The life history strategy of *Carex pumila* Thunb. (Cyperaceae), a rhizomatous perennial pioneer species on the sand plains of the dune system of coastal Manawatu

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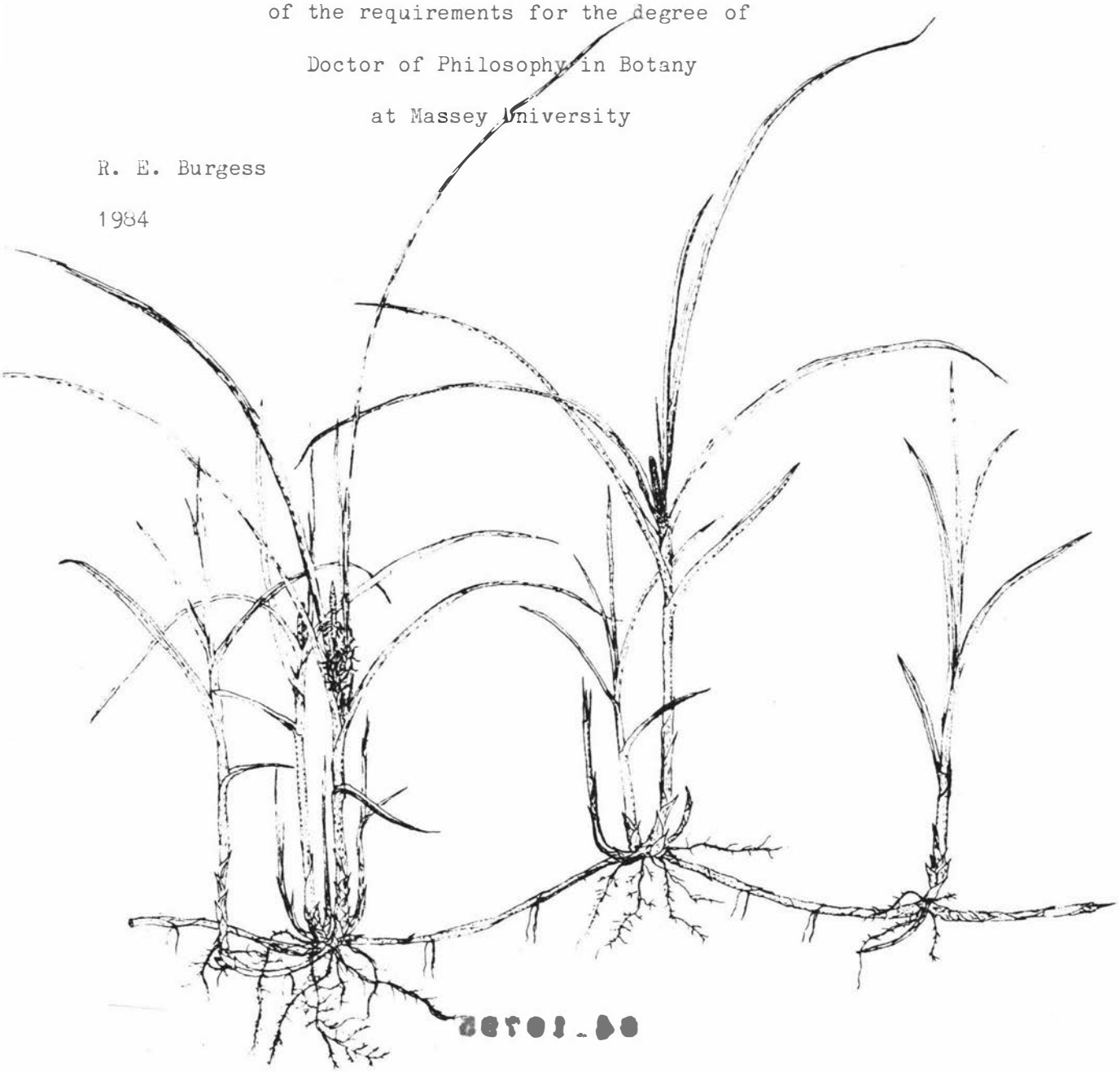

