Canopy Architecture and Radiation Profiles in Natural *Typha × glauca* Stand

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부들(*Typha × glauca*) 自然群落의 葉層部 構造와 受光狀態

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ABSTRACT

To verify the cause of high productivity in *Typha* stand, leaf area index(LAI), leaf orientation and inclination, specific leaf area (SLA), and radiation interception profiles were determined in a natural *Typha×glauca* stand. Throughout the growing season, the leaf inclination has been kept at near-right angle and leaf orientation has been random. These chracteristics were responsible for an uniform spatial arrangement of the leaves within the canopy and could be explained by the SLA value, which increased in their higher strata. The extinction coefficient (K) of the canopy, 0.12 to 0.20, was one of the smallest value out of terrestrial plant communities. At least more than 25% of full radiation penetrated into the lowest stratum of the canopy. High productivity of the *Typha* would be attributed to efficient penetration of the radiation in virtue of the stiff and straight leaves even though rather small LAI.

INTRODUCTION

Cattail plant (*Typha*) is the most productive with aboveground standing crops often exceeding 15 tons/ha (van der Valk and Davis, 1978) and with total biomass often exceeding 40 tons/ha (Fox, 1975; Andrews and Pratt, 1978). The eminent efficiency of *Typha* as a solar collector is due to the following factors: (1) water is not a limiting factor in a habitat, (2) nutrient availability from run-off and decomposition is high (Pearsall, 1954; Boyd and Hess, 1970; Boyd, 1971), (3) owing to its perennial habit the canopy expands rapidly in early spring at the expense of carbohydrates stored for the previous season (Bray *et al.*, 1959; Bray, 1960; Jervis, 1969; Linde *et al.*, 1976; Gustafson, 1976), (4) a canopy architecture which optimizes both leaf area and the penetration of light throughout the canopy.

Kvet *et al.* (1969) and Dykyjová (1971a and b) analyzed the canopy architecture of the

Typha community and emphasized the received radiation efficiency. Fox (1975) and Gustafson (1976) recognized the importance of leaf inclination and orientation on dry matter production in *Typha* but did not analyze it in detail.

STUDY AREA

The study area, located in the Carlos Avery Wildlife Management Area at Anoka county, Minnesota, U.S.A., is a large homogeneous stand (ca. 2 ha) of *Typha×glauca* surrounded by wetland forest. The water level was artificially maintained at approximately 20cm throughout the growing season.

MATERIALS AND METHODS

Canopy analysis. To analyze the seasonal growth pattern of the canopy, aboveground materials within seven (50×50)cm quadrats were harvested on each sampling date. Shoots were clipped off at the ground surface, placed in plastic bag, and taken to the laboratory where each shoot was washed, cut off on the water level apart 20cm from shoot base and then cut into successive 40cm segments upper than the water level. Their materials were subdivied into the following categories: (1) leaves, (2) stems and leaf sheaths, (3) reproductive organs and (4) dead materials, Leaf area was measured for each zone using a Hayashi Denko AAM-5 automatic leaf area meter and converted into leaf area index (LAI), surface area of leaves/ground area, m²/m². All materials were then dried to constant weight at 70°C.

Light measurement. The vertical distribution of light intensity was determined using a Licor Model LI-185A photometer and a LI-190x quantum sensor (PhAR) *in situ*. A grid was established by running string horizontally between two stakes. Starting at water level strings were placed at 20cm intervals and light intensity was measured at least 40 points at each level within the canopy with above canopy readings serving as the controls. All light measurements were taken in the time interval 30 min. before and 30 min. after noon on clear, calm days.

Leaf orientation and inclination. To describe leaf configuration within the canopy, leaf orientation was determined using a compass and a large plexiglass plate marked off at 15° interval. The center of the plexiglass plate was horizontally set on right above the center of the plant stump. The leaf azimuth was measured overlooking the plate. The orientation of the apices of least 70 leaves for each interval were recorded. Leaf inclination, the angle of the leaf lamina to a horizontal plane, was measured using a plexiglass plate marked off at 5°C intervals and a plumb line. The angles of thirty leaves were determined for each 40cm interval of the shoots. All measurements of leaf orientation and inclination were made during periods when there was little or no detectable air

movement.

