

# More lightweight and isodiametric seeds for C<sub>4</sub> than for C<sub>3</sub> grasses are associated with preference for open habitats of C<sub>4</sub> grasses in a temperate flora

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## Abstract

Seed mass and shape of grasses were analysed in a temperate flora containing 178 and 26 species belonging to C<sub>3</sub> and C<sub>4</sub> photosynthetic types respectively. The weedy character and the annual or perennial status were also considered. On the basis of the seed traits studied, three groups were distinguished: C<sub>4</sub> grasses, annual C<sub>3</sub> grasses of weedy character and perennial non-weedy C<sub>3</sub> grasses. The C<sub>4</sub> group had more isodiametric (same diameter in all directions) seed shape and lower average seed mass than the C<sub>3</sub> group. To our knowledge, this has not yet been described for temperate C<sub>4</sub> grasses and is certainly associated with their preference for open habitats where competition for light is small. Weedy annual C<sub>3</sub> grasses had heavier and less isodiametric seeds than C<sub>4</sub> grasses did. These species are mostly specialized to establish in the dense cover of perennial vegetation, and this ability distinguishes them from the C<sub>4</sub> group. Non-weedy perennial C<sub>3</sub> species possessed less isodiametric seeds than did C<sub>4</sub> grasses, but did not differ from weedy annual C<sub>3</sub> grasses. As most alien C<sub>4</sub> grasses naturalized in Hungary are annuals with small, isodiametric seeds, these traits are good candidates to be included in screening for potential future invasives in open habitats.

**Keywords:** C<sub>4</sub> grasses, photosynthetic types, seed ecology, seed slenderness, thousand-seed weight, weeds

## Introduction

Seed properties (e.g. size, shape, amount of stored reserves, longevity, dormancy etc.) play a key role in plant dispersal in space and time, and different sets of properties contribute to success in different environments (Fenner and Thompson, 2005). A great deal of knowledge has already accumulated on the ecological significance of various seed properties. For example, seed mass distributions were found to change characteristically with increasing community maturity during vegetation succession (Salisbury, 1942). The survival of seedlings in shade was found to be correlated with the amount of storage material available in the seeds (Grime and Jeffrey, 1965). The general approach for most of such works (reviewed by, e.g., Leishman *et al.*, 2000; Fenner and Thompson, 2005; Bolmgren and Eriksson, 2010) was the quantification of seed mass (or other seed related trait) and its environmental correlates in whole-vegetation types. Only few studies have focused on certain plant functional or taxonomic groups (Zhao *et al.* 2011; Azcarate *et al.*, 2010), or tried to predict seed attributes from plant traits (Thomson *et al.*, 2010).

Grasses as a subset of the vegetation were rarely the subjects of such investigations, although grasses represent both a distinct taxonomic group and a characteristic functional group. Rabinowitz (1978) studied seven species of perennial grasses native to tall-grass prairie. Three of the species were common dominants in the studied prairie, whereas the other four were rare and were not dominant in any habitat. She found that species abundance in the vegetation and diaspore weight were positively correlated, i.e., the common species have heavy dispersal units, whereas the infrequent species have light ones. It was hypothesized that rare grasses may be colonizers of rare microsites and thus have seeds adapted for long-distance dis-

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persal. Furthermore, the strategy of small-seeded grasses was interpreted as related to their weedy character (Rabinowitz, 1978). Thompson's (1987) study on thirty two British grasses provided evidence that seeds of grasses with well-developed soil seed banks are small and compact. This finding can be considered as supporting the weedy character of small-seeded grasses, if we accept that species with remarkable ability to maintain seed banks are often weeds.

In this study, we examine whether seed properties of C<sub>3</sub> and C<sub>4</sub> photosynthetic-type grasses are different in the temperate flora of Hungary. Our approach is based on the following three results known from earlier investigations. (i) In a detailed ecological analysis of C<sub>3</sub> and C<sub>4</sub> grasses in the Hungarian flora, Kalapos (1991) showed that the C<sub>4</sub> group has a more pronounced weedy character than the C<sub>3</sub> group. (ii) Numerous authors demonstrated for various field situations that weeds more frequently establish persistent soil seed bank than non-weedy species do in a given vegetation (see e.g. in Leck *et al.*, 1989). (iii) Thompson *et al.* (1993) formed a theory that the seeds of species maintaining persistent soil seed bank are generally smaller and more spherical than those of transient species.

From facts i to iii, we hypothesize that the seeds of C<sub>3</sub> grasses should be heavier and less isodiametric in shape than the seeds of C<sub>4</sub> species, or – in other words – seeds of C<sub>4</sub> species should be more lightweight and more isodiametric. This hypothesis and related comparisons between grass groups based on life forms and weediness are investigated here.

