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How Much of a Stress-tolerant Ruderal is the Arctic-Annual, *Koenigia islandica* L.

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Abstract: The comparative effects of different stresses on growth and flowering of a stress-tolerant plants, *Koenigia islandica* L., were examined in controlled growth experiments alongside a typical ruderal, *Stellaria media* (L) ViLL., and a typical stress-tolerant plant, *Minuartia verna* (L.) Hiern. *Koenigia islandica* is fully tolerant of low nutrient supply and low temperature as *Minuartia verna*. There was relatively little effect of low nutrient supply on concentration of total nitrogen and phosphorus in *Koenigia* and *Minuartia* plants, while the size and concentrations of nitrogen and phosphorus in *Stellaria* was markedly reduced. *Koenigia* can grow adequately and flower under 8 cm of standing water which neither *Minuartia* or *Stellaria* could tolerate. Unlike *Minuartia* and *Stellaria*, *Koenigia* is relatively intolerant to drought. The growth of all three species was reduced by moderate to heavy shading. *Koenigia* was able to flower and set seed as quickly or slightly before *Stellaria* when grown at the same temperature or level of nutrient. *Koenigia* can complete its life cycle in the same length of time as *Stellaria*, i. e. less than 50 days, and is considered fully ruderal. *Koenigia* contradicts one of the main assumptions of the CSR life-strategy theory and a more flexible approach to the ordination of plants along three-main axis of competition, disturbance and stress is suggested.

Keywords: *Minuartia verna*, *Stellaria media*, stress-tolerant, CSR life-strategy theory

Introduction

The CSR life strategy theory of Grime (1979) has been very influential in the developing of ideas in plant ecology over recent decades with many workers providing supporting evidence for the theory (Grime *et al.*, 1997); Kachi & Rorison 1991), or adapting it to plant groups other than herbaceous vascular plants to which it was originally devised (Cooke & Rayner, 1984; Reynolds, 1989). There are however a number of papers questioning some of the assumptions of the theory (Oksanen, 1996 and Onipchenko *et al.*, 1998). Loehle (1988) specifically criticized the model because it 'distorts the data, results in lack of information and generates overly restrictive assumptions about strategic or environmental trade-off and suggested that the plants can tolerate both high levels of competition and stress are excluded given the way in which the triangular ordination is constructed from a three-dimensional matrix. Kautsky (1988) presented evidence from aquatic macrophyte communities to question another of the underlying assumptions of the CSR strategy theory: that there is no viable strategy available for plants to occupy environment with high levels of stress and disturbance. The three primary strategies of stress tolerators, ruderals and competitors were further supplemented by Grime (1974) to give four secondary strategies. It includes stress-tolerant ruderals, which allegedly can only tolerate moderate levels of stress and disturbance. Grime (1979) suggested that the arctic annual, *Koenigia islandica* L., should be placed in this category along with annuals. Is *Koenigia* and other plants like it, only 50 % stress-tolerant and only tolerant of moderate level of disturbance, or does it lie outside the triangle in a region of high disturbance (high-levels of frost-heave and soil erosion) and stress (low temperature and nutrient levels)?

Many of the critical examinations of the three primary axes of the growth strategy theory are based on field observations and not on the use of comparative experimental manipulation or laboratory tests, those used by Grime *et al.* (1997). This paper presents a quantitative assessment of the ability of *Koenigia islandica* to tolerate stress and disturbance in a comparative approach with typical stress-tolerator, *Minuartia verna* (L). Hiern and a typical ruderal, *Stellaria media* (L.) Vill. *Koenigia* can therefore be used as a test of one of Grime's primary assumptions that there is a simple trade-off between stress-tolerance and ruderalness. Grime (1974) has provided units for measuring the competitive ability and stress tolerance of plants, but unfortunately not for disturbance. Tolerance to disturbance can include the ability of a plant to recover from grazing or how rapidly it can reproduce before the vegetative part of the plant is destroyed by some regular, but catastrophic event. The ability to tolerate disturbance is taken here as the rapidity with which a plant can produce its disseminules and the allocation of resources to these structures.

