invaded by *Typha* during the period of the study. Palynological studies also indicate that *Gleichenia* has been partially replaced by *Typha* at Kaitoke Swamp during the last c. 650 years, before which *Typha* was absent or much less common (Horrocks et al. 1999). Thus, relatively small changes in environmental conditions, such as water depth, could influence the competitive balance between clones of these species, which in turn influences the rate of peat accumulation.

Conclusions

This study emphasises that, before rates of peat accumulation can be accurately estimated, the whole entrainment process must be quantified. Different plant components have different residence times at different levels, and different decomposition rates. Using leaves only is at best an approximation, especially for the decay of rhizomes, which are themselves anatomically complex structures. However, obtaining these values for large macrophytes is not easy, and the data are presented to guide and compare with future studies. Notwithstanding these qualifications, the following conclusions are possible.

Annual productivity of dense *T. orientalis* stands at Kaitoke Swamp is c. $3.0 \text{ kg m}^{-2} \text{ yr}^{-1}$, which is similar to other estimates for this species elsewhere.

Such dense stands are composed of both living and dead shoots, with the latter comprising at least a third of the total (live + dead) dry matter.

Living root and rhizome biomass is at least 46% of the living biomass total, more in winter.

Above-surface standing dead biomass remains reasonably constant over an annual cycle.

Decomposition rates (mean k values) of recently dead *T. orientalis* leaves are in the range 0.18–0.39 yr⁻¹, which suggest slow decomposition that may account for the large necromass in the stands.

Using the above values and some estimated rates of entrainment, we estimate that c. 6.5% of the annual biomass production (dry weight) eventually becomes fixed in the system as peat. A confidence interval cannot be reliably assigned to this figure. It is based on the mean weights and mean decomposition rates at each stage of the entrainment process.

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