RESULTS AND DISCUSSION

Shoot biomass. The overwintering shoots began to expand in mid-May, 1979. The maximum shoot dry weight, 1,960 g/m², and average stem dry weight, 960 g/m², were obtained in late August while maximum leaf dry weihgt, 663 g/m², occurred in mid-July. Moss *et al.* (1977) reported 4,000 g/m² of annual net production of managed *Typha* stand, including above- and below-ground. Dead material, most of which was leaves, was first noticed in mid-July and gradually increased to 44% of the total leaf biomass and 22% of the stem biomass in the final September 13 sampling date. The male
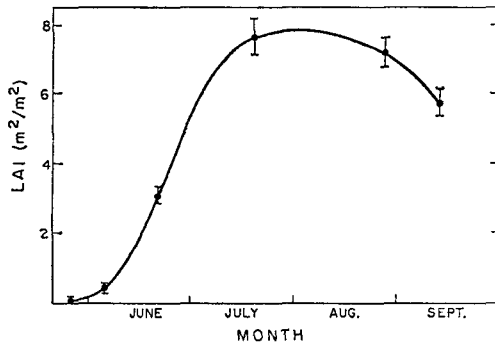

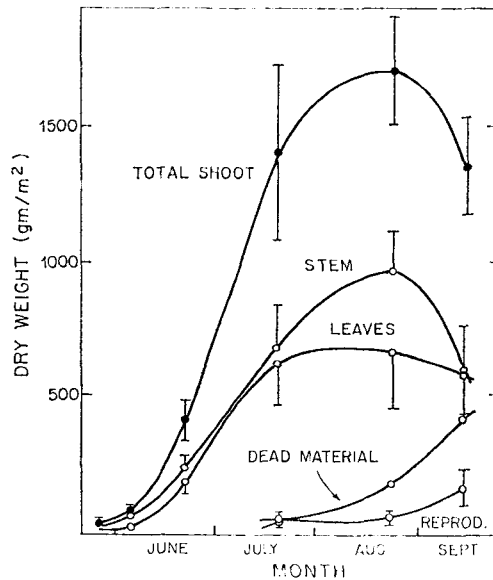Fig. 2. Seasonal changes in leaf area index (LAI) for the *Typha* stand.

Fig. 1. The seasonal distribution of above ground biomass and dead material.

and female reproductive organs were first observed on July 21 after which total dry weight increased to an average dry weight of 88 gm/m² by September 13 (Fig. 1). The decline in total shoot biomass after the seasonal maximum in late August can be attributed to the following factors: (1) the loss of leaves (Penfound, 1956; Boyd, 1971; Dykyjová, 1971b; Gustafson, 1976), (2) translocation of photosynthate to reproductive organs (Linde *et al.*, 1976), and (3) translocation of photosynthate from shoots to rhizomes (Andrews and Pratt, 1978).

Leaf area index. The maximum LAI occurred in mid-July, was sustained through late August and then diminished. Thus for *Typha* the maximum canopy coverage is maintained over an interval of approximately 50 days (Fig. 2). The maximum LAI obtained in this study, 7.6, is substantially less than the range 9.3~17.4 reported by many investigators(Jervis, 1969; Dykyjová *et al.*, 1971; Moss *et al.*, 1977; Andrews and Pratt, 1978). This discrepancy may be due in part to the various methods used to measure
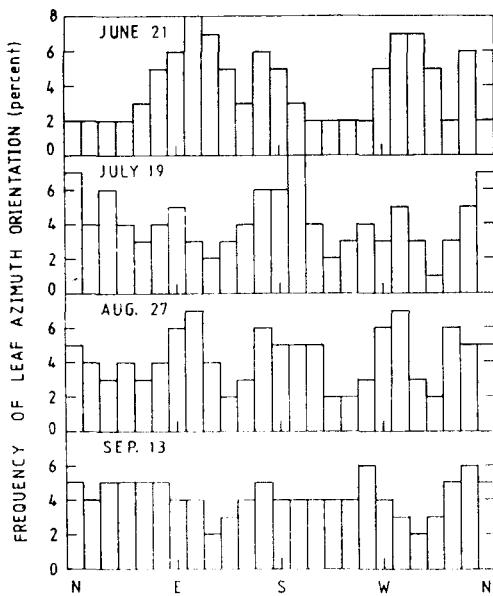
Fig. 3. Leaf orientation within the *Typha* canopy.

LAI (Gustafson, 1976) since the maximum total shoot biomass obtained in this study $(1,963g/m^2)$ equals or exceeds those reported in the articles cited above.

Leaf orientation and inclination. In the earlier stages of canopy development the leaf azimuth orientation tended to be oriented to the south and northwest (June 21) and north and south (July 19) (Fig. 3). This pattern appears to be due to the alternate production of leavse as shown by Linde *et al.* (1976). As the season progressed leaf orientation was being randomly distributed (August 29, September 13). This uniform spatial arrangement of the leaves within the canopy allows for maximum penetration of incident radiation per unit area.