Materials and Methods

Seeds of *Stellaria* were collected from Campus vicinity of Bradford, whilst the seeds of *Minuartia* were obtained from commercial seed merchant (Chiltrens, Cumbria). Seeds of *Koenigia* were collected from plants growing near Storr (57°31' 6°10'W) on the Isles of Skye, Scotland. Seeds of *Koenigia* required scarification in order to induce germination. The mean dry weight of the seeds of *Koenigia*, *Stellaria* and *Minuartia* are 0.44, 0.35 and 0.26 mg seed^{-1}, respectively.

Single plant of each species were planted 10 days after germination into individuals 210 cm^3 pots containing acid-washed sand that was thoroughly rinsed prior to planting. Plants were grown in cabinets with 16 h photoperiod at photosynthetically active photon flux density of 110 μmoles m^{-2} s^{-1} and temperature of 15°C. Nutrients were supplied as full-strength Rorison's nutrient solution (Hendry & Grime, 1993), except where otherwise stated. The eight hour long dark period was kept at 5° C. The temperature was ramped up to 15°C and down from 15° C in the first hour and last hour of the photoperiod, respectively. The nutrient solution was changed twice a week. During the growth period, the appearance of the first flowers and fruits was noted. The plants were grown for 50 days. Before the plants were harvested, the roots thoroughly rinsed with deionised water. Plants were dried at 80° C for 48 h prior to being weighed. The concentrations of nitrogen, phosphorus and potassium in the plant tissues were determined using methods of Allen (1989).

The effect of temperature on the growth of three species was investigated by altering both the photoperiod and dark periods by 5° C intervals, such that the dark period was always 10°C lower than photoperiod. The temperatures of photoperiods were 5, 10, 15, 20 and 25° C.

Table 1: The concentration (mg g^{-1}) of total nitrogen (N), phosphorus (P) and potassium (K) in *Koenigia islandica, Minuartia verna* and *Stellaria media* plants grown for 50 days in 0.4, 1 and 100% of full-strength Rorison's nutrient solution

Concentration of nutrient solution (% of full strength)	*Koenigia*			*Minuartia*			*Stellaria*		
	N	P	K	N	P	K	N	P	K
0.4	11.5	0.6	18.3	11.0	0.6	18.7	8.2	0.4	8.5
1	11.8	0.7	17.6	11.4	0.7	19.0	8.9	0.4	13.8
100	13.2	1.0	19.0	10.7	0.7	20.9	14.2	1.3	25.0

The effect of nutrient stress on plant growth was investigated by diluting the standard Rorison's nutrient solution by 50, 90, 95, 98, 99 and 99.6% with deionised water, pH 5.5. Plants of each species were also grown at different concentrations of nitrate-nitrogen supplied as HNO_3 in a background solution of full-strength Rorison's nutrient solution. Phosphorus was tested in same way,but with phosphate added to the nutrient solution as H_3PO_4 (Hendry & Grime 1993). The pH of all nutrient solutions was adjusted to 5.5.

The ability of different species to tolerate waterlogging was assessed by growing the plants in 0.5 dm^3 pots containing John Inns compost No. 2. The height of pots was relative to the levels of deionised water within a glass tank was manipulated such that 2, 4, 6, 8 cm of water above the soil surface. Control plants were well watered in the same size pots, but without standing water. The tank containing the plants was kept in an unheated glasshouse for fifty days before harvesting the plants.

The effect of fluctuating water stress was investigated by growing 10 days old seedling in 0.5 dm^3 pots for further 40 days in a glasshouse under different number of layers of white muslin cloth. The ambient photon flux density was reduced by 62 % with single layer of muslin, whilst two and three layers of cloth reduced it by 76 and 86 %. The aboveground parts of the plant were harvested, dried and weighed after 50 days of growth under the different number of layers of cloth.

