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EXPERIMENTAL ECOLOGY OF *DRYAS OCTOPETALA* ECOTYPES: RELATIVE RESPONSE TO COMPETITORS

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SUMMARY

A competition experiment was performed to determine the relative competitive abilities of fellfield and snowbed ecotypes of *Dryas octopetala* L. under conditions of high nutrients, high light, and high water availability. Pots were designed to allow the effects of root competition and shoot competition to be assessed separately. The large-leaved snowbed ecotype responded positively to shoot competition, producing larger leaves and higher biomass than in control pots (no competition). Root competition resulted in a decrease in leaf size and an increase in root:shoot ratio, but no significant effect on shoot number or biomass accumulation. In contrast, the fellfield ecotype responded to shoot competition with an increase in root:shoot ratio, with no effect on biomass or shoot numbers. However, root competition caused a reduction in plant growth. Under growth chamber conditions of high resource availability, the snowbed ecotype is the superior competitor, probably due to ecotypic differences in both root and shoot characteristics.

Key words: Competition, ecotypes, root competition, shoot competition.

INTRODUCTION

The study of competition has long occupied a central role in the development of ecological and evolutionary theory. Variation in competitive ability among individuals within a population is thought to be of general importance in the operation of natural selection (Darwin, 1859). Until recently studies demonstrating a genetic basis for differences in competitive ability in natural populations of plants have been few. Experimental work has now established that genetic variation in competitive ability exists within and between plant populations (Shontz & Shontz, 1971; Khan, Antonovics & Bradshaw, 1976; Solbrig & Simpson, 1977; Weaver & Warwick, 1982). Moreover, competitive advantage may vary as a function of the physical environment (Snaydon, 1971) or the biotic environment (Sakai, 1957; Turkington & Harper, 1979; Martin & Harding, 1981), with locally adapted populations being better competitors in their 'home' sites.

All of the foregoing studies examined variation in competitive ability in relatively short-lived herbaceous, weed or crop species. Field and growth chamber manipulations with *Dryas octopetala* L. (Rosaceae) have suggested that differential competitive ability may also be important in the distribution and selection of two ecotypes in natural, undisturbed environments in long-lived perennial plant species (McGraw & Antonovics, 1983; McGraw, 1985). Indirect evidence came from field experiments in which nutrients were added factorially. A fellfield ecotype responded negatively in terms of plant growth to fertilizer addition while

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a snowbed ecotype responded positively. The fellfield and snowbed community responses were virtually the same with graminoid species becoming dominant and community production increasing by a factor of 2·4. The contrasting response of the two ecotypes was attributed to genetic differences in competitive ability, possibly conferred by genetic differences in plasticity of petiole and leaf length (McGraw & Antonovics, 1983) and by differential physiological tolerance to shade (McGraw, 1985).

The present study was designed to test the relative response to competitors of fellfield and snowbed ecotypes of *D. octopetala* by placing them in direct competition with each other. Based on previous work, I predicted that the snowbed ecotype would be a superior competitor under conditions of high light, water, and nutrient availability. Moreover, since previous work showed that the selective differential was probably due to a difference in shade-tolerance and canopy characteristics, I predicted that the mechanism of competitive suppression of the fellfield ecotype would be through shoot competition, and not through root effects.

Materials and Methods

Seeds were collected from natural fellfield and snowbed populations of *Dryas octopetala* near Eagle Summit, Alaska at mile 106 on the Steese Highway (65° 26′ N, 145° 30′ W; elevation 1050 m). The site consists of a gradient from a ridgetop to a snowbank in the lee of the ridge. The ridgetop is dry, nutrient-poor, and exposed to wind and snowblast, while the snowbank is relatively moist, nutrient-rich, and protected from exposure. The fellfield ecotype of *D. octopetala* is abundant on the ridgetop and the snowbed ecotype is most abundant in areas of late-lying snow. The zone between the ridgetop and the snowbed contains individuals of both ecotypes as well as individuals which are phenotypically intermediate. Detailed descriptions of the changes in vegetation and environment along this gradient may be found elsewhere (Miller, 1982; McGraw & Antonovics, 1983).

