Plant competition for light analyzed with a multispecies canopy model

III. Influence of canopy structure in mixtures and monocultures of wheat and wild oat

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Summary. A multispecies canopy photosynthesis simulation model was used to examine the importance of canopy structure in influencing light interception and carbon gain in mixed and pure stands of wheat (*Triticum aestivum* L.) and wild oat (*Avena fatua* L.), a common weedy competitor of wheat. In the mixtures, the fraction of the simulated canopy photosynthesis contributed by wheat was found to decline during the growing season and this decline was closely related to reductions in the amount of leaf area in upper canopy layers. For both species in mixture and in monoculture, simulated photosynthesis was greatest in the middle or upper-middle canopy layers and sensitivity analyses revealed that canopy photosynthesis was most sensitive to changes in leaf area and leaf inclination in these layers. Changes in LAI and leaf inclination affected canopy carbon gain differently for mixtures and monocultures, but the responses were not the same for the two species. Results from simulations where the structural characteristics of the two species were substituted indicated that species differences in leaf inclination, sheath area and the fraction of leaf area alive were of minor consequence compared with the differences in total leaf area in influencing relative canopy carbon gain in mixtures. Competition for light in these species mixtures appears to be influenced most by differences in the positioning of leaf area in upper canopy layers which determines, to a great extent, the amount of light intercepted.

Key words: Canopy structure – Competition for light – Leaf area index-LAI – Leaf inclination – Canopy photosynthesis

Plant architecture affects the penetration and distribution of visible radiation in canopies (Warren Wilson 1967; Stoner et al. 1978; Caldwell et al. 1983a; Neufeld et al. 1988) and would thus be expected to be an important factor in determining competitive ability of plants for light (Caldwell 1987). Because of the rapid extinction of visible radiation in canopies (Saeki 1963), the ability of a plant to place foliage in upper, well lit canopy layers (Black 1958, 1960; Williams 1963; Harper and Clatworthy 1963) should be an important structural trait contributing to competitive ability. Indeed, plant height alone can often be used to predict competitive outcome (Benjamin 1984). In addition to the amount and height of foliage, competitive ability has also been related to foliage orientation (Jennings and Aquino 1968).

A quantitative evaluation of the role of plant architecture in competition for light between species of similar height and growth form is difficult, experimentally. In mixed-species canopies the species may differ slightly in foliage orientation and there will likely be considerable foliage overlap both within and among species in the canopy. Thus, accurate measurements of the light intercepted by different plants are difficult to obtain. Furthermore, species can differ in the photosynthetic utilization of intercepted light within the canopy (Beyschlag et al. 1990). The importance of species differences in canopy structure as opposed to leaf physiological characteristics may, therefore, not always be readily apparent.

The present study utilized the multispecies canopy photosynthesis model described by Ryel et al. (1990) to investigate the importance of canopy structure in influencing the simulated carbon gain of two annual grasses, wheat (*Triticum aestivum*) and wild oat (*Avena fatua*), a common weedy competitor of wheat, growing in mixed and monoculture stands in the field. In general, these species are rather similar in height and growth form but they do differ slightly in the timing of leaf area development and location in the canopy, leaf inclination, leaf senescence patterns (Barnes et al. 1988) and individual leaf photosynthetic characteristics (Beyschlag et al. 1988; 1990). The model was used to specifically evaluate (1) which part of the canopy was most important for the total carbon gain of each species and (2) which structural traits are most important in influencing competition for light.
Methods

Plants of wheat (cv. Bannock) and wild oat were sown to an overall density of 816 m$^{-2}$ in monocultures and 1:1 mixtures from 29 to 30 May 1987 in field plots (1.2 x 1.8 m) located near Logan, Utah, USA (1460 m elevation; 41.5° N), as described by Barnes et al. (1988). Plots were irrigated periodically during the growing season (29 May to 3 August 1987) so that the total precipitation (natural + augmented) received by the plants during June and July was 161 mm, which was 200% of normal. For both species, mean predawn leaf water potentials (measured with a pressure chamber) ranged from $-0.3$ to $-1.0$ MPa during June and July.