Results and Discussion

Temperature: The optimum temperature for the growth of all three species tested is 15° C (Fig. 1). Not surprisingly, the *Stellaria* plants are heavier than *Koenigia* or *Minuartia* plants at all growth temperatures (Fig. 1). The growth of all three species is reduced markedly with reduction in temperature, but the relative reduction in growth of *Koenigia* was less than other two species tested, at 5 and 10° C. The total dry weight of the *Stellaria* plants at 5° C was only 1.5 % of that 15° C, whilst the growth of *Minuartia* and *Koenigia* was reduced by 97.1 and 95.3%, respectively, for the same reduction in temperature. The flowering and setting of seeds by *Koenigia* was between two and six days before that of *Stellaria* at temperature between 10 and 25° C (Fig. 1). There was no flowering by *Minuartia* within the 50-days growth period at any temperature or nutrient regime. None of the *Stellaria* and *Koenigia* plants had flowered by the time of harvest at 50-days when grown at 5° C (Fig. 1)

Nutrient stress: The growth of Stellaria was reduced far more by increasing dilution of the Rorison's nutrient solution than *Koenigia* or *Minuartia* (Fig. 2). The *Stellaria* seedlings were, however, still heavier than either *Koenigia* or *Minuartia* seedlings at the lowest level of dilution (0.4%) of the nutrient solution (Fig. 2). *Koenigia* behaved in simlar manner to

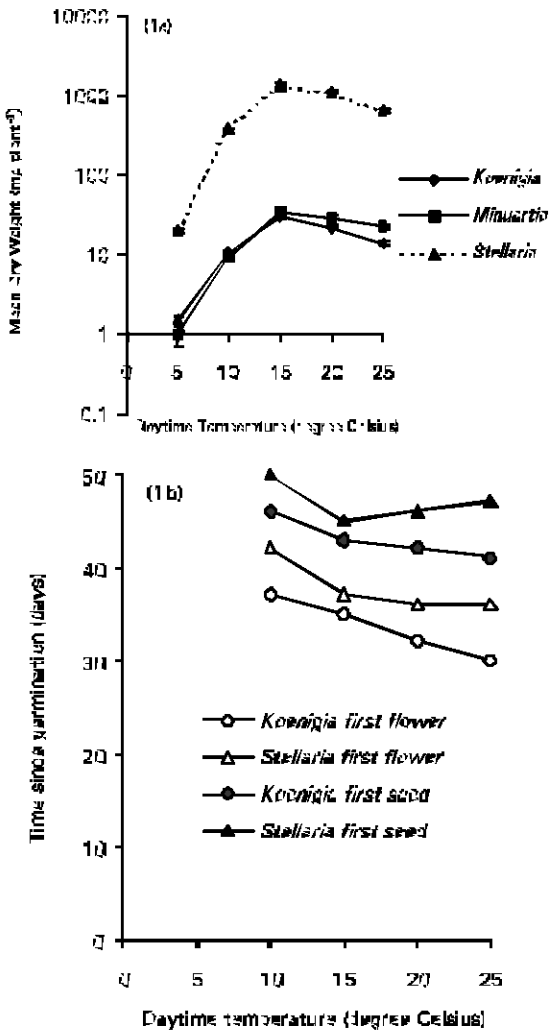

Fig. 1: The effect of day time temperature (° C) on (a) the mean dry weight (mg plant^{-1}) and (b) time taken for the first plants of *Koenigia islandica, Stellaria media and Minuartia verna* to flower and set seed when grown for 50 days in full-strength Rorison's nutrient solution. Means of 5 replicate plant with ± one standard error bars shown.

Minuartia as a stress-tolerator by maintaining leaf nitrogen and phosphorus concentrations similar to those of control plants at low rates of nutrient supply (Table 1). In contrast, the nitrogen and phosphorus concentrations in the leaves of *Stellaria* were markedly reduced with increasing dilution of the nutrient solution (Table 1). Decreasing the concentration of the nutrient solution only increased the length of time to the production of the first flowers by a few days for *Koenigia* and *Stellaria* (Fig. 3).