Seeds were placed in petri dishes at 17 °C with a 20 h day/4 h night light cycle on 2 September, 1981. Upon emergence of the radicle (about 10 September, seeds were placed in the competition pots. The 6 cm wide pots were designed to hold space available to roots and shoots of each plant constant, while varying the presence or absence of roots and/or shoots of a single competing plant. Each pot had plastic partitions below ground and clear plexiglass partitions aboveground. Plants were grown in isolation [no competition, Fig. 1(a)], in the presence of roots of the other ecotype [root competition, Fig. 1(b)], in the presence of shoots of the other ecotype [shoot competition, Fig. 1(c)], and in the presence of both roots and shoots of the other ecotype [full competition, Fig. 1(d)], using above- or below-ground partitions to effect each treatment. The technique is a modification of that used by Donald (1958). The plant growth medium consisted of finely chipped pieces of arcillite clay (commercially available as 'Turface' from International Minerals Corporation). The advantage of Turface for the present work is that upon harvest the soil can be easily washed from the roots allowing a complete biomass determination.

In this study, the effect of competition is measured by the difference in growth between plants growing alone and those growing in the presence of roots, shoots, or both roots and shoots of a competitor. This measure indicates the degree to which the two competing plants utilize common limiting resources. Density is

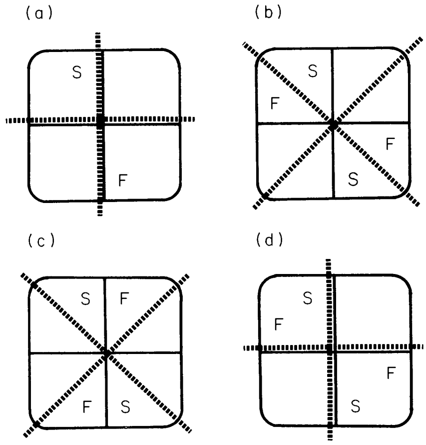

Fig. 1. Schematic diagram of competition pots showing above-ground partitions (----) and below-ground partitions (——) used to separate and enclose roots and shoots of the snowbed ecotype (S) and the fellfield ecotype (F); (a) no competition, (b) root competition, (c) shoot competition, (d) full competition.

purposely varied to observe its effects, unlike in 'de Wit' competition trials where density is held constant to observe relative performance in mixed and pure cultures (de Wit, 1960). Since the density effect depends critically on the distance between plants, care was taken to place two competing plants the same distance apart (1·8 cm), whether roots, shoots, or roots and shoots were being juxtaposed.

Seedlings were kept in germination conditions until 27 September. During this time, all seedlings which failed to emerge completely were replaced by others. By 27 September, 13 to 23 replicate pots remained in each treatment. The pots were then transferred to a growth chamber equipped with high intensity discharge lamps. Nutrients, light, and water were administered at constant high levels. Nutrients were added at the rate of one complete application (pots watered until dripping) of half-strength Hoagland's solution daily. Photosynthetically active radiation in the chambers was approximately 1000 μmol m^{-2} s^{-1} at the level of the pots, nearly the level found on clear days at the field site. In addition to daily nutrient applications, pots were watered with distilled water twice daily. Temperature in the growth chamber was maintained at 17 °C during a 20 h light period and at 4 °C during the 4 h dark period. Relative humidity in the chamber was maintained at 90% ($\pm$10%) in order to prevent extreme water loss and drought stress in the small pots at the high light intensities used in the experiment. At weekly intervals approximately one half of the pots were moved to new random locations within the growth chamber to avoid possible effects of spatial heterogeneity of the chamber environment.

Plants were harvested on 16 and 17 December, 1981, 15 weeks after seed germination began. Leaf length and root:shoot ratio were measured to assess the morphological effects of competition. The plant growth response was measured in terms of shoot numbers, above-ground dry weight, root dry weight, and total plant dry weight attained by the end of the experiment. The data were analyzed with two-way ANOVAs carried out separately for each ecotype. Within the competition treatments, the relationship between the growth and morphology of

Table 1. *F-statistics for two-way ANOVAs on root and shoot competition effects on plant growth and morphology of the fellfield and snowbed ecotypes of* Dryas octopetala L.