## Materials and methods

The flora of Hungary contains 204 grass species of which twenty six belong to the C<sub>4</sub> photosynthetic type, the rest are C<sub>3</sub> species (Kalapos, 1991). Seed size and shape data were extracted from published literature, mainly from the seed atlas of Schermann (1967), or were based on direct measurements. In the latter case, mature seeds were harvested from populations growing in the wild in habitats typical for the species. Whenever possible, attention was paid to collect pooled seed samples from several mother plants of the same stand to avoid bias caused by maternal effects. Seed samples were placed in labelled paper bags and stored at room temperature till the end of the vegetation period. Thousand-seed mass data were calculated from measurements of 3 × 100 fully ripened seeds, weighed at an accuracy of 0.1 mg. (For some species where sample size was small, fewer, but at least 100, seeds were measured.) Seed shape was characterized by the slenderness (length per width) of the seeds, based on the measurements of ten seeds, with 0.1-mm accuracy. Slenderness was chosen to describe seed shape because this ratio is

known to be more characteristic to the species than seed length or width alone (Antkowiak *et al.*, 2010). In practice, caryopses or caryopses with persistent lemmas (in the case of strongly attached lemmas) were measured, but in any case without awns. Inclusion of awns would strongly modify seed shape, although these appendages are not persistent enough and break or wear away easily during seed dispersal in the field. Theoretically, the observation on seed shape could be more complete by considering not only the slenderness but the flatness too, or simply encountering the three-dimensional shape of seeds, as it was used for a subset of British species to quantify their seeds' deviation from the isodiametric shape (Thompson *et al.*, 1993). However, among grasses, there is a very limited variation in seed flatness, as most species have seeds like a tiny stick, longer or shorter, but always almost round in cross-section. Therefore, in practice, flatness would have added very little information to the seed shape of grasses.

In addition to the photosynthetic type, seed attributes were also compared between annuals and perennials. Relationship between 'weediness' and seed mass and seed shape was investigated by comparing groups of weedy and non-weedy grasses. The annual/perennial status and weediness groups were also used to form sub-groups of the C<sub>3</sub> grasses and then these groups were compared to C<sub>4</sub> grasses. Such sub-groups of C<sub>4</sub> grasses were not formed as a result of the very few perennial and non-weedy members (only five and six species respectively). The status of each species according to photosynthetic type, annual/perennial habit and weedy character is listed in the Appendix.

Data were log-transformed prior to statistical analyses to meet the normality and homoscedasticity assumptions of the tests. Comparisons between two groups were made by Student's *t*-test, or in case of non-normally distributed data (despite log transformation), the groups were compared by using non-parametric Mann–Whitney *U*-test (Quinn and Keough, 2002). Comparisons among three groups were made by one-way analysis of variance. If the ANOVA assumptions failed, a Kruskal–Wallis test with Dunn's multiple comparisons test was used. The relationship between the two seed traits, size and shape was analysed by calculating Pearson correlation of log-transformed data. In all comparisons, differences were considered significant at *P* < 0.05 probability level. For all the analyses, the Statistica 8.0 package was used (StatSoft, 2008).

## Results

Average seed mass was three-times higher for the C<sub>3</sub> group than for the C<sub>4</sub> group (3.44 and 1.13 g respectively). Mean seed slenderness was 4.46 for the

C<sub>3</sub> group, which is considerably higher than that of the C<sub>4</sub> group (2.54,  $P < 0.0001$ ).

There was a strong positive correlation between seed mass and seed slenderness for the C<sub>3</sub> group ( $r = 0.329$ ,  $P < 0.0001$ ,  $n = 137$ ), i.e., heavier seeds are less isodiametric in this group. Despite a similar trend, the relationship was not significant for the C<sub>4</sub> group ( $r = 0.035$ ,  $P = 0.876$ ,  $n = 22$ ), even after excluding *Cenchrus incertus*, a large-seeded epizoochorous grass ( $r = 0.247$ ,  $P = 0.281$ ,  $n = 21$ ).

Regarding weed versus non-weed groups comparisons, mean thousand-seed weight was not significantly different, 3.33 g for weedy and 3.06 g for non-weedy grasses altogether (C<sub>3</sub> and C<sub>4</sub> species combined). For the same groups of species, seed slenderness was significantly higher for non-weedy grasses than for grass weeds (4.51 and 3.39 respectively,  $P < 0.01$ ).

In a more detailed analysis of weediness, when groups of C<sub>3</sub> weeds, C<sub>3</sub> non-weeds and C<sub>4</sub> species (weeds + non-weeds) were compared, the C<sub>4</sub> group showed significantly smaller (lighter) and more isodiametric seeds on average than any of the C<sub>3</sub> groups (Table 1). Within C<sub>3</sub> species neither seed mass nor seed shape differed significantly between weed and non-weed groups, although the former had somewhat higher average seed mass (Table 1).