In the leaf inclination data presented in Fig. 4, the thin lines within each stratum of the canopy depict the mean angle of the leaves from the horizontal. Although the frequency distribution of leaf inclination varies with plant height as well as leaf age, the canopy is dominated by long narrow spiralling leaves ("ribbonlike") with steep leaf angles even though by end of the growing season. Thus, leaf shading is kept to a minimum, while light penetration into the lower strata of the canopy is maximized. Near-vertical
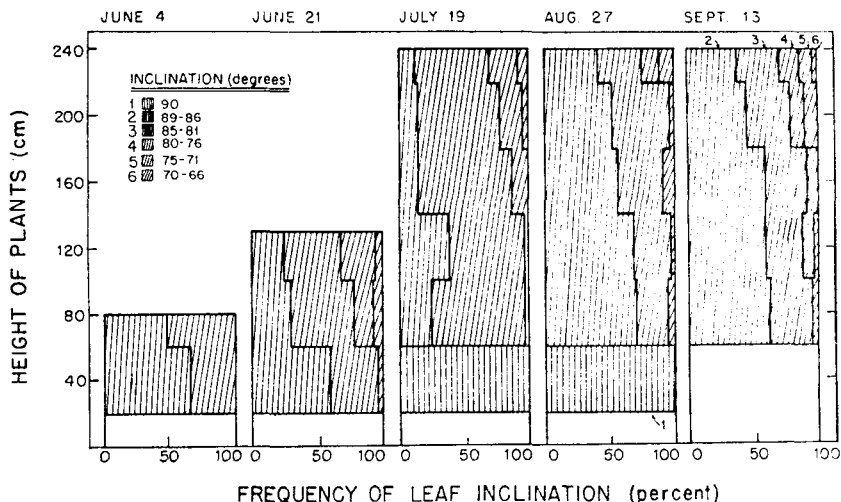

Fig. 4. Frequency of leaf inclination throughout the *Typha* canopy. Lines in each stratum mean the mean angle of leaves.

leaves were abundant in the lower and middle strata of the canopy, while the upper strata contained a minor subset of gently-sloping angle leaves which increased as the season progressed.

The leaf angles of *Typha* are steeper than those reported for wheat (Nichiporovich, 1961), corn (Loomis *et al.*, 1968), or sugar cane (Hodanova, 1972). The architecture of the *Typha* canopy is classified as "erectophile" (de Wit, 1965) owing to the high percentage of steep-angle or vertically oriented leaves. Duncan *et al.* (1967) reported that plant productivity was directly related to leaf angle for many plant communities. The vertical distribution of mean leaf inclination in the *Typha* canopy approaches the theoretically most efficient canopy structure for maximum productivity described by Kuroiwa (1970) and Duncan (1971).

Specific leaf area (SLA, cm²/g) is distinguished into two parts; upper and lower leaf lamina. The SLA in the upper part, above than about 100cm, is directly proportional to shoot height while lower part. below than 100cm, is inversely proportional to shoot height (Fig. 5). The left ward shift of the SLA curves as the season progresses is due to leaf elongation as the stand reaches its maximum height. Such a feature of the SLA due to the thick and stiff leaf might contribute to vertical erection and random distribution of the leaves within the conopy.

Productive structure and vertical light destribution. The productive structure of the *Typha* stand is characterized by the narrow leaf type (Monsi and Saeki, 1953) and by the substantial leaf area in the middle and lower strata of the canopy (Fig. 6). In a mature stand the green leaf area is distributed vertically between 60~240cm. Radiation profiles,
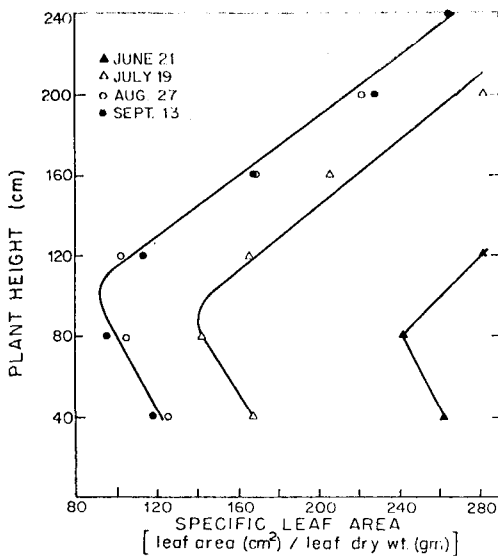

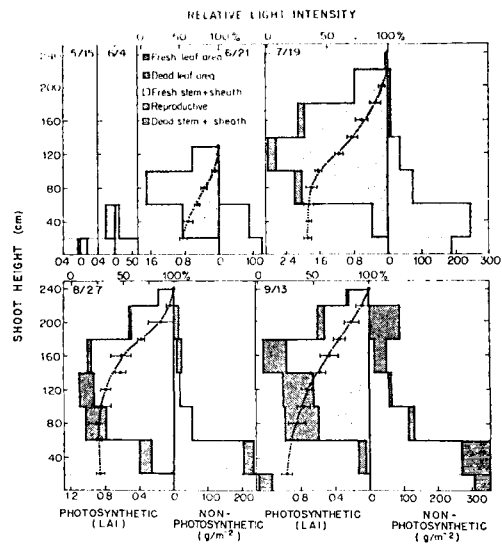Fig. 5. Specific leaf area (SLA) in *Typha* leaves.