Not surprisingly, the growth of *Stellaria* was affected by low concentrations of nitrogen supplied as nitrate (Fig. 3). *Minuartia* was tolerated by low rates of nitrate supply than *Koenigia* in terms of absolute dry weight per plant and relative reduction in dry weight as compared to control. *Koenigia* is

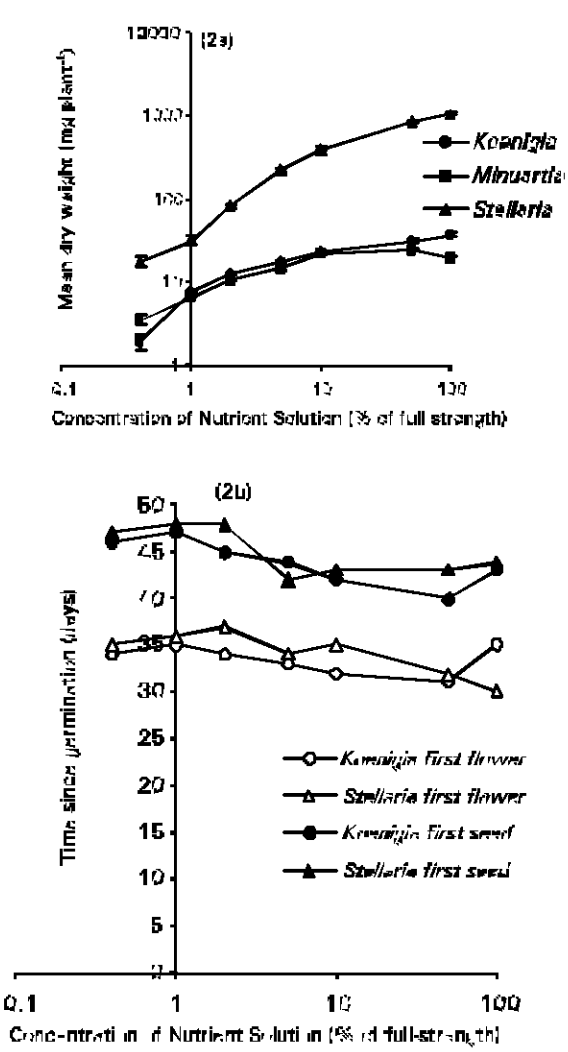

Fig. 2: The effect of concentration of nutrient solution (% of full-strength) on (a) the mean dry weight (mg plant^{-1}) and (b) time taken for the first plants of *Koenigia islandica*, *Stellaria media* and *Minuartia verna* to flower and set seed when grown for 50 days at 15/5°C. Means of 5 replicate plant with ± one standard error bars shown.

however more tolerant of low concentrations of orthophosphate in the nutrient solution than *Minuartia* and *Stellaria* on the relative basis (Fig. 3).

Water availability: The growth of *Koenigia* seedlings was least affected by waterlogging compared to *Stellaria* and *Minuartia* seedlings (Fig. 4). All plants of *Stellaria* and *Minuartia* died under 8 cm standing water (Fig. 4), while plants of *Koenigia* were 21% of the weight of control plants grown under 2 cm of water. The plants of *Koenigia* are also capable of flowering and setting seed under 8 cm of standing water (Fig. 4), partly because it is self-fertile cleistogamous annual.