Population	Source of variation	Root weight	Above ground weight	Total weight	Number of shoots	Length longest leaf	Root: shoot
Fellfield	Root competition	2·82 a	4·35*	4·18*	6·32*	8·84**	0·00
	Shoot competition	0·53	0·48	0·04	2·96	0·61	5·00*
	Root:shoot interaction	0·18	0·67	0·51	2·28	0·42	0·06
Snowbed	Root competition	0·01	2·75	1·32	2·55	12·47***	11·15**
	Shoot competition	9·44**	13·91***	13·06***	1·86	25·04***	0·74
	Root:shoot interaction	0·15	0·67	0·49	0·00	0·72	0·26

Significance levels are; $*P < 0{\cdot}05$; $** P < 0{\cdot}01$; $*** P < 0{\cdot}001$; a $0{\cdot}05 < P < 0{\cdot}10$.

one ecotype and the growth and morphology of the other ecotype was determined by correlation.

Results

In the snowbed ecotype, shoot competition had stronger effects on above and below ground biomass and leaf length than did root competition (Table 1). The effect of shoot competition was unusual in that root, shoot and total weight of the snowbed ecotype all increased in response to addition of shoots (shoot competition and full competition) of a fellfield plant to the pot (Fig. 2), regardless of whether roots of the fellfield plant were present or not. This effect was not due to greater allocation to shoots *vis-à-vis* roots since the root: shoot ratio of snowbed plants was unaffected by shoot competition. The harvested above-ground biomass was therefore further separated into photosynthetic (leaf blades) and non-photosynthetic (petiole and stem) tissue to determine whether shoot competition may have stimulated greater allocation to leaf material within the above-ground biomass. This was not the case at the time of harvest. However, with shoot competition, snowbed plants produced longer leaves (Table 1, Fig. 2). These leaves projected farther away from the meristem horizontally and vertically than shorter leaves. Root competition resulted in a significant decrease in leaf size and an increase in the root: shoot ratio, with no significant effect on biomass accumulation of snowbed plants.

The fellfield ecotype responded to root and shoot competition in a manner very different from the snowbed ecotype. Shoot competition had no effect on biomass accumulation, although the root: shoot ratio increased significantly (Table 1). Root competition caused a reduction in number of shoots, aboveground weight, and total plant weight, with a similar trend in root weight. Leaf length also declined under root competition.

Root and shoot competition effects on all plant attributes were surprisingly additive across treatments as indicated by the parallelograms in Figure 2. There was no significant interaction between root and shoot effects in growth or morphology of a competitor in either ecotype (two-way ANOVA, Table 1).

Within the full competition treatment, components of biomass and total biomass of an individual of the fellfield ecotype were negatively correlated with all biomass measures of the competing individual of the snowbed ecotype (Table 2). That all