Fig. 6. Radiation profiles and leaf area index within the *Typha* canopy.

the vertical distribution of light intensity within the canopy, show exponential attenuation from full sunlight above the canopy to water level. The relative radiation intensities at water level of 20cm from base were 53.3, 32.5, 34.0 and 25.4% on June 21, July 19, August 29 and September 13, respectively.

Gustafson (1976) reported that saturation radiation intensity for gross photosynthesis with *Typha* was $600\sim800\mu Em^{-2} s^{-1}$. In this study the photosynthetically active radiation (400~700nm) at noon was measured at 2000 $\mu Em^{-2}s^{-1}$. It is assumed, therefore, that all of the leaves within the *Typha* canopy are light saturated at noon on clear days. The quantitative analysis of the vertical productive structure and the radiation distributions reported here are similar to those described by Kvĕt *et al.* (1969) and Dykyjová (1971a and b) for natural *Typha* stands.

The radiation profile for the canopy is closely related to the vertical distribution of leaf area. The structure of the upper stratum of the canopy is the most critical in determining radiation penetration. To assess the efficiency of received radiation, the relationship between LAI and vertical radiation penetration was determined using the Beer-Lambert law:

$$I=I_0e^{-KL}$$

where, I and I_0 refer to radiation intensities on a horizontal surface within and above the canopy; L is the leaf area index; K is the extinction coefficient.

The K is a constant determined by leaf angle, leaf thickness, reflectivity and chlorophyll content of a particular species. Despite the limitations of this formula (Anderson, 1966) it is well adapted for use with the *Typha* canopy structure. Radiation interception profiles (Fig. 6) were characterized using the log of the relative radiation intensity (log I/I_0) and the cumulative LAI starting 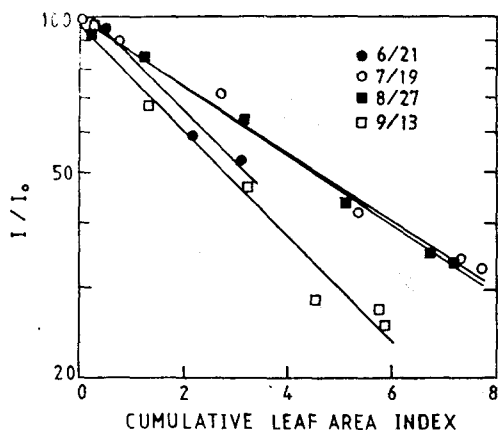from the uppermost canopy (Fig. 7). The K derived from the data were 0.20, 0.12, 0.12, and 0.20 on June 21, July 19, August 29 and September 13, respectively. Such a difference of the K values as the season progresses should be derived from a little changes of the leaf orientation and leaf inclination. The K for *Typha* is close or equal to that for *Miscanthus sacchariflorus* which has the smallest value out of the investigated plants, but less than those reported for *M. sinensis* (Monsi and Saeki, 1953), corn (Loomis *et al.*, 1968), barley (Udagawa and Uchijima, 1969), or sugar beet (Hodanova, 1972). The maximum daily rate of photosynthesis in a *Typha* stand is ap-

Fig. 7. Relationship between radiation interception and cumulative leaf area index within the *Typha* canopy.

proximately 8 g carbon m^{-2} (Gustafson, 1976) which is less than half of the maximum rate reported for corn (Loomis *et al.*, 1968). In spite of this the annual biomass yield from corn is often only half that of *Typha* (Andrews and Pratt, 1978). *Typha's* high productivity can be attributed to its efficient canopy structure including the steep leaf angles, the random leaf orientation and the uniform spatial arrangement.

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摘　　要

부들(*Typha×glauca*)의 生產性이 높은 원인을 밝히기 위하여 葉面積指數, 比葉面積, 잎의 方位와 傾斜 및 放射量의 수직분포를 측정하였다. 생육기간 중 잎은 거의 直立하였고 方位는 무작위한 分布를 유지하였다. 이러한 葉層部의 균일한 空間配置는 비엽면적이 지상 100cm 높이를 경계로하여 上·下에 깊수록 커지는 것으로 보아 葉身이 두껍음으로서 유지된다. 엽층부의 消滅係數 K는 0.12~0.20으로 육상식물군락 중에서 가장 작은 값이있다. 엽층부 最下層에 투입되는 相對放射量은 성숙한 군락에서도 25% 이상이었다. 부들의 엽면적지수가 과이 크지 않은데도 생산성이 높은 이유는 햇빛이 효과적으로 투입되는 엽층부 구조의 특징에 기인하였다.

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