When seed traits of grass groups were compared according to annual and perennial life-history categories, thousand-seed mass was significantly higher for annuals than for perennials (3.87 and 2.72 g respectively). There was a similar tendency in seed slenderness, yet it was not significant (4.41 for annuals and 3.82 for perennials,  $P = 0.084$ ). In a subsequent analysis with three species groups – C<sub>3</sub> annuals, C<sub>3</sub> perennials and C<sub>4</sub> species (annuals and perennials combined) – mean thousand-seed mass was significantly higher for C<sub>3</sub> annuals than for the other two groups (Table 2). As for seed slenderness, C<sub>4</sub> species had lower mean value (i.e. more isodiametric seeds) than any of the two C<sub>3</sub> groups, which in turn were not different in this respect (Table 2).

**Table 1** Thousand-seed mass (TSM; g) and seed slenderness (seed length per width; Slen.) comparisons among grass species groups of the Hungarian flora with respect to their weed vs. non-weed characters and C<sub>3</sub> vs. C<sub>4</sub> photosynthetic types. Number of records are indicated in parentheses for each seed trait – grass group combination. Capital letters in superscript indicate significant differences.

Seed trait	C <sub>3</sub> weed	C <sub>3</sub> non-weed	C <sub>4</sub> Weed+ non-weed
TSM	4.408 <sup>A</sup> (31)	3.174 <sup>A</sup> (112)	1.132 <sup>B</sup> (22)
Slen.	4.560 <sup>A</sup> (30)	4.055 <sup>A</sup> (126)	2.544 <sup>B</sup> (23)

**Table 2** Thousand-seed mass (TSM; g) and seed slenderness (seed length per width; Slen.) comparisons among grass species groups of the Hungarian flora with respect to their annual vs. perennial life histories and C<sub>3</sub> vs. C<sub>4</sub> photosynthetic types. Number of known records are indicated in parentheses for each seed trait – grass group combination. Capital letters in superscript indicate significant differences.

Seed trait	C <sub>3</sub> annual	C <sub>3</sub> perennial	C <sub>4</sub> annual+ perennial
TSM	5.060 <sup>A</sup> (42)	2.769 <sup>B</sup> (101)	1.132 <sup>B</sup> (22)
Slen.	4.529 <sup>A</sup> (40)	4.440 <sup>A</sup> (116)	2.544 <sup>B</sup> (23)

## Discussion

### Seed mass comparisons

Thousand-seed mass comparisons in this study showed that seeds of C<sub>3</sub> grasses are heavier in general than seeds of C<sub>4</sub> grasses in the temperate grass flora of Hungary. This is consistent with our hypothesis that the seeds of C<sub>4</sub> species should be more lightweight than the seeds of C<sub>3</sub> grasses. However, despite the threefold difference in the averages, the deviation is significant only at  $P < 0.1$ . This is most probably due to the uneven sample sizes (143 and 22 species respectively) and the presence of *Cenchrus incertus* in the smaller (C<sub>4</sub>) group. The seeds of this grass are almost ten times heavier than the seeds of other species in the group. Indeed, when the analysis was repeated by omitting *C. incertus*, the difference in mean thousand-seed mass became significant between C<sub>3</sub> and C<sub>4</sub> grasses ( $P = 0.018$ ). *Cenchrus incertus* is unique in expressing remarkable morphological adaptation to zoochory as opposed to the vast majority of grasses that are wind dispersed. Species with seeds dispersed by animals are known to have significantly heavier seeds than that of species with wind-dispersed or unassisted seeds (Leishman *et al.*, 2000). Furthermore, for the interpretation of statistical significance in the present comparison, it must be emphasized that sampling intensity was above 80 per cent for both grass groups, (i.e. we sampled a considerable majority of the statistical population). Therefore, the obtained difference could be considered biologically meaningful and reliable.

The comparison of weedy and non-weedy grasses (irrespective of photosynthetic pathway type) yielded no difference in average seed mass. This is not consistent with the general concept that weeds (colonizers) are usually producing high number of small seeds (Comes and Grubb, 2003). This finding can be better interpreted if the photosynthetic pathway type is also considered by distinguishing three groups, that is, C<sub>3</sub> weeds, C<sub>3</sub> non-weeds and C<sub>4</sub> grasses. In this case, the C<sub>4</sub> group expressed significantly lighter seeds than either of the two C<sub>3</sub> groups. It is in line with the

finding that C<sub>4</sub> grass species are associated with open, disturbed or abiotically stressed habitats in the Hungarian flora (Kalapos, 1991).