Measurements of canopy leaf blade area index (LAI) and leaf sheath area index (SAI) were conducted with a fiber-optic, inclined point quadrat system (Caldwell et al. 1983b) at an inclination of 12.5° (Warren Wilson 1960, 1963). Point quadrat sampling was conducted three times during the growing season in the mixtures (22 to 24 June, 6 to 8 July and 19 to 21 July; n = 4 to 6) and twice during the season in the monocultures (30 June and 14 July; n = 2). For analysis, canopies were arbitrarily divided into strata 5 cm in height; sampling in the field was conducted so that upper layers of each replicate canopy were sampled more intensively (ca. 100 quadrats/layer) than lower layers (ca. 80 quadrats/layer).

Leaf blade inclination was determined on representative individuals (n = 3 to 6) which had been removed from borders of the experimental plots. The borders were at least 30 cm wide and the border plants chosen for sampling were immediately adjacent to the experimental plants. Immediately after removal, all leaves were traced on graph paper and the surface area of leaf segments of similar inclination was determined using a leaf area meter (Model LI-3000, LICOR, Inc., Lincoln, Nebraska, USA). Leaf blade inclination from the horizontal was measured with a protractor and then weighted by leaf area to obtain a measure of the mean weighted leaf inclination for each layer in the canopy. Sheaths were assumed to be vertical.

Simulations of daily canopy net photosynthesis and light interception were conducted using the model described by Ryle et al. (1990). For each canopy layer, the following structural data were input parameters: LAI, SAI, foliage inclination and the fraction of the LAI in the layer which was alive (Caldwell et al. 1986). The individual leaf gas exchange parameters used in the model are described by Beyschlag et al. (1990). The model included leaf sheath material in the calculations of radiation penetration but did not include any photosynthetic contribution by this tissue, since sheath photosynthetic capacity is small in comparison to leaf blade capacity (W. Beyschlag unpublished data; Araus and Tapia 1987), the amount of sheath area is small compared to leaf blade area and most of the sheath material occurs at depth in the canopy where light is low. Leaf absorbance, transmittance and reflectance of photosynthetically active radiation (400–700 nm) were assumed to be 0.85, 0.11 and 0.04, respectively, for both species. These represent typical spectral characteristics of normal green foliage (Ross 1975).

Meteorological data used in the simulations were collected at the field site and are given by Beyschlag et al. (1990). To evaluate and compare the influence of canopy structure on photosynthesis in canopies at different times during the season, one set of meteorological data representative of the different times was used in all simulations. Meteorological records from the field site indicated that the daily courses of air temperature, humidity, wind speed and solar irradiance used in the simulations could occur at all sampling periods.

Results

Canopy structure

The mean leaf area index (LAI) of the mixed-species stands was 1.9 on 24 June, reached a maximum of 5.5 by 8 July, and then declined to 4.5 by 21 July. Total LAI of wheat in mixture was greater than wild oat early in the growth period (24 June) but became gradually less than wild oat as the season progressed (Fig. 1). The height profile of LAI was typical of grasses (Monsi et al. 1973) and generally similar for both species though a definite shift in the species composition of LAI in the upper canopy layers was observed with time. In the upper half of the mixed canopy layers, wheat contributed 59% of the total LAI in the mixture in late June, 49% in early July and 43% by late July. Dead and senescent LAI and sheath area index (SAI) increased during the season for both species and were consistently greater in wheat than wild oat.

Total LAI in monoculture was similar for the two species early in the season (30 June) but was substantially greater for wild oat at midseason (14 July) (Fig. 1). As
in the mixtures, the fraction of the canopy leaf area that was alive remained greater in wild oat monocultures than in wheat monocultures throughout the season. No apparent differences existed between the species for total SAI in the monocultures.

