The analyses described here were done to determine chemical composition of seed unsaturated fatty acids in a wide range of species and persistence in the soil. Results showed no relationship between seed lipids and persistence in the soil. Therefore, there was no evidence to support the hypothesis that the oily seeds may be short lived and the relationship between oil content and seed longevity hypothesis is complex.

Keywords: seed chemistry, seed persistence

INTRODUCTION

The longevity of seeds in the soil is of considerable importance to both agronomists and ecologists. Many buried weed seeds can remain viable for years, posing serious problems of control for the farmer. To the ecologist, on the other hand, the persistence of seed banks in the soil is a major component of plant succession and plays a substantial role in the development of plant communities (Grime, 1979; Cook, 1980; Roberts, 1981).

Chemically, seed storage lipids are mainly triacylglycerols, most of which are oils, i.e., they are liquid above about 20°C. Some seeds may also contain appreciable quantities of phospholipids, glycolipids, and sterols generally associated with membranes. The predominant fatty acids in some seeds are unsaturated ones, and of these oleic (18:1) and linoleic (18:2) account for more than 60% by weight of all oils in some oil seed crops. These seed oils are of nutritional value because of their higher unsaturated fatty acid content. However, the seeds with oils rich in unsaturated fatty acids might pay the price of declining seed viability (Kaloyereas, 1958). In the presence of oxygen, fatty acid hydrocarbon chains may spontaneously oxidise producing highly reactive free radical intermediates, a class of compound called hydroperoxides, and a wide variety of secondary products from hydroperoxide decomposition. The rate of this reaction is greatly accelerated by lipooxygenases which are found in many seeds. Once a free radical reaction is produced, usually by oxygen attack, a chain reaction is initiated which creates additional reaction cycles and free radicals. However, the lipids in seed tissue may be protected by natural antioxidants which, by scavenging free radicals, can break the chain reaction cycle (Tappel, 1980).

Oxidative damage to membranes caused by free radicals has been suggested as one causative factor of poor seed longevity (Parish & Leopold, 1978; Pearce & Abdel Samad, 1980; Bewly, 1986). In the presence of oxygen, ageing of seeds has been associated with peroxidation of polyunsaturated fatty acids (Stewart & Bewly, 1980; Wilson & McDonald, 1986; Hendry, 1993). As free radical induced damage is believed to be greater in oily seeds, there would be a strong selection pressure for reduction of lipid content in persistent seeds (Ponquet, et al., 1992). However, the higher energetic costs of lipid production compared to carbohydrate synthesis could produce a selection pressure against energy storage in seeds in the form of fats.

The mechanisms that determine long-term seed persistence in the soil are largely unknown. Some physical attributes, such as seed size, shape and chemical composition (e.g. ortho-dihydroxyphenol content) have already been discussed in relation to persistence (Thompson, 1987; Thompson, et al., 1993; Hendry, et al., 1994). The relationship between seed persistence and seed lipids (unsaturated fatty acids) was analysed in the present study. Specifically, we tested the hypothesis that the greater danger of oxidation damage in oily seeds leads to a negative relationship between seed persistence and fatty acid content.

MATERIALS AND METHODS

Plant Material

ISP and other species seeds

More recent material of 43 ISP (Integrated Screening Program) species and 9 other species were from the seed stocks of the Unit of Comparative Plant Ecology. Most of these seeds were collected from semi-natural sites within a 25 km radius around Sheffield, UK. The list of species is shown in Table 1.

Biochemical analyses

Fatty acid analysis

Unsaturated fatty acids were determined as described by Hendry and Thorpe (1993) where 50 mg of ground tissue was extracted with 1.5 ml of borate buffer pH
9.0, 3 ml of KOH was added to 1 ml of extract and incubated in sealed tubes for 6 hours at 80°C. Following centrifugation at 3000 x g for 3 minutes, the saponified extract was incubated with lipoxidase enzyme (60,000 U/ml; Sigma Chemicals) for 20 minutes at 25°C. Absorbance was recorded at 234 nm for both active and boiled enzyme and the treatment responses estimated against a lineolic acid (Sigma Chemicals) standard. All replications consist of 5 samples.