Annual grasses displayed significantly heavier average seed mass than perennial grasses. However, when the photosynthetic pathway type was also taken into account, C<sub>4</sub> grasses showed the most lightweight seeds, C<sub>3</sub> perennials were intermediate, and C<sub>3</sub> annuals differed from both former groups by possessing the heaviest seeds. It is especially interesting because most of the C<sub>4</sub> grasses in our study are also annuals (Kalapos, 1991). Thus, the opposite tendency in seed mass between the two weed-like group, C<sub>3</sub> annuals and C<sub>4</sub> species, requires further interpretation.

The dominance of the annual life history among C<sub>4</sub> grasses (and also C<sub>4</sub> Cyperaceae) in Hungary is rooted in their increased heat demand compared to that of C<sub>3</sub> species (Williams, 1974; Kalapos *et al.*, 1997). Owing to their lower temperature requirements, C<sub>3</sub> species start their vegetative development earlier in the growth season than C<sub>4</sub> species do under seasonal temperate climate (e.g. Williams, 1974; Monson and Williams, 1982; Barnes *et al.*, 1983; Kalapos, 1991). Thus, C<sub>3</sub> grasses outcompete C<sub>4</sub> grasses via site pre-emption in undisturbed habitats where the early spring plant growth is not hindered by the environmental constraints (Allen, 1982), and thus closed canopy can develop, mainly from perennial tussocks, soon after the growing season began. Under such circumstances, C<sub>3</sub> annuals need to support their seedlings with larger budget of resources, i.e., with heavier seeds, for a successful establishment. Correlation between seed size and success of seedling establishment in shade has been shown (Grime and Jeffrey, 1965; Mazer, 1989).

The lower quantum yield of C<sub>4</sub> photosynthesis relative to C<sub>3</sub> metabolism makes C<sub>4</sub> plants less suited to shaded environments than C<sub>3</sub> plants (Ehleringer, 1978; Long, 1983). Therefore, C<sub>4</sub> species can be successful in habitats where either (i) vegetation development is suppressed during (early) spring (e.g. by low resource levels or other adverse conditions) or (ii) springtime disturbance removes the early sprouting C<sub>3</sub> vegetation. In such habitats, small seed size is not a drawback, but its benefit for quick colonization dominates instead. Typical examples of (i) are the inundation zones of floodplain rivers in Hungary, where wide corridors of bare mud surfaces become available for plant life after the retreat of spring floods. For case (ii), good examples include the fields of maize, a late-sown cereal, where massive disturbance happens after the main germination period of C<sub>3</sub> species. Significantly higher contribution of C<sub>4</sub> species was found in the weed flora of maize fields when compared to that of wheat fields in an extensive study of two agricultural regions of Hungary (Cseresnyés *et al.*, 2009).

### Seed slenderness comparisons

Seed slenderness difference between C<sub>3</sub> and C<sub>4</sub> grass groups proved to be extremely significant, i.e., C<sub>4</sub> grass species produce seeds more close to the isodiametric shape. An earlier study on British grasses concluded that seeds of species with persistent soil seed banks are compact, whereas those of species that lack seed banks are attenuated (Thompson, 1987). Later, this rule was extended, and in general, those species with small and round-shaped seeds were associated with their persistent soil seed bank (Thompson *et al.*, 1993). In our work, the species' ability to form persistent seed banks was not studied. Notwithstanding this, the more isodiametric seeds of C<sub>4</sub> grasses could be a sign of their greater ability to form persistent seed bank in the soil, and this would be consistent with their smaller seed size, and their strategy to colonize open, disturbed or stressed habitats (Venable and Brown, 1988). When photosynthetic pathway type was ignored, weedy grasses had more isodiametric seeds than non-weedy grasses. In a subsequent, refined analysis with three groups distinguished, C<sub>4</sub> grasses expressed more isodiametric seed shape than either the weedy C<sub>3</sub> grass group or the non-weed C<sub>3</sub> grass group. Considering the C<sub>4</sub> group, this result is in accordance with the habitat preference of the group as discussed earlier. However, the less isodiametric seeds in the C<sub>3</sub> weedy group need interpretation. According to Fenner and Thompson (2005), penetration of seeds into the soil is a crucial step of seed-bank formation. Spherical shape of a seed facilitates, whereas flat or elongated shape precludes penetration. Large seeds are known to be subjected to intensive predation (Reader, 1993; but see Moles *et al.*, 2003), thus they tend to minimize residence time in the soil and avoid seed banking (Fenner and Thompson, 2005). We identified C<sub>3</sub> weedy grasses as having relatively large seeds, thus their less isodiametric seed shape could be considered as an adaptive trait in avoiding burial in the soil and ensuring quick germination.

It is in accordance with the results of the seed shape versus life-history comparison where seeds of the C<sub>4</sub> grasses again showed more isodiametric shape and differed significantly from both the annual and perennial groups of the C<sub>3</sub> species. The similarity of results regarding weediness and life form can be related to the partial interdependence of these traits as most of the weedy grasses are annuals, whereas the non-weedy group is mostly formed by perennial species.