Mean leaf blade inclination ranged from 40 to 80° from the horizontal for both species and, for the most part, tended to become more horizontal with depth in both mixed and monoculture canopies (Fig. 1). The uppermost layers of wild oat, however, exhibited somewhat more horizontal leaf inclinations which reflected the longer and more pendulous nature of the leaves of this species.

Canopy photosynthesis and light interception

The simulated daily net photosynthesis (expressed on a ground area basis, $A_{can}$) for wheat in mixture was highest early in the season and declined at all subsequent periods under both clear and overcast sky conditions (Fig. 2). By comparison, $A_{can}$ of wild oat in mixture increased slightly over time under clear skies and was less affected by overcast skies. In monocultures, $A_{can}$ of both species under clear skies declined from early- to midseason. Under clear skies, shaded leaves contributed about 20% of $A_{can}$ early in the season for both species in mixture and monoculture (data not shown). The contribution of shaded leaves to the total canopy carbon gain was minimal or slightly negative in all later-season canopies except the midseason wild oat monoculture where daily carbon losses from these leaves were about 14% of $A_{can}$.

Canopy net photosynthesis, expressed on a leaf surface area basis, was highest for early season canopies of mixtures and monocultures, and with the exception of the midseason monoculture of wild oat, was similar between the species at all times and under both clear and overcast sky conditions (data not shown, but see Beyschlag et al. 1990). In the midseason monocultures, wheat exhibited 45% greater photosynthesis rates per unit leaf area than wild oat.

The middle and/or upper-middle canopy layers made disproportionately large contributions to $A_{can}$ for both species and in all canopies (Fig. 2). For example, in the early July canopy, which exhibited the highest total LAI of the mixtures, the upper half of the canopy layers comprised 30 to 40% of the total LAI for both species yet contributed 90 to 95% of the canopy carbon gain under clear skies. The layer in the canopy where daily net photosynthesis became negative increased in height in the canopy through time and was generally similar for both species, with the exception of the midseason monocultures.

Daily carbon gain of the different canopy layers was closely related to the integrated daily intercepted light (photon flux density, 400-700 nm, expressed on a ground area basis, PFD$_{int}$) (Fig. 2). For both species, the ratio of $A_{can}$/PFD$_{int}$ was highest in the early-season canopies.

Fig. 2. Simulated daily total canopy net photosynthesis (expressed on a ground area basis, $A_{can}$, mmol CO$_2$ m$^{-2}$ ground area d$^{-1}$) and height profiles of $A_{can}$ (open bars) and light interception (PFD$_{int}$, mol quanta m$^{-2}$ ground area d$^{-1}$; lines and solid circles) for wheat and wild oat in mixture and monoculture under clear and overcast conditions. Below the arrows, $A_{can}$ is negative. The daily total $A_{can}$ for each species is given in the upper part of each figure

The proportion of $A_{can}$ in the mixture which was contributed by wheat was greatest in June and declined at later dates with a greater decrease evident under overcast conditions (Fig. 3). In June, the fractional $A_{can}$ contribution of wheat was closely related to the fraction
of total LAI composed of wheat in the canopy. Later in the season, the fractional contribution of wheat was more closely related to the proportion of wheat LAI in the upper half or upper third of the canopy layers.

Sensitivity analyses

When structural characteristics of a species in a mixture are altered in a sensitivity analysis, this affected $A_{\text{can}}$ not only of the species whose traits were altered but also of the species whose characteristics remained unaltered. Therefore, to determine how structural changes might influence competitive ability, it is useful to illustrate the effect of these structural changes on the fractional contribution of the species to $A_{\text{can}}$ of the mixture canopy. Sensitivity analyses were conducted both by altering plant structural characteristics in individual canopy layers or by simultaneously altering characteristics in several layers. Single-layer sensitivity analyses were conducted by altering either LAI ($\pm 20\%$) or leaf inclination ($\pm 20^\circ$) of both species in individual canopy layers while holding all other parameters constant (Fig. 4). The results are expressed as percent changes in the contribution of wheat to total canopy $A_{\text{can}}$ with the base case as $A_{\text{can}}$ of unaltered canopies for clear sky conditions (Fig. 2). As expected, simulated canopy photosynthesis of both species was less affected by structural changes under overcast skies than under clear skies (not shown).