Data source

Seed chemistry and persistence

In order to determine whether the fatty acid composition of seed lipids could be correlated with seed survival, the unsaturated fatty acid content of a wide range of species was determined and compared with information on persistence of these species.

Data on seed persistence were taken from Thompson, Bakker and Bekker (1996). The mean seed persistence class (where 1 is transient <1 year), 2 is short-term persistent (>1 and <5 years) and 3 is long-term persistent (> 4 years) over all measurements was calculated and used as a measure of seed persistence.

RESULTS

In the series of experiments, marked differences were observed in the concentrations of unsaturated fatty acids (UFA) in seeds of 52 species. The maximum concentration recorded was 35.0% of dry seed weight in *Urtica dioica* and the minimum was 0.80% of dry seed weight in *Galium aparine*. The percentage contents of UFA and seed persistence are summarised in table 1. No correlation was found between seed UFA and persistence in the soil (Fig. 1). There were marked differences in unsaturated fatty acid content in monocot and dicot species seeds; most monocots have less unsaturated fatty acids than dicots (Fig. 2).

DISCUSSION

This study provides no evidence to support the hypothesis that long-lived seeds would be less likely to store energy in the form of unsaturated fats. However, some interesting differences in unsaturated fatty acids contents between monocots and dicots emerge from Fig. 2. Results showed that dicot species seeds have generally more lipids (UFA) than monocots. This is only the most obvious example of the role of phylogeny in determining seed chemical composition.

Table. List of 52 species tested for unsaturated fatty acid contents.

<table>
<thead>
<tr>
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<tbody>
<tr>
<td><em>Agrostis capillaris</em></td>
<td><em>Dactylis glomerata</em></td>
</tr>
<tr>
<td><em>Anisantha sterilis</em></td>
<td><em>Deschampsia flexuosa</em></td>
</tr>
<tr>
<td><em>Anthoxanthum odoratum</em></td>
<td><em>Catapodium rigidum</em></td>
</tr>
<tr>
<td><em>Anthmiscus sylvestris</em></td>
<td><em>Digitalis purpurea</em></td>
</tr>
<tr>
<td><em>Arabidopsis thaliana</em></td>
<td><em>Dryas octopetala</em></td>
</tr>
<tr>
<td><em>Arrhenatherum elatius</em></td>
<td><em>Epilobium hirsutum</em></td>
</tr>
<tr>
<td><em>Bidens tripartita</em></td>
<td><em>Eriophorum vaginatum</em></td>
</tr>
<tr>
<td><em>Brachypodium pinnatum</em></td>
<td><em>Eupatorium cannabinum</em></td>
</tr>
<tr>
<td><em>Briza media</em></td>
<td><em>Festuca ovina</em></td>
</tr>
<tr>
<td><em>Bromopsis erecta</em></td>
<td><em>Festuca rubra</em></td>
</tr>
<tr>
<td><em>Campanula rotundifolia</em></td>
<td><em>Galium aparine</em></td>
</tr>
<tr>
<td><em>Carex flacca</em></td>
<td><em>Helianthus annus</em></td>
</tr>
<tr>
<td><em>Centaurea scabiosa</em></td>
<td><em>Helicotrichon pratensis</em></td>
</tr>
<tr>
<td><em>Cerastium fontanum</em></td>
<td><em>Helianthemum nummularium</em></td>
</tr>
<tr>
<td><em>Chamerion angustifolium</em></td>
<td><em>Holcus lanatus</em></td>
</tr>
<tr>
<td><em>Chenopodium album</em></td>
<td><em>Koeleria macrantha</em></td>
</tr>
<tr>
<td><em>Chenopodium rubrum</em></td>
<td><em>Leontodon hispidus</em></td>
</tr>
<tr>
<td><em>Coryza canadensis</em></td>
<td><em>Lolium perenne</em></td>
</tr>
</tbody>
</table>

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**Correlation of unsaturated fatty acids with seed persistence**

*Compositae* are generally high in fats, while *Gramineae* are generally low. The simple correlation in Fig. 1 does not take account of these phylogenetic constraints. However, an analysis conducted by Hodkinson (1996), using a large number of species and modern phylogenetically independent contrast (PIC) methods (Purvis & Rambaut 1995a) also failed to reveal any relationship between seed persistence and fatty acid content.