Although, in this work, grasses of the Hungarian flora were analysed, it is supposed that the same seed morphological differences prevail in other geographical regions characterized with four-season continental



climate similar to that of Hungary. On the other hand, we do not think that the same seed size and shape differences between  $C_4$  and  $C_3$  grass groups would express under (sub)tropical climate, where the seasonal dormancy of the vegetation is missing. Evidence from Australian flora underlines this as variation between species in seed-biology attributes was largely independent of variation in other traits (Leishman and Westoby, 1992).

Finally, our results suggest certain prediction regarding successful establishment of alien  $C_4$  grasses in open habitats. Considering already naturalized  $C_4$  aliens in Hungary, the most prominent candidates could be equipped with small seeds and with isodiametric seed shape and with annual life history. In earlier studies, small seed size and therophyte life form were found to have importance in the invasiveness in other floras or species groups (Hamilton *et al.*, 2005; McIntyre *et al.*, 2005). In a global examination, Mason *et al.* (2008) found invasive species to express a strategy of greater seed production both overall and per unit seed mass compared with natives. Isodiametric seed shape is newly associated with invasive success of species and most probably it operates via facilitating seed burial and formation of a persistent soil seed bank (Bekker *et al.*, 1998), a feature long known to be linked to invasibility (Newsome and Noble, 1986; Pyšek and Richardson, 2007).

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## APPENDIX

Seed mass and seed slenderness of C<sub>3</sub> and C<sub>4</sub> photosynthetic type grasses in the Hungarian flora with reference to their life-history and weediness categories. Nomenclature follows Horváth *et al.* (1995).

Abbreviations: A, annual; P, perennial; W, weed; N, non-weed; TSM, thousand-seed mass in grams; Slen., slenderness (length/width).

Type	Life history	Weed/Non-weed	Genus	Species	TSM (g)	Slen.
C3	A	N	<i>Aegilops</i>	<i>cylindrica</i>	34.35	3.549
C3	A	N	<i>Aira</i>	<i>caryophylla</i>	0.13	4.75
C3	A	N	<i>Aira</i>	<i>elegantissima</i>	0.05	5
C3	A	W	<i>Alopecurus</i>	<i>myosuroides</i>	2.045	2.6
C3	A	W	<i>Alopecurus</i>	<i>rendlei</i>	1.12	
C3	A	W	<i>Apera</i>	<i>interrupta</i>	0.09	8
C3	A	W	<i>Apera</i>	<i>spica-venti</i>	0.145	6
C3	A	W	<i>Avena</i>	<i>fatua</i>	30	5
C3	A	W	<i>Avena</i>	<i>sterilis</i>	16.74	3.04
C3	A	W	<i>Avena</i>	<i>strigosa</i>	18.5	4.06
C3	A	N	<i>Bromus</i>	<i>brachystachys</i>	2.31	
C3	A	N	<i>Bromus</i>	<i>commutatus</i>	4.35	5.25
C3	A	N	<i>Bromus</i>	<i>hordeaceus</i>	3.15	3.2695
C3	A	N	<i>Bromus</i>	<i>madritensis</i>	2.455	9.204
C3	A	N	<i>Bromus</i>	<i>racemosus</i>	4.18	3.85
C3	A	N	<i>Bromus</i>	<i>rigidus</i>	10.66	3.47
C3	A	N	<i>Bromus</i>	<i>squarrosus</i>	2.75	2.4
C3	A	N	<i>Bromus</i>	<i>tectorum</i>	3.05	6.5
C3	A	W	<i>Bromus</i>	<i>arvensis</i>	2.05	3.8
C3	A	W	<i>Bromus</i>	<i>japonicus</i>	3.4	3.75
C3	A	W	<i>Bromus</i>	<i>lepidus</i>	2.8	
C3	A	W	<i>Bromus</i>	<i>mollis</i>	2.45	2.75
C3	A	W	<i>Bromus</i>	<i>secalinus</i>	7.6	3.75
C3	A	W	<i>Bromus</i>	<i>sterilis</i>	7.8	10
C3	A	N	<i>Cynosurus</i>	<i>cristatus</i>	0.45	3.75
C3	A	W	<i>Cynosurus</i>	<i>echinatus</i>	1.586	3.75
C3	A	N	<i>Gaudinia</i>	<i>fragilis</i>	1.97	3.92
C3	A	W	<i>Haynaldia</i>	<i>villosa</i>	5.3	3.75
C3	A	W	<i>Hordeum</i>	<i>hystrix</i>	2.37	4.63
C3	A	W	<i>Hordeum</i>	<i>marinum</i>	2.631	2.642
C3	A	W	<i>Hordeum</i>	<i>murinum</i>	7.8	5.5
C3	A	W	<i>Lolium</i>	<i>multiflorum</i>	2.1	4
C3	A	W	<i>Lolium</i>	<i>remotum</i>	3.35	2.5
C3	A	W	<i>Lolium</i>	<i>temulentum</i>	8.3	2.3
C3	A	W	<i>Phleum</i>	<i>paniculatum</i>	0.249	1.68
C3	A	N	<i>Pholiurus</i>	<i>pannonicus</i>	1.9	3.5
C3	A	W	<i>Poa</i>	<i>annua</i>	0.27	3.5
C3	A	W	<i>Sclerochloa</i>	<i>dura</i>	0.98	3.75
C3	A	N	<i>Secale</i>	<i>sylvestre</i>	6.9	5.5
C3	A	N	<i>Taeniatherum</i>	<i>asperum</i>	2.96	5
C3	A	N	<i>Ventenata</i>	<i>dubia</i>		4
C3	A	N	<i>Vulpia</i>	<i>bromoides</i>	0.8	8
C3	A	N	<i>Vulpia</i>	<i>myuros</i>	0.43	9.5
C3	P	N	<i>Agropyron</i>	<i>caninum</i>	4.4	6