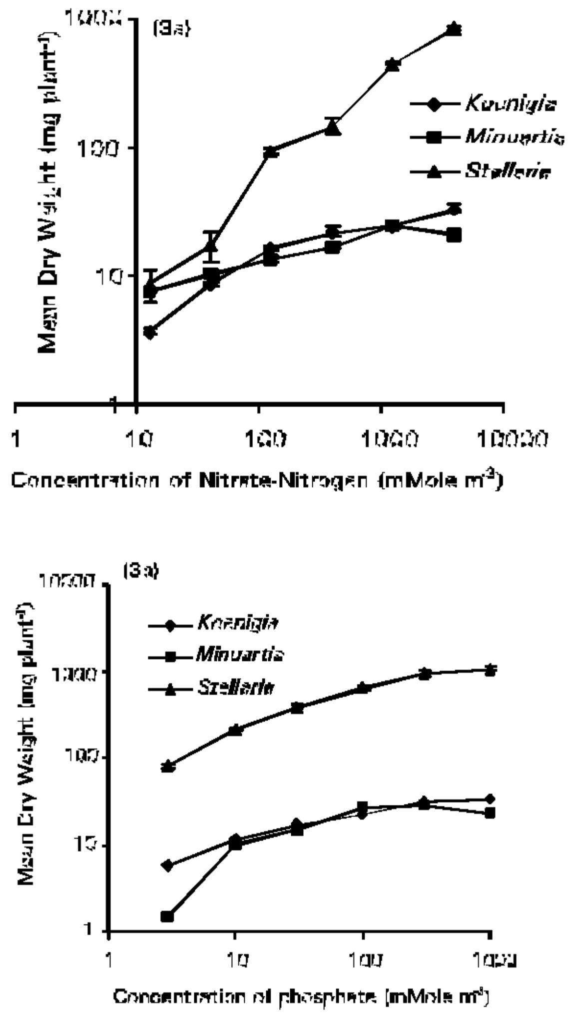

Fig. 3: The effect of (a) nitrate-nitrogen concentration and (b) orthophosphate concentration (mmole m^{-3}) in full-strength Rorison's nutrient solution on the mean dry weight (mg plant^{-1}) of *Koenigia islandica, Stellaria media* and *Minuartia verna* plants grown for 50 days at 15/5 °C. Means of 5 replicate plant with ± one standard error bars shown.

From three species *Koenigia* is least tolerant to fluctuating water stress (Fig. 5). Growth was at its maximum when plants were watered for eight days in every 12 days watering cycle. The growth of *Stellaria* and *Minuartia* was greatest with lowest level of watering. The high organic matter content of the John Innes compost No. 2 will have increased the water holding capacity of the substratum and therefore maintained high soil water potential over a longer period than for a purely based growing medium.

Availability of light: None of three species tested are particularly shade tolerant as growth was markedly reduced by moderate levels of shading (Fig. 6). However *Koenigia* is the least tolerant to highest level of shading as mean weights of

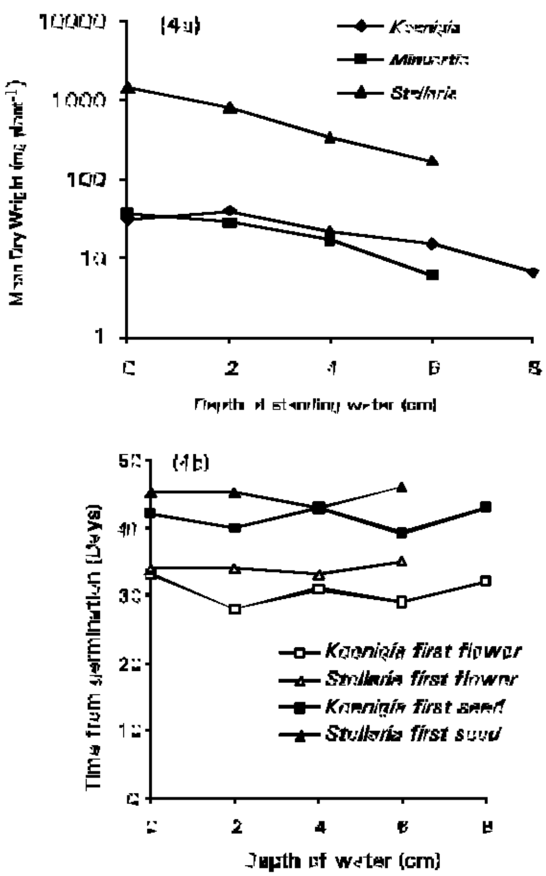

Fig. 4: The effect of water level (cm) above the soil surface on (a) the mean dry weight (mg plant^{-1}) and (b) the time taken for the first plants of *Koenigia islandica, Stellaria media* and *Minuartia verna* to flower and set seed when grown for 50 days in Jhon Innes compost. Means of five replicate plants with ± one standard error bars shown.