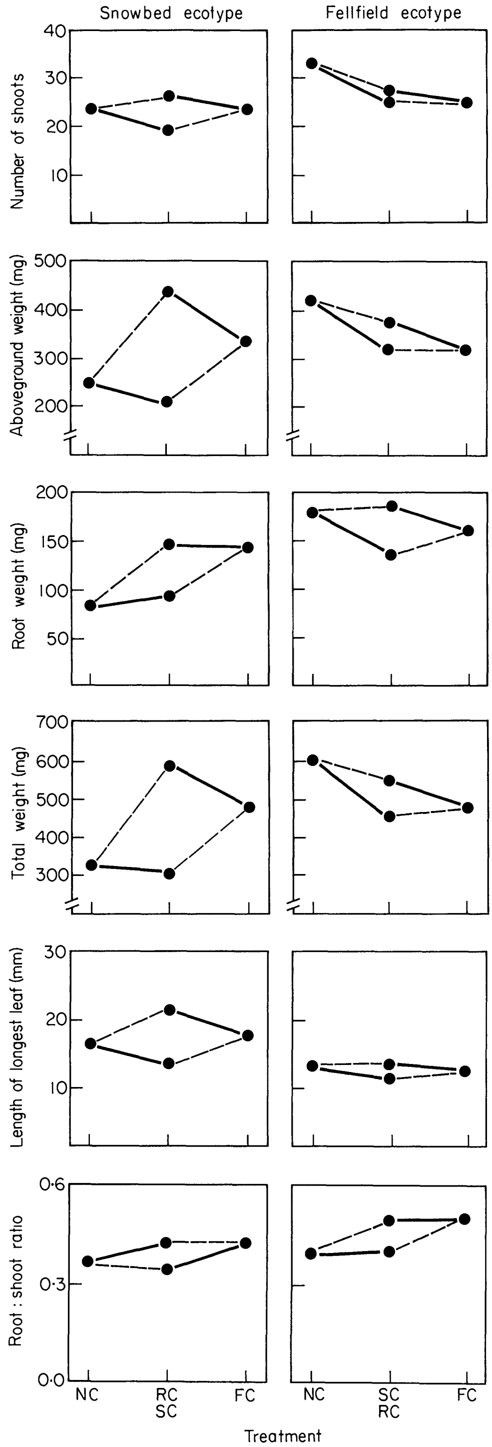

Fig. 2. Response of growth parameters to root competition (——) and shoot competition (----); NC, no competition; SC shoot competition; RC root competition; FC, full competition.

Table 2. *Pearson product-moment correlation coefficients for various measures of plant growth and plant morphology between competing populations of* Dryas octopetala *L. in the full competition experiment*

Fellfield ecotype	Snowbed ecotype: Shoot number	Shoot weight	Root weight	Total weight	Root: shoot	Length longest leaf
Shoot number	−0·60*	−0·65**	−0·62*	−0·64**	−0·06	−0·46
Shoot weight	−0·59*	−0·58*	−0·52*	−0·57*	0·07	−0·17
Root weight	−0·73**	−0·71**	−0·64**	−0·69**	−0·04	−0·36
Total weight	−0·68**	−0·67**	−0·60*	−0·65**	0·03	−0·26
Root:shoot	−0·39	−0·39	−0·36	−0·38	−0·15	−0·34
Length longest leaf	−0·35	−0·28	−0·10	−0·22	0·57*	0·07

Significance levels as in Table 1.

of these correlations were significant is due to a strong positive correlation among the characters within an ecotype ($P < 0{\cdot}01$ in all cases, data not shown). For example, within the snowbed ecotype root biomass and shoot biomass are positively correlated ($r = 0{\cdot}95$, $P < 0{\cdot}0001$), therefore both root and shoot biomass of the snowbed ecotype are negatively correlated with a competitor's total biomass ($r = -0{\cdot}60$ and $r = -0{\cdot}67$, respectively). Hence, the mechanism (root or shoot effects) by which one plant effects another is not clarified by the analysis. None of the biomass values were correlated with root:shoot ratio or leaf length of the competitor (Table 2). However, leaf length of the fellfield ecotype was positively correlated with the root: shoot ratio of the snowbed ecotype. Correlation coefficients for attributes of the competitors were smaller (in absolute value) and of lower statistical significance in the root competition and shoot competition treatments (data not shown).

Discussion

In previous work, the snowbed ecotype showed a potential for producing larger leaves than the fellfield ecotype in response to both experimental and field conditions (McGraw & Antonovics, 1983; McGraw, 1985). In addition, snowbed plants had a lower root:shoot ratio (greater allocation to shoots) than fellfield plants at high nutrient and light levels. Both greater allocation to above-ground biomass and longer leaves have been strongly implicated as important arbiters of the outcome of competition in other studies (Black, 1960; Snaydon, 1971; Solbrig & Simpson, 1977).

The results of the competition experiment verified the prediction that the snowbed ecotype would be competitively superior, but pointed to ecotypic differences in response to root competition as well as shoot competition as the cause. The lack of growth depression of the fellfield ecotype in response to shoot competition is enigmatic since snowbed plants again produced much larger leaves and were overtopping the fellfield plants. In addition the root: shoot ratio increased in response to shoot competition. Both overtopping and an increase in the root:shoot ratio should theoretically lead to reduced growth by fellfield plants. Overtopping and higher root:shoot ratios may have developed late in the course of competition, and therefore had not produced an effect by the time of the final harvest.