## Appendix (continued)

Type	Life history	Weed/ Non-weed	Genus	Species	TSM (g)	Slen.
C3	P	N	<i>Agropyron</i>	<i>intermedium</i>	5.55	4.75
C3	P	N	<i>Agropyron</i>	<i>pectinatum</i>	1.5	7
C3	P	W	<i>Agropyron</i>	<i>repens</i>	3.65	5.75
C3	P	N	<i>Agrostis</i>	<i>canina</i>	0.08	3.88
C3	P	N	<i>Agrostis</i>	<i>capillaris</i>	0.385	3.05
C3	P	N	<i>Agrostis</i>	<i>stolonifera</i>	0.085	3.5
C3	P	N	<i>Agrostis</i>	<i>vinealis</i>	0.06	3.29
C3	P	N	<i>Alopecurus</i>	<i>geniculatus</i>	0.38	2.5
C3	P	N	<i>Alopecurus</i>	<i>pratensis</i>	0.85	1.75
C3	P	W	<i>Alopecurus</i>	<i>aequalis</i>	0.36	2
C3	P	N	<i>Anthoxanthum</i>	<i>odoratum</i>	0.58	2.5
C3	P	N	<i>Arrhenatherum</i>	<i>elatus</i>	3.35	4
C3	P	N	<i>Arundo</i>	<i>donax</i>	0.1	4
C3	P	N	<i>Beckmannia</i>	<i>eruciformis</i>	0.4	4
C3	P	N	<i>Brachypodium</i>	<i>pinnatum</i>	4.3	5
C3	P	N	<i>Brachypodium</i>	<i>sylvaticum</i>	5.1	5
C3	P	N	<i>Briza</i>	<i>media</i>	0.535	1.5
C3	P	N	<i>Bromus</i>	<i>benekenii</i>	2.9	5.5
C3	P	N	<i>Bromus</i>	<i>erectus</i>	5.05	5.5
C3	P	N	<i>Bromus</i>	<i>inermis</i>	3.95	4.75
C3	P	N	<i>Bromus</i>	<i>pannonicus</i>	6.579	6.88
C3	P	N	<i>Bromus</i>	<i>ramosus</i>	5.865	4.69
C3	P	N	<i>Calamagrostis</i>	<i>arundinacea</i>		5
C3	P	N	<i>Calamagrostis</i>	<i>canescens</i>	0.07	3.43
C3	P	N	<i>Calamagrostis</i>	<i>pseudophragmites</i>	0.06	7.5
C3	P	N	<i>Calamagrostis</i>	<i>stricta</i>	0.197	2.55
C3	P	N	<i>Calamagrostis</i>	<i>varia</i>	0.24	3.24
C3	P	W	<i>Calamagrostis</i>	<i>epigeios</i>	0.062	5.25
C3	P	N	<i>Catabrosa</i>	<i>aquatica</i>	0.46	2.4
C3	P	N	<i>Corynephorus</i>	<i>canescens</i>	0.11	4.5
C3	P	N	<i>Dactylis</i>	<i>polygama</i>		3.54
C3	P	W	<i>Dactylis</i>	<i>glomerata</i>	0.883	5.5
C3	P	N	<i>Danthonia</i>	<i>alpina</i>		3.75
C3	P	N	<i>Deschampsia</i>	<i>cespitosa</i>	0.2	3
C3	P	N	<i>Deschampsia</i>	<i>flexuosa</i>	0.43	4.5
C3	P	N	<i>Festuca</i>	<i>altissima</i>	0.66	4.75
C3	P	N	<i>Festuca</i>	<i>amethystina</i>		3.92
C3	P	N	<i>Festuca</i>	<i>arundinacea</i>	1.52	4.5
C3	P	N	<i>Festuca</i>	<i>dalmatica</i>		4.55
C3	P	N	<i>Festuca</i>	<i>drymeia</i>	0.87	3.6
C3	P	N	<i>Festuca</i>	<i>gigantea</i>	2.27	4.75
C3	P	N	<i>Festuca</i>	<i>heterophylla</i>	1.04	6.5
C3	P	N	<i>Festuca</i>	<i>nigrescens</i>	0.89	4.53
C3	P	N	<i>Festuca</i>	<i>ovina</i>	0.635	5.5
C3	P	N	<i>Festuca</i>	<i>pallens</i>	1.037	5.754
C3	P	N	<i>Festuca</i>	<i>pratensis</i>	1.75	4.25
C3	P	N	<i>Festuca</i>	<i>pseudodalmatica</i>		3.85
C3	P	N	<i>Festuca</i>	<i>pseudovina</i>	0.38	3.575
C3	P	N	<i>Festuca</i>	<i>rubra</i>	1.1	5