The magnitude of the change in $A_{\text{can}}$ due to altering the structure of individual canopy layers was small because these layers contributed a small proportion of the total canopy foliage area. However, the results do reveal which canopy layers would be most responsive to alterations in LAI and leaf inclination and, at least in a qualitative sense, illustrate the effect on competitive balance of these structural changes (Fig. 4). In general, decreasing LAI or increasing leaf inclination in one species decreased the fraction of the total canopy carbon gain of that species while increasing LAI or decreasing leaf inclination had the opposite effect. With the exception of the lower canopy layers in mid and late season, changes in LAI of $\pm 20\%$ produced larger changes in the relative $A_{\text{can}}$ contribution of each species than changes in leaf inclination of $\pm 20^\circ$. The most sensitive layers to changes in LAI were the middle and upper-middle layers; these are the layers that have the greatest contribution to $A_{\text{can}}$ (Fig. 3). By comparison, layers most sensitive to leaf inclination changes were somewhat lower in the canopy. For mid- and late-season canopies, the lowermost canopy layers were largely insensitive to changes in either LAI or leaf inclination.

Altering LAI or leaf inclination for several canopy layers simultaneously revealed different responses for the same species in mixtures and monocultures (Fig. 5). As in the single-layer sensitivity analyses, decreasing leaf inclination or increasing LAI simultaneously in several layers of mixtures increased the relative $A_{\text{can}}$ contribution of the species altered and the effects were greatest in the middle of the canopy. Increases or decreases of leaf inclination in wheat monocultures reduced $A_{\text{can}}$ in nearly all cases. In contrast, more erect foliage in upper regions of the wild oat monoculture canopy increased $A_{\text{can}}$ while more steeply inclined leaves in lower regions
of the canopy reduced $A_{can}$. The responses were generally opposite for the alterations in leaf inclination in the other direction. Increases and decreases in LAI in all canopy regions of the wheat monoculture increased and decreased $A_{can}$, respectively. Alterations of LAI had the opposite effect in wild oat monocultures.

The relative importance of differences in canopy structure of the two species in influencing carbon gain was evaluated by substituting the structural attributes (LAI, leaf inclination, SAI and LAI live fraction) of wild oat to wheat, or the reverse, so that both species had the same structural attributes. Results of a substitution where wheat was provided with wild oat parameter values indicated that species differences in LAI were much more important than species differences in leaf inclination, LAI live fraction or SAI (Fig. 6). Similar results were obtained by the reverse substitution (not shown).

**Discussion**

The ability of a plant to successfully compete for light in mixed-species stands is determined both by its ability to intercept light and by its effectiveness in utilizing this light in photosynthesis. Simulations of canopy carbon gain by Beyschlag et al. (1990) indicate that in mixed stands of wheat and wild oat, competition for light is influenced more by differences in canopy structure than by differences in physiological characteristics of individual leaves. Similarly, Pearcy et al. (1981) showed, through simulation modeling, that physiological differences between competing $C_3$ and $C_4$ species would be less important for plant carbon gain than foliage placement under closed canopy conditions. Wilson and Ludlow (1983) found that in mixtures of a $C_4$ grass and a $C_3$ legume, differences in photosynthetic capacity were only important for leaves in the upper canopy layers. In the canopy layers with the greatest LAI, which were lower in the canopy, carbon uptake rates were similar for the two species. Studies on hedgerow trees and shrubs by Küppers (1984, 1985) also indicated that competitive status was more closely related to crown architectural features than single-leaf photosynthetic characteristics. Thus, the findings in our work with wheat and wild oat that plant architecture plays a much more important role in competition for light than do single-leaf photosynthetic characteristics is corroborated by studies with several other species.