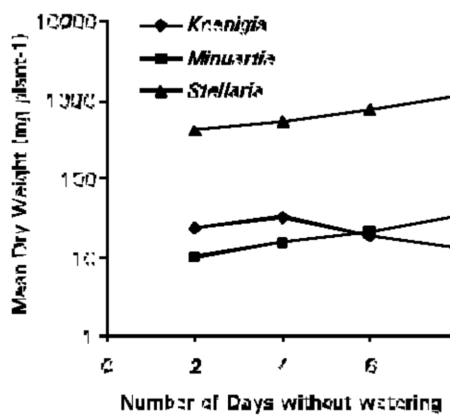

Fig. 5: The effect of length of drought period (days) within 12 days watering cycle on the mean dry weight (mg plant^{-1}) of *Koenigia islandica, Stellaria media and Minuartia verna* plants. Means of five replicate plants with ± one standard error bars shown.

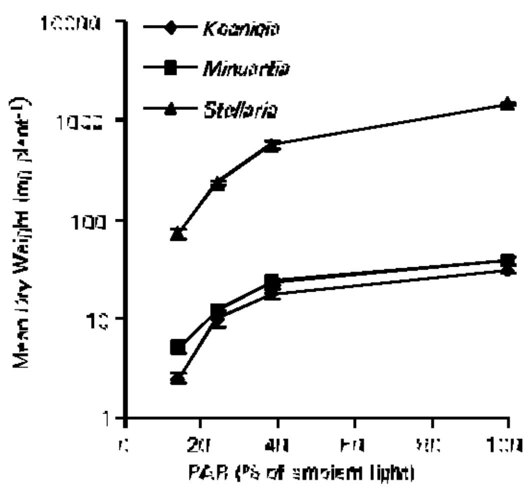

Fig. 6: The effect of different levels of shading (% of full-strength) on the mean dry weight (mg plant^{-1}) of *Koenigia islandica, Stellaria media* and *Minuartia verna* plants. Means of five replicate plants with ± one standard error bars shown.

the plants at this level of shading were reduced markedly (Fig. 6).

Length of life cycle: The minimum time taken by *Koenigia* to complete its life cycle in the laboratory was between 39 and 47 days depending on the temperature, water and nutrient regime. This is slightly quicker than that for *Stellaria*, (42 and 50 days). After 6 days of flowering, *Koenigia* set viable seed. When Campbell & Grime (1992) tested CSR life-strategy theory using seven contrasting species of grass the result did not coincide with the predictions of theory. The examination of the regenerative and established strategies of *Koenigia islandica* in the field and laboratory also provide evidence that this species does not fit into the prediction given by Grime (1979) as to its position within the CSR strategy theory. Using the definition of a stress-tolerator *Koenigia* is highly stress tolerant species. The mean dry weights of *Koenigia* were very close to those of the stress-tolerator *Minuartia* when grown under the same temperature and nutrient conditions (Figs. 1, 2, 3, and 4). The mean relative growth rate of *Koenigia* plants was estimated to be 0.6 mg mg^{-1} week^{-1}. This is slightly less than that for *Minuartia* (0.7 mg mg^{-1} week^{-1}) grown under exactly the same conditions. Although low temperature had the same relative reduction in growth (Fig. 2), but *Koenigia* is clearly better able to grow and reproduce at lower temperature than the other species as it is widespread in arctic and alpine tundra (Hultén, 1968). It was found as 80° N on Savalbard (Jalas & Suominen, 1986) where mean July temperature was only 5°C (Meteorological office 1972).
Koenigia was also typical of most arctic plants in being able to tolerate considerable nutrient stress (Chapin, 1980). Nutrient stress has similar effects on absolute weight and relative