## Appendix (continued)

Type	Life history	Weed/ Non-weed	Genus	Species	TSM (g)	Slen.
C3	P	N	<i>Festuca</i>	<i>rupicola</i>	0.775	3.28
C3	P	N	<i>Festuca</i>	<i>tenuifolia</i>	0.3	3.1
C3	P	N	<i>Festuca</i>	<i>vaginata</i>	0.6	4.5
C3	P	N	<i>Festuca</i>	<i>valesiaca</i>	0.48	3.7
C3	P	N	<i>Glyceria</i>	<i>arundinacea</i>	1.79	
C3	P	N	<i>Glyceria</i>	<i>declinata</i>	1.31	2.416
C3	P	N	<i>Glyceria</i>	<i>fluitans</i>	2.3	3.75
C3	P	N	<i>Glyceria</i>	<i>maxima</i>	0.9	3.25
C3	P	N	<i>Glyceria</i>	<i>plicata</i>	1.31	
C3	P	N	<i>Helictotrichon</i>	<i>praeustum</i>		4.55
C3	P	N	<i>Helictotrichon</i>	<i>pratense</i>	2.08	
C3	P	N	<i>Helictotrichon</i>	<i>pubescens</i>	2.03	5.5
C3	P	N	<i>Hierochloë</i>	<i>australis</i>		2.15
C3	P	N	<i>Hierochloë</i>	<i>repens</i>	0.45	3
C3	P	N	<i>Holcus</i>	<i>lanatus</i>	0.34	2.75
C3	P	N	<i>Holcus</i>	<i>mollis</i>	0.19	4
C3	P	N	<i>Hordelymus</i>	<i>europaeus</i>	5.77	5
C3	P	N	<i>Koeleria</i>	<i>cristata</i>	0.37	5
C3	P	N	<i>Koeleria</i>	<i>glauca</i>	0.153	4.42
C3	P	N	<i>Koeleria</i>	<i>grandis</i>	0.23	4.18
C3	P	N	<i>Koeleria</i>	<i>pyramidata</i>		3.53
C3	P	N	<i>Leersia</i>	<i>oryzoides</i>	1.06	2.8
C3	P	W	<i>Lolium</i>	<i>perenne</i>	1.3	4
C3	P	N	<i>Melica</i>	<i>altissima</i>	2	2.75
C3	P	N	<i>Melica</i>	<i>ciliata</i>	0.46	3
C3	P	N	<i>Melica</i>	<i>nutans</i>	0.47	2.4
C3	P	N	<i>Melica</i>	<i>picta</i>		2.31
C3	P	N	<i>Melica</i>	<i>transsilvanica</i>	0.844	2.26
C3	P	N	<i>Melica</i>	<i>uniflora</i>	4.5	2.25
C3	P	N	<i>Milium</i>	<i>effusum</i>	1.2	3
C3	P	N	<i>Molinia</i>	<i>arundinacea</i>		2.6
C3	P	N	<i>Molinia</i>	<i>coerulea</i>	0.85	3.25
C3	P	N	<i>Nardus</i>	<i>stricta</i>	0.38	10
C3	P	N	<i>Phalaroides</i>	<i>arundinacea</i>	0.73	3.5
C3	P	N	<i>Phleum</i>	<i>hubbardii</i>		1.89
C3	P	N	<i>Phleum</i>	<i>phleoides</i>	0.075	2.25
C3	P	N	<i>Phleum</i>	<i>pratense</i>	0.475	1.9
C3	P	N	<i>Phragmites</i>	<i>australis</i>	0.25	3.415
C3	P	N	<i>Piptatherum</i>	<i>virescens</i>	2.8	2.1
C3	P	W	<i>Piptatherum</i>	<i>miliaceum</i>	0.519	2.633
C3	P	N	<i>Poa</i>	<i>angustifolia</i>	0.19	3.926
C3	P	N	<i>Poa</i>	<i>badensis</i>	0.35	3.75
C3	P	N	<i>Poa</i>	<i>bulbosa</i>	1.2	3.75
C3	P	N	<i>Poa</i>	<i>nemoralis</i>	0.19	4
C3	P	N	<i>Poa</i>	<i>palustris</i>	0.187	4.25
C3	P	N	<i>Poa</i>	<i>annonica</i>		4.75
C3	P	N	<i>Poa</i>	<i>pratensis</i>	0.225	3.75
C3	P	N	<i>Poa</i>	<i>remota</i>	0.29	3.55
C3	P	N	<i>Poa</i>	<i>subcoerulea</i>		3.36