Given the higher metabolic costs associated with energy storage as lipids one might expect storage as starch (which may be more common in monocots than in dicots) to be selected, independently of any selection on the basis of longevity. Lipids, however, are a more efficient carbon storage form, with an energy yield approximately double that of carbohydrate and lipid storage may be favored in small seeds. The relationship between seed size and lipid content has not been investigated.

In a study of 7 species, Ponquett *et al.* (1992) found no correlation between longevity in dry storage and total oil content, but there was a significant relationship between the ratio of linoleic acid to tocopherols (an antioxidant) and longevity. Extrapolation from this study is limited, firstly because of the small number of species considered and secondly because it included 6 species of legume and is therefore phylogenetically unbalanced. Furthermore, longevity in dry storage may be unrelated to persistence in the field.

It has been shown that dormant imbibed (buried) seeds can respire, and can carry out protein synthesis in the formation of various cellular organelles and membranes. There is little doubt, therefore, that such seeds can also undertake at least some of the cellular repair and maintenance activities which are part of the normal metabolism of all tissues. The fluid environment provided by water allows for the diffusion of substrates to active sites of enzymes and also serves as a protectant of macromolecular structure (Vertucci & Farrant 1995). Villiers (1974) demonstrated that fully-imbibed seeds can maintain tissues cytoplasmic and nuclear components in good order by repair mechanisms and turn-over. It is probable that repair and turn-over would be unlikely in dry stored seeds, but may be possible in fully hydrated, but non-germinating, seeds.

The relationship between fats and persistence have mostly been concerned with dry storage. The records for dry storage and prolonged longevity are held mostly by legumes with starchy seeds (Harrington, 1972). Seventeen different crop seeds were stored over a period of twelve years and in general, leguminous seeds were found to maintain longest viability (Sonavne, 1934). Oily seeds usually exhibit poor storage life, e.g. sesame, mustard and linseed stored up to 12 months showed marked decrease in germinability (Nandi *et al.*, 1982). Cotton and lettuce Calmer cultivar seeds showed significant decline in viability, when stored for 3 to 6 years in a warehouse (Towers & Harrison, 1949, Harrington, 1973). Reduction of seed lipid content is not the only solution to the problem of reducing oxidative damage - it is also possible to increase the levels of antioxidants. The above observations by Ponquett *et al.* (1992) suggested that reducing the ratio of lipids to antioxidants may be a key to increased seed tonqevity of lipid storing seeds. In various types of plant tissues, “protective solutes” e.g. sugars and polysaccharides have been shown to decrease membrane damage in conditions of environmental stress. In a study of *Inga* species, Pritchard *et al.* (1995) showed that sensitivity to desiccation stress of *Inga* embryos was associated with low internal levels of soluble sugars. Depending upon the evolutionary and ecological constraints upon a species, seed persistence may be facilitated by either changing the energy storage chemical or by increasing antioxidant production. The latter possibility will confound any relationship between seed longevity and seed lipid content.

Of course seed persistence in the soil is dependent on many factors. Seed size, shape, colour, dormancy mechanism, soil environment and resistance to pathogens also contribute to persistence (Thompson *et al.*, 1993; Khan *et al.*, 1996; Kremer, 1986; Hendry *et al.*, 1994). It would be of interest to investigate the proportions of polysaccharides and total lipids in seed reserves of the species examined here for a better understanding of seed persistence mechanisms in the soil.
Fig. 2. Percentage Unsaturated Fatty Acids Content of Monocot and Dicot Species Seeds