The present results support the findings of others that root competition develops before shoot competition in depressing growth of 'loser' plants (Donald, 1958; Aspinall, 1960). Suppression of growth of the fellfield ecotype by roots of the snowbed ecotype occurred despite daily inputs of half-strength Hoagland's solution. The difference between ecotypes in response to root competition was accentuated by the finding that fellfield plants had greater root weights under all treatments. The competitive difference in response to root competition was therefore not due to root biomass. How do roots of the snowbed ecotype suppress growth of fellfield plants? The advantage of snowbed plants is suggested by the general observation that in wild plants, species or ecotypes from moderate to high nutrient sites have roots with a higher nutrient uptake capacity (per gram of root) than plants from low nutrient sites (Chapin, 1980). From previous work, it is known that the snowbed is a more fertile site than the fellfield (Miller, 1982). If the snowbed ecotype possessed a higher nutrient uptake capacity, it could take advantage of the daily nutrient pulse of Hoagland's solution to a greater degree than the fellfield ecotype. In addition, root competition produced no compensating shift in the root:shoot ratio of fellfield plants. In contrast, the root:shoot ratio of snowbed plants increased in response to root competition, thus compensating for the competition.

The ecotypic difference in response to shoot competition was that the snowbed ecotype showed an increase in above- and below-ground biomass while the fellfield ecotype was not affected. A trend toward the same response has been observed in competition experiments with *Lolium* and *Phalaris* (Donald, 1958). This response in snowbed *Dryas octopetala* was not due to greater allocation to above-ground biomass. Neither was it attributable to a greater allocation to photosynthetic tissue within the above-ground biomass. However, shoot competition stimulated greater leaf length (and overall leaf size) in the snowbed ecotype. The cause of the enhanced leaf expansion was probably an effect of the competing shoot on the water balance of the expanding leaves. Leaf expansion (even more so than photosynthesis) is extremely sensitive to drought stress (Sands & Rutter, 1959; Lister *et al.*, 1967; Boyer, 1970; Acevedo, Hsiao & Henderson, 1971; Garrett & Zahner, 1973). The competing shoot, by transpiration, would maintain a higher relative humidity in the canopy of the snowbed plant, thus reducing the vapor pressure deficit and, in turn, reducing water loss from the plant. Reduced water loss and the resulting higher water potential of leaves would allow greater leaf expansion. Consistent with this hypothesis is the overall pattern of leaf size in the competition treatments (Fig. 2). If soil water availability was reduced by roots of a competitor with no shoot effect (root competition treatment), inhibition of leaf expansion would occur more quickly and leaf size would be reduced; this was the observed effect of root competition. The negative root effect and positive shoot effect on leaf size is clearly shown in Figure 2 and appears to be additive. Equally clear is the lack of response of leaf length in the fellfield ecotype exposed to shoot competition. This ecotypic difference is consistent with previously shown genetic differences in leaf plasticity (McGraw & Antonovics, 1983).

The production of longer leaves by the snowbed ecotype allowed light capture over a greater horizontal area in the treatments with shoot competition than in other treatments. In this way, self-shading was probably reduced. Therefore, although percentage allocation of biomass to leaves was the same among treatments, shoot competition had a positive effect through its effect on leaf length and hence, canopy architecture. Since the unusual effect of shoot competition on snowbed plants was not anticipated, no quantitative measurements of canopy architecture were made. However, in future work, more detailed examination of canopy light interception and microclimate would probably be useful in the interpretation of such competition experiments.

The evidence for significant within-species (or within-genus) variation in competitive ability is strong (Shontz & Shontz, 1971; Mahmoud & Grime, 1976; Solbrig & Simpson, 1977; Turkington & Harper, 1979; Grace & Wetzel, 1981; Martin & Harding, 1981). Frequently such evidence is used to infer that one biotype or species is 'more competitive' than another. However, relative competitive ability may reverse as a function of the environment (Snaydon, 1971; Turkington & Harper, 1979), such that local populations are competitively superior only in specific local environments. Since the present study was carried out under only one set of conditions, it would be premature to identify one ecotype as competitively superior. However, from this study, I conclude that natural populations of long-lived perennial plants found in stable environments may be genetically differentiated with respect to competitive ability, as has been shown in relatively short-lived species. In *D. octopetala*, the snowbed ecotype was better able to withstand, and even to take advantage of, competition under growth chamber conditions of high resource availability.