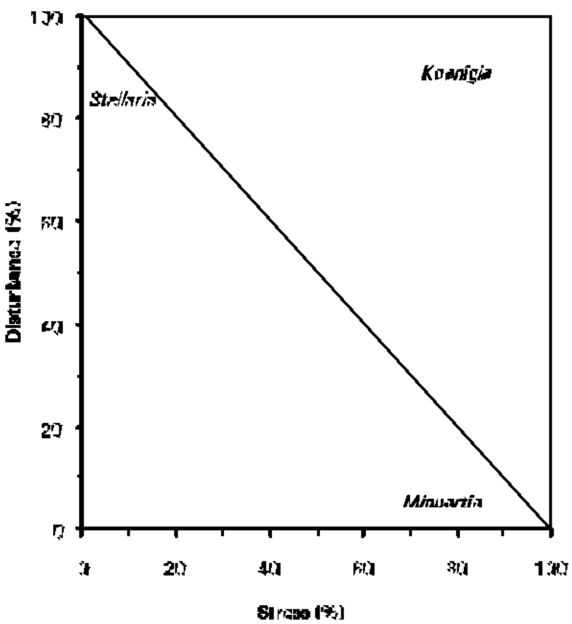

Fig. 7: The position of *Koenigia islandica* , *Stellaria media* and *Minuartia verna* within CSR strategy theory triangle.

growth rate as that observed in *Minuartia*. It was also typical of stress-tolerators in that concentrations of nitrogen and phosphorus in the leaves was not reduced significantly with decreasing rates of nutrient supply (Grime *et al.*, 1997).

Grime (1979) does not use any units to quantify the degree to which plants can tolerate disturbance. However a morphological index is used to quantify the competitive ability of the plant and by plotting this value with logarithm of its relative growth on a triangular plot. The degree to which a plant is tolerant of disturbance automatically falls out (Grime, 1974). This is, however not as rigorous as having some objective and independent measure of ruderalness, which would enable genuine triangulation to be established and thus gave a measure of error to the plants position within the triangular plot. One possible independent measure of how well a plant can tolerate devastating disturbance, as opposed to grazing is the minimum time required for a species to complete its life cycle. Other attributes might include the proportional allocation to reproduction, which is normally greater in ruderals (Salisbury, 1942).

Koenigia is annual and can complete its life cycle in 39 days in the laboratory and it was a few days ahead of *Stellaria* In the field it has been observed to complete its life cycle within 35 to 40 days in Rocky Mountains of USA (Reynolds, 1984) and 42 days in one of its extant Scottish localities (pers. Obs.). It also allocated a significant proportion of its biomass to seed production (29%) with typical between and seven seeds produced per plant in Scotland. It was normally found in mobile substrata, such as solifluction lobes, lake shores, stone polygons, mud blisters and other locations that experience intensive soil movement due to erosion or freeze-thaw cycles (Polunin, 1959). In its Scottish localities, the concentrations of nitrate-nitrogen, ammonium-nitrogen and phosphate in the soil were 0.59, 0.28 and 0.93 $\mu g\ g^{-1}$ dry weight, respectively.

Not surprisingly *Koenigia* has virtually no competitive ability, and has a morphological index of 0.5 (Grime, 1974). It was however very stress-tolerant (100% according to Grime's own criteria) and fully ruderal in terms of its rapidity of reproduction. *Koenigia* therefore lies well outside the triangle of CSR strategy theory, in half of the graph where plants cannot allegedly occupy high levels of stress and disturbance (Fig. 7).

Loehl (1988) suggested, plants should be ordinated in three-dimensional space with respect to their competitive ability, stress-tolerance and ruderalness. It would also be preferable to use an absolute scale rather than relative units. If such an approach is taken, then one can envisage that most plants will occupy the area of low to moderate levels of stress and disturbance, but moderate to high levels of competition. It is unlikely that plants are likely to occur in the corner of such a hypothetical space where there is virtually no competition, stress or disturbance: i. e. the origin for all three axes. Conversely, the physical environment of highly disturbed and stressful environments is such that plants are likely to be so far apart that significant competition for resources will never occur.

The application of CSR life-strategy theory to arctic vegetation not only appears to be flawed (Oksanen, 1996; Crawford 1997), but needs to be modified to take into account the exceptions found in temperate herbaceous and woody vegetation. It was also evident that plants that tolerate one particular stress, such as low temperature and waterlogging, are not going to be able to tolerate the opposite extreme of a stress-gradient, i. e. high temperature and drought. It is clear that use of single axis for stress-tolerance is unrealistic given the wide array of stresses that species of plants may have to tolerate and survive (Grubb, 1985).

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