Wheat and wild oat are morphologically quite similar yet they were found to differ slightly in the amount and placement of foliage in the canopy, foliage inclination, and foliage longevity (Fig. 1). However, the species differences in structural characteristics apart from LAI appeared to be of minor consequence in influencing canopy carbon gain by the two species (Fig. 6). Early in the season, the total amount of leaf area of wheat was
found to be well correlated with the fraction of $A_{can}$ contributed by wheat, while later in the season carbon gain of wheat appeared to be better associated with the amount of leaf area in the upper half or upper third of the canopy layers (Fig. 3). These findings agree with other studies which have shown that the total LAI for each of the species in a mixture may not always accurately predict the ultimate competitive status (Kropff et al. 1987; Légère and Schreiber 1989).

Results from our simulations support the contention by many authors (e.g., Eagles 1983; Saeki 1963; Rhodes and Stern 1978) that plant structural attributes which are advantageous for increased production in pure stands may not necessarily be of advantage for competition in mixed stands. For example, the sensitivity analyses (Figs. 4, 5) revealed, as one might expect, that increased LAI or more horizontally oriented foliage in upper canopy layers would be advantageous for a species competing in a mixture, but not necessarily of benefit for production in a monoculture. Simulations by Duncan (1971) and Ross (1970) showed that, when canopy LAI exceeded 3 to 4, canopy photosynthesis in pure stands was increased by more erect foliage, especially in upper layers. Results from our simulations of canopy photosynthesis in wild oat monocultures agree with these calculations of Duncan and Ross (Figs. 4, 5). However, alterations of leaf angle for wheat was found to reduce $A_{can}$ of this species in monoculture (Fig. 5) which suggests that, at least under these growth conditions, foliage inclination of wheat may presently be near optimal for canopy photosynthesis.

Leaves of wild oat are produced at a slower rate but live longer than those of wheat. As a result, wild oat had more live foliage in lower canopy layers and a greater fraction of live LAI for the entire canopy (Fig. 1). In mixtures, slightly greater ability to photosynthesize at low light and/or lower dark respiration rates in wild oat (Bayschlag et al. 1990) appeared to compensate for these leaf age differences since the respiratory carbon loss of lower canopy layers was not substantially different for the two species. However, in monocultures, the lower canopy leaves appeared to represent a considerable carbon drain in monocultures of wild oat but not in monocultures of wheat. The importance of lower-canopy leaves in wild oat monocultures was suggested by the sensitivity analyses which showed that $A_{can}$ was reduced appreciably by reducing inclination of leaves above these lower layers, which would lead to more shading of the lower layers, or by increasing LAI in lower layers (Fig. 5). In wheat monocultures, increased LAI in lower canopy layers was found to increase $A_{can}$ slightly. It seems that optimal leaf area indices were exceeded in monocultures of wild oat but not in wheat, according to this analysis.

Our objective in this paper is not to predict the competitive balance between these species based on simulations of canopy photosynthesis, but rather to identify the canopy structural features which would be most important in influencing competition for light. The ultimate competitive balance is usually dependent upon belowground as well as aboveground interactions (Martin and Field 1987). Furthermore, the simulated canopy photosynthesis of these species can differ depending on climatic conditions (Bayschlag et al. 1990).

Because of the overriding importance of canopy structure in influencing canopy carbon gain of these species, even subtle changes in the placement of foliage in the canopy can substantially alter the balance of competition between these species. Shifts in competitive balance between these species have been found to occur under conditions of ultraviolet-B radiation (UV-B, 280–320 nm) enhancement (Barnes et al. 1988). These competitive shifts were associated with shifts in the extent of overtopping of wild oat by wheat but not with any changes in single-leaf photosynthesis characteristics (Barnes et al. 1988; Bayschlag et al. 1988). Our findings here, as well as those by Ryel et al. (1990), suggest that the subtle UV-B-induced changes in canopy structure led to alterations in light interception and canopy photosynthesis, which, when integrated over time, caused the observed shifts in competitive balance. In monocultures of these species, there were no changes in stand production when exposed to enhanced UV-B (Barnes et al. 1988).

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