- [ ] Monocot
- [ ] Dicot

Species List:
- Galium aparine
- Agrostis capillaris
- Artemisia absinthium
- Brachypodium pinnatum
- Lolium perenne
- Deschampsia flexuosa
- Festuca ovina
- Pae inana
- Bromus erectus
- Rumex acetosella
- Calocephalus rigidum
- Persicaria maculosa
- Pultenaea dysenterica
- Daunus glomerata
- Mentha arvensis
- Pae amphibia
- Cramus fontanum
- Festuca rubra
- Lycopus europaeus
- Plantago lanceolata
- Daunus purpurea
- Helianthemum nummularium
- Chenopodium rubrum
- Lotus corniculatus
- Koelreuteria macrantha
- Santolina chamaem
- Antennaria alyssoides
- Antennaria alyssoides
- Nasturtium officinale
- Zea mays
- Chenopodium album
- Spinacia oleracea
- Arabidopsis thaliana
- Carex flaccida
- Rorippa islandica
- Pilosella officinarum
- Anthriscus sylvestris
- Bidens tripartita
- Euphorium vagum
- Girgentanum vulgare
- Chaerophyllum temulum
- Lepidium hirsutum
- Holcus lanatus
- Centaurea calcituba
- Crispa octopetala
- Capsaicum annuum
- Capparis spinosa
- Thymus polytrichus
- Erica medica
- Epilobium hirsutum
- Campanula rotundifolia
- Helianthus annuus
- Urtica dioica
Table 1. Unaturated fatty acids) and seed persistence score of 52 species.
Persistence scores are given only for species with at least 10 records.