## Appendix (continued)

Type	Life history	Weed/ Non-weed	Genus	Species	TSM (g)	Slen.
C3	P	N	<i>Poa</i>	<i>trivialis</i>	0.195	4
C3	P	W	<i>Poa</i>	<i>compressa</i>	0.2	3.75
C3	P	W	<i>Poa</i>	<i>supina</i>		2
C3	P	N	<i>Puccinellia</i>	<i>distans</i>	0.24	2.6
C3	P	N	<i>Puccinellia</i>	<i>limosa</i>	0.1323	3.398
C3	P	N	<i>Sesleria</i>	<i>heuflerana</i>		1.9
C3	P	N	<i>Sesleria</i>	<i>sadlerana</i>	2.2	3.5
C3	P	N	<i>Sesleria</i>	<i>uliginosa</i>		2.94
C3	P	N	<i>Sesleria</i>	<i>varia</i>	1.5	3.44
C3	P	N	<i>Sieglingia</i>	<i>decumbens</i>	0.87	2.5
C3	P	N	<i>Stipa</i>	<i>borysthénica</i>	15.277	12.97
C3	P	N	<i>Stipa</i>	<i>bromoides</i>	3.039	6.002
C3	P	N	<i>Stipa</i>	<i>capillata</i>	4.6	11.5
C3	P	N	<i>Stipa</i>	<i>crassiculmis</i>		8.7
C3	P	N	<i>Stipa</i>	<i>dasyphylla</i>	18.666	14.49
C3	P	N	<i>Stipa</i>	<i>eriocaulis</i>	25.302	12.792
C3	P	N	<i>Stipa</i>	<i>joannis</i>	37.77	10.8
C3	P	N	<i>Stipa</i>	<i>pulcherrima</i>	40.4	12.992
C3	P	N	<i>Stipa</i>	<i>tirsa</i>	15.975	11.308
C3	P	N	<i>Trisetum</i>	<i>flavescens</i>	0.5	6
C4	A	W	<i>Cenchrus</i>	<i>incertus</i>	4.98	1.13
C4	A	N	<i>Crypsis</i>	<i>aculeata</i>	0.361	3.75
C4	A	W	<i>Digitaria</i>	<i>ciliaris</i>	0.59	2.53
C4	A	W	<i>Digitaria</i>	<i>ischaemum</i>	0.48	2.2
C4	A	W	<i>Digitaria</i>	<i>sanguinalis</i>	0.61	4
C4	A	W	<i>Echinochloa</i>	<i>crus-galli</i>	2	1.9
C4	A	W	<i>Echinochloa</i>	<i>oryzoides</i>		1.175
C4	A	W	<i>Eleusine</i>	<i>indica</i>	0.363	2.5
C4	A	W	<i>Eragrostis</i>	<i>megastachya</i>	0.14	1.2
C4	A	W	<i>Eragrostis</i>	<i>minor</i>	0.11	2.2
C4	A	W	<i>Eragrostis</i>	<i>pilosa</i>	0.08	2
C4	A	N	<i>Heleochloa</i>	<i>alopecuroides</i>	0.357	2
C4	A	N	<i>Heleochloa</i>	<i>schoenoides</i>	0.29	2.13
C4	A	W	<i>Panicum</i>	<i>capillare</i>	0.47	2
C4	A	W	<i>Setaria</i>	<i>pumila</i>	2.75	1.5
C4	A	W	<i>Setaria</i>	<i>verticillata</i>	1.15	1.8
C4	A	W	<i>Setaria</i>	<i>viridis</i>	0.9	2
C4	A	W	<i>Tragus</i>	<i>racemosus</i>	0.429	4.25
C4	P	N	<i>Bothriochloa</i>	<i>ischaemum</i>	0.3	3
C4	P	N	<i>Chrysopogon</i>	<i>gryllus</i>	2.6	5
C4	P	N	<i>Cleistogenes</i>	<i>serotina</i>	1.1055	5
C4	P	W	<i>Cynodon</i>	<i>dactylon</i>	0.335	2.25
C4	P	W	<i>Sorghum</i>	<i>halepense</i>	4.5	3