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References

Acevedo, E., Hsiao, T. C. & Henderson, D. W. (1971). Immediate and subsequent growth response of maize leaves to changes in water status. *Plant Physiology*, **48**, 631–636.

Aspinall, D. (1960). An analysis of competition between barley and white persicaria. II. Factors determining the course of competition. *Annals of Applied Biology*, **48**, 637–654.

Black, J. N. (1960). The significance of petiole length, leaf area and light interception in competition between strains of subterranean clover (*Trifolium subterraneum* L.) grown in swards. *Australian Journal of Agricultural Research* **11**, 277–291.

Boyer, J. S. (1970). Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. *Plant Physiology*, **46**, 233–235.

Chapin, III F. S. (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233–260.

Darwin, C. (1859). *On the Origin of Species*. A facsimile of the first edition, 1964. Harvard University Press. Cambridge, Massachusetts.

Donald, C. M. (1958). The interaction of competition for light and for nutrients. *Australian Journal of Agricultural Research*, **9**, 421–432.

Garrett, P. W. & Zahner, R. (1973). Fascicle density and needle growth responses of red pine to water supply over two seasons. *Ecology*, **54**, 1328–1334.

Grace, J. B. & Wetzel, R. G. (1981). Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist*, **118**, 463–474.

Khan, M. A., Antonovics, J. & Bradshaw, A. D. (1976). Adaptation to heterogeneous environments. III. The inheritance of response to spacing in flax and linseed (*Linum usitatissimum*). *Australian Journal of Agricultural Research*, **27**, 649–659.

Lister, G. T., Slankis, V., Krotkov, G. & Nelson, C. D. (1967). Physiology of *Pinus strobus* L. seedlings grown under high or low soil moisture conditions. *Annals of Botany*, **31**, 121–132.

McGraw, J. B. (1985). Experimental ecology of *Dryas octopetala* ecotypes. III. Environmental factors and plant growth. *Arctic and Alpine Research*, **17**, in press.

McGraw, J. B. & Antonovics, J. (1983). Experimental ecology of *Dryas octopetala* ecotypes. I. Ecotypic differentiation and life-cycle stages of selection. *Journal of Ecology*, **71**, 879–897.

Mahmoud, A. & Grime, J. P. (1976). An analysis of competitive ability in three perennial grasses. *The New Phytologist* **77**, 431–435.

Martin, M. M. & Harding, J. (1981). Evidence for the evolution of competition between two species of annual plants. *Evolution*, **35**, 975–987.

Miller, P. C. (1982). Environmental and vegetational variation across a snow accumulation area in montane tundra in central Alaska. *Holarctic Ecology*, **5**, 85–98.

Sakai, K.-I. (1957). Studies on competition in plants. VII. Effect on competition of a varying number of competing and non-competing individuals. *Journal of Genetics*. **55**, 227–234.

Sands, K. & Rutter, A. J. (1959). Studies in the growth of young plants of *Pinus sylvestris* L. II. The relation of growth to soil moisture tension. *Annals of Botany*, **23**, 269–284.

Shontz, N. N. & Shontz, J. P. (1971). Competition for nutrients between ecotypes of *Galinsoga ciliata*. *Journal of Ecology*, **60**, 89–92.

Snaydon, R. W. (1971). An analysis of competition between plants of *Trifolium repens* L. populations collected from contrasting soils. *Journal of Applied Ecology*, **8**, 687–697.

Solbrig, O. T. & Simpson, B. B. (1977). A garden experiment on competition between two biotypes of the common dandelion (Taraxacum officinale). Journal of Ecology, **65**, 427–486.

Turkington, R. & Harper, J. L. (1979). The growth, distribution, and neighbour relationships of *Trifolium repens* in a permanent pasture. IV. Fine scale biotic differentiation. *Journal of Ecology*, **67**, 245–254.

Weaver, S. E. & Warwick, S. I. (1982). Competitive relationships between atrazine resistant and susceptible populations of *Amaranthus retroflexus* and *A. powellii* from southern Ontario. *The New Phytologist*, **92**, 131–139.

Wit, C. T. de (1960). On competition. *Agricultural Research Reports* (*Verslagen van Landbouwkundingen Onderzoekingen*), **66**, 108–118.