<table>
<thead>
<tr>
<th>Species</th>
<th>% oil (UFA) content</th>
<th>Persistence score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agrostis capillaries</td>
<td>1.3 ± 0.02</td>
<td>1.77</td>
</tr>
<tr>
<td>Anisantha sterilis</td>
<td>7.4 ± 0.06</td>
<td>1.21</td>
</tr>
<tr>
<td>Anthoxanthum odoratum</td>
<td>15.5 ± 0.34</td>
<td>1.00</td>
</tr>
<tr>
<td>Anthriscus sylvestris</td>
<td>7.4 ± 0.18</td>
<td>2.08</td>
</tr>
<tr>
<td>Arabidopsis thaliana</td>
<td>10.2 ± 0.23</td>
<td>1.14</td>
</tr>
<tr>
<td>Arrhenatherum elatius</td>
<td>1.4 ± 0.02</td>
<td>1.70</td>
</tr>
<tr>
<td>Bidens tripartite</td>
<td>16.2 ± 0.05</td>
<td>1.70</td>
</tr>
<tr>
<td>Brachypodium pinnatum</td>
<td>1.4 ± 0.06</td>
<td>1.05</td>
</tr>
<tr>
<td>Brassica</td>
<td>21.6 ± 0.22</td>
<td>1.00</td>
</tr>
<tr>
<td>Bromopsis erecta</td>
<td>2.3 ± 0.05</td>
<td>1.43</td>
</tr>
<tr>
<td>Campanula rotundifolia</td>
<td>17.1 ± 0.18</td>
<td>1.34</td>
</tr>
<tr>
<td>Carex flacea</td>
<td>10.9 ± 0.30</td>
<td>1.54</td>
</tr>
<tr>
<td>Cerastium fontanum</td>
<td>2.8 ± 0.07</td>
<td>1.17</td>
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<tr>
<td>Centaurea scabiosa</td>
<td>18.2 ± 0.35</td>
<td>1.78</td>
</tr>
<tr>
<td>Ceratum angustifolium</td>
<td>3.6 ± 0.09</td>
<td>1.57</td>
</tr>
<tr>
<td>Chenopodium album</td>
<td>7.5 ± 0.22</td>
<td>2.22</td>
</tr>
<tr>
<td>Chenopodium rubrum</td>
<td>6.5 ± 0.30</td>
<td>2.20</td>
</tr>
<tr>
<td>Cynara canadensis</td>
<td>19.6 ± 0.36</td>
<td>1.92</td>
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<tr>
<td>Dactylis glomerata</td>
<td>3.1 ± 0.09</td>
<td>1.22</td>
</tr>
<tr>
<td>Deschampsia flexuosa</td>
<td>2.0 ± 0.08</td>
<td>1.11</td>
</tr>
<tr>
<td>Digitalis purpurea</td>
<td>6.0 ± 0.06</td>
<td>2.28</td>
</tr>
<tr>
<td>Dryas octopetala</td>
<td>18.4 ± 0.37</td>
<td>1.78</td>
</tr>
<tr>
<td>Epilobium hirsutum</td>
<td>23.2 ± 0.17</td>
<td>1.80</td>
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<tr>
<td>Erhophorum vaginatum</td>
<td>16.5 ± 0.64</td>
<td>1.50</td>
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<tr>
<td>Eupatorium cannabinum</td>
<td>19.6 ± 0.72</td>
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<td>Festuca ovina</td>
<td>2.0 ± 0.07</td>
<td>1.12</td>
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<tr>
<td>Festuca rubra</td>
<td>3.7 ± 0.09</td>
<td>1.16</td>
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<tr>
<td>Galium aparine</td>
<td>0.8 ± 0.04</td>
<td>1.24</td>
</tr>
<tr>
<td>Helianthus annuus</td>
<td>34.3 ± 0.71</td>
<td>2.34</td>
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<tr>
<td>Helianthemum nummularium</td>
<td>7.5 ± 0.16</td>
<td>1.93</td>
</tr>
<tr>
<td>Holcus lanatus</td>
<td>18.2 ± 0.30</td>
<td>1.63</td>
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<td>Holchole macrantha</td>
<td>7.1 ± 0.12</td>
<td>1.10</td>
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<tr>
<td>Leontodon hispidus</td>
<td>17.3 ± 0.38</td>
<td>1.34</td>
</tr>
<tr>
<td>Lolium perenne</td>
<td>1.8 ± 0.05</td>
<td>1.26</td>
</tr>
<tr>
<td>Lotus comiculatus</td>
<td>6.8 ± 0.13</td>
<td>1.41</td>
</tr>
<tr>
<td>Lycopus europaeus</td>
<td>3.9 ± 0.14</td>
<td>1.64</td>
</tr>
<tr>
<td>Mentha arvensis</td>
<td>3.1 ± 0.09</td>
<td>1.64</td>
</tr>
<tr>
<td>Origanum vulgare</td>
<td>16.6 ± 0.53</td>
<td>2.00</td>
</tr>
<tr>
<td>Persicaria maculosa</td>
<td>2.8 ± 0.14</td>
<td>1.28</td>
</tr>
<tr>
<td>Pilosella officinalis</td>
<td>14.5 ± 0.41</td>
<td>1.71</td>
</tr>
<tr>
<td>Plantago lanceolata</td>
<td>4.7 ± 0.11</td>
<td>1.41</td>
</tr>
<tr>
<td>Poa annua</td>
<td>2.2 ± 0.06</td>
<td>2.12</td>
</tr>
<tr>
<td>Poa trivialis</td>
<td>3.2 ± 0.08</td>
<td>2.01</td>
</tr>
<tr>
<td>Pulsatilla dysenterica</td>
<td>2.9 ± 0.15</td>
<td>2.33</td>
</tr>
<tr>
<td>Rottkoppa islandica</td>
<td>13.1 ± 0.22</td>
<td>2.33</td>
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<tr>
<td>Rumex acetosella</td>
<td>2.6 ± 0.07</td>
<td>2.02</td>
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<tr>
<td>Scirpus sylvesteri</td>
<td>8.3 ± 0.08</td>
<td>1.26</td>
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<tr>
<td>Thymus polytrichus</td>
<td>20.4 ± 0.77</td>
<td>1.93</td>
</tr>
<tr>
<td>Urtica dioica</td>
<td>35.0 ± 0.79</td>
<td>1.93</td>
</tr>
<tr>
<td>Urea mays</td>
<td>7.5 ± 0.23</td>
<td>1.93</td>
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</table>
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from deterioration in storage. pp. 27-45 in
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