ABSTRACT

The life history strategy of *Carex pumila* Thunb. (Cyperaceae), a major colonist of raw moist sand on the sand plains of coastal Manawatu, New Zealand, is outlined. By virtue of the continuous formation of sand plains, sites suitable for colonization are a permanent feature of this habitat and vegetation of increasing seral maturity is represented at any one time across a series of adjoining deflation hollows and low dunes. It is proposed that the species is an r-strategist well suited to exposure, nutrient stress and seasonal flooding. Amelioration of these conditions by deliberate perturbation treatments resulted in this seral species responding in a way that ultimately lead to its more rapid demise.

The species has a rhizomatous perennial growth habit. The modular construction of its rhizome system is described for the first time. Similarly, the occurrence of both long and short sympodial rhizome branches and of large-diameter sinker roots have not been previously described in the literature on this species. Its floral development appears to be environmentally cued. Emergence of inflorescences occurrs in early October. Maximum size of dissemules is obtained by early January. Subsequently seeds are shed and the shoots bearing them die. The species is essentially allogamous, although in a laboratory experiment, it was found to be partially self-compatible. Self-pollination must be expected in the field since neighbouring shoots are likely to be part of the same genet.

Field studies are reported in which the performance of *Carex pumila* was monitored, firstly at sites of increasing seral maturity both in space and in time, and secondly in response to perturbation treatments. Populations showed a pattern of development that included

a juvenile phase of rhizome expansion, an adolescent phase of increasing shoot density, a mature phase in which a proportion of the shoots were reproductive, and a senile phase of diminished growth and seed production. Phasic development was more protracted on the more stressed and more exposed sites. Other species more rapidly filled the space made available by the death and decay of Carex pumila shoots, than the colonist itself. As a pioneer, the species is doomed to extinction on the sites it colonizes.

In a perturbation experiment, the sward mass of the total vegetation per unit area was increased at all sites by nitrogen fertilizer, applied as ammonium ions at a rate of 50 kg N / ha. Where the Carex pumila population was in a senile phase in an old deflation hollow, the increase was made mainly by other species. In younger populations on a low dune, the density of shoots and expanding buds of Carex pumila were markedly increased by the fertilizer treatment. Associated with this, a significant increase occurred in the proportion of the total dry weight of vegetative branches in rhizomes and in green leaves.

A nitrogen limitation to seed yeild was indicated at the older low dune site. Here nitrogen fertilizer addition increased seed output per unit area by increasing both seed number per culm and seed size. By contrast on the younger low dune site, seed output per unit area was unchanged by the perturbation. In this population, reallocation of resources within fertile shoots, which was seen as an increased number of seeds per culm, was offset however by a reduction in fertile shoot density.

Seed reproductive effort varied between 0 and 16% of total biomass, whereas rhizome allocation was more variable; up to 100% of biomass where the species was invading an embryonic deflation hollow. As a proportion of the biomass of fertile shoots alone, seed reproductive effort estimates of up to 32% were obtained.

The post-anthesis photosynthetic contribution of female spikes to final seed weight was estimated at 26%, in a growth room experiment. This estimate is considered conservative given that final seed weight was not significantly reduced by defoliation and shading of the culm. Thus, the allocation of biomass to seeds cannot be considered a drain on the carbon resources of the plant that might otherwise be allocated to growth or some other plant function.

Total nitrogen concentrations were dissimilar in different plant parts and, for comparable organs, between populations of different ages. Thus, allocation patterns to component parts based on dry weight and total nitrogen were different. Given that nitrogen was seen to be limiting growth in this seral habitat, the allocation of this resource is likely to be of greater significance in the evolution of life history strategies than is that of